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Morphometrical relationships between South-east Asian deer (Cervidae, tribe Cervini): evolutionary and biogeographic implications

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Abstract

Two hundred and fourteen skulls of Asian deer species (Cervini) were measured and the resulting craniometric data analysed using multivariate statistics. Our results suggest that elements of skull shape as determined by morphometrics can be used as phylogenetic characters and depict phylogenetic relationships among Cervini deer species that is not far removed from the picture given by molecular studies and other characters. Morphometrics-based phylogeny was used in combination with other phylogenies and palaeoenvironmental reconstructions to investigate factors that may have influenced evolutionary changes. Our data indicate the need for a revision of the genus and subgenus level taxonomy of the Cervini.

Key words: Asia, deer, evolution, morphometrics, palaeoenvironment, Cervidae

INTRODUCTION

True antlered deer (tribe Cervini; see Groves & Grubb, 1987) occur naturally in Asia, Europe, northern Africa and North America. In the tropical and subtropical part of their range in East, South and South-east Asia, three genera are presently recognized, *Cervus*, *Axis* and *Elaphurus*, containing 15 species (Table 1, for locations see Fig. 1). The high species richness of deer is partly the result of their ecological characteristics. According to Geist (1998), deer do not thrive in mature, species-rich environments, but they flourish in young, poorly stocked ecosystems. The occurrence of such systems increased during the Late Tertiary and especially the Quaternary when alternating glacial and interglacials resulted in a change from relatively stable to more unstable, shifting vegetation types. Furthermore, deer benefited from the sweeping megafaunal extinctions that occurred as humans rose to ecological dominance and caused major landscape changes in recent times (Geist, 1998). The speed of these changes, however, makes it difficult to determine how species are related to each other, as their phylogenetic branching patterns become more difficult to analyse.

Based on an analysis of morphological and karyotypic data, Groves & Grubb (1987) proposed the subdivision of *Cervus* into four subgenera: *Rusa* (*C. alfredi*, *C. mariannus*, *C. unicolor* and *C. timorensis*); *Rucervus* (*C. eldi*, *C. duvauceli* and *C. schomburgki*); *Przewalskium* (*C. albirostris*); the subgenus *Cervus* with *C. nippon* and *C. elaphus*. They also suggested that within the genus *Axis*, the subgenus *Hyelaphus* containing *A. porcinus*, *A. calamianensis* and *A. kuhli* may not be as phylogenetically close to the subgenus *Axis*, which contains *A. axis*, as is often implied. According to Groves & Grubb (1987), this did, however, not preclude the genus *Axis* from being monophyletic.

The evolutionary relationships within the Cervini were further investigated by Emerson & Tate (1993) who analysed electrophoretic patterns for 22 proteins. They found that the genus *Cervus* split into two distinct groups with *Cervus elaphus* and *C. nippon* in one clade, and *C. unicolor* and *C. timorensis* in another. They also found a close relationship between the genus *Elaphurus* and the *C. elaphus/C. nippon* group, whereas *C. unicolor* and *C. timorensis* grouped more closely with the genera *Dama* and *Axis*. *Cervus* therefore seemed to be paraphyletic. Cronin *et al*. (1996), who analysed (κ)-casein sequences to assess phylogenetic relationships, also supported this conclusion. They similarly found that *Elaphurus* grouped with *C. elaphus* and *C. nippon*, whereas *C. unicolor* formed a monophyletic clade with *C. duvauceli*.

Following this, research by Randi, Mucci, Claro-Hergueta *et al*. (2001) elucidated the evolutionary relationships in the *Cervus* group using sequences from complete mitochondrial DNA control regions. Their data suggested that *Elaphurus* should be merged with *Rucervus*, because it associated closely with *C. eldi* in a phylogenetic analysis, while the two species *C. timorensis* and *C. unicolor* did not group with

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Table 1. Species of Cervinae in East, South, and South-east Asia (Lekagul & McNeely, 1977; Corbet & Hill, 1992; Wemmer, 1998), and numbers of specimens and their sex used in this research

Species name	Subgenus	Distribution range	No. of specimens used in research Males, females
Axis axis (chital)	*Axis*	Most of India and Sri Lanka,	5, 6
A. calamianensis (Calamian deer)	*Hyelaphus*	Calamian Islands, north of Palawan	1, 3
A. kuhli (Bawean or Kuhl's deer)	*Hyelaphus*	Bawean Island (Java Sea)	6, 7
A. porcinus (hog deer)	*Hyelaphus*	Pakistan, northern India, Nepal, Bhutan, Bangladesh, Sri Lanka, southern China, Burma, southern Thailand, Vietnam, Cambodia, and Laos	7, 2
C. unicolor (sambar)	*Rusa*	India, South China, Bangladesh, Burma, Thailand, Cambodia, Laos, Vietnam, Malaya, Sumatra, and Borneo	10, 20
C. timorensis (Timor deer)	*Rusa*	Java, through the Lesser Sunda Islands, Sulawesi, and most of the Moluccan Islands	11, 5
Cervus alfredi (Philippine spotted deer)	*Rusa*	Negros and Panay, Central Philippines	3, 2
C. mariannus (Philippine deer)	*Rusa*	Luzon, Mindoro, Samar, Leyte, and Mindanao Islands	14, 7
C. duvauceli (barasignha)	*Rucervus*	Nepal, India	18, 2
C. eldi (Eld's deer)	*Rucervus*	India, Burma, Thailand, Cambodia, China, Laos, and Vietnam	4, 2
C. schomburgki (Schomburgk's deer)	*Rucervus*	Now extinct. Historically in the central plains of Thailand, and possibly Laos and Yunnan	6, 0
C. elaphus (red deer)	*Cervus*	West Europe, northern Africa, East Asia and eastern North America	20, 4
Elaphurus davidianus (Père David's deer)		South-eastern China (re-introduced from captivity)	8, 7
C. nippon (sika deer)	*Cervus*	Across East Asia	not used in this research
C. albirostris	*Przewalskium*	Tibet, Kansu, and Szechwan	not used in this research

C. alfredi, thus suggesting that the subgenus *Rusa* is not monophyletic. X.-H. Liu *et al*. (2003), who analysed sequences of the cytochrome *b* gene, similarly found a close relationship between *Elaphurus* and *C*. (*Rucervus*) *eldi*, while *C*. (*Rusa*) *unicolor* grouped with *Axis porcinus*, and *C. albirostris* with *C. elaphus* and *C. nippon*.

Groves & Grubb (1987) noted that one of the difficulties of determining phylogenetic relationships within the Cervini is that workers have tended to study fossil or recent material independently, using different morphological characters, and that indeed most research has relied on very few characters. Groves & Grubb therefore incorporated many different characters in their research, including internal and external morphology and karyotypes. Still, the discrepancies between the phylogenetic relationships proposed by Groves & Grubb (1987) and the more recent ones based on protein and molecular data by Emerson & Tate (1993) and Randi, Mucci, Claro-Hergueta *et al*. (2001) show that further work is needed to explore the evolutionary history of Asian deer species.

In the present research multivariate statistical analyses of craniometric data of the modern Asian species were used and these combined with some measurements on fossil deer from Java. One of us (EM) has investigated the palaeoenvironments of the South-east Asian region in the Late Tertiary to Late Quaternary (Meijaard, 2003*a*,*b*; Meijaard & Groves, in press), and that knowledge was combined with the findings from our craniometric analysis and other data in the literature with the specific aim to: (1) investigate the monophyly of the genera *Cervus* and *Axis* and their subgenera *Rusa*, *Rucervus*, *Cervus*, *Axis* and *Hyelaphus*; (2) assess the relationships between taxa on the South-east Asian islands and those on the mainland; (3) develop a historic biogeographical model explaining the dispersal and divergence of Cervini in island South-east Asia.

METHODS

EM measured 159 deer skulls, including 19 cranial fragments of *A. lydekkeri*, a Pleistocene species of Java, in the following museums: Zoological Museum Cibinong (ZMC), Indonesia; National Museum of Natural History (NMHM), Leiden, The Netherlands; Zoological Museum Amsterdam (ZMA), The Netherlands; the Field Museum (FMNH), Chicago, U.S.A.; The Natural History Museum, London (BMNH). CG measured an additional 55 skulls in the following museums: BMNH; ZMA; NMHM; Indian Forestry College, Dehra Dun (IFC); Van Ingen Taxidermy, Mysore (VI); Natur-Museum und Forschungs-Institut Senckenberg, Franfurt-am-Main (SMF); Bombay Natural History Society, Bombay (BNHS); Muséum National d'Histoire Naturelle, Paris (MNHP).

Measurements of 17 variables were taken following the same methods as Lowe & Gardiner (1974) (for details see the figure in their publication): greatest length

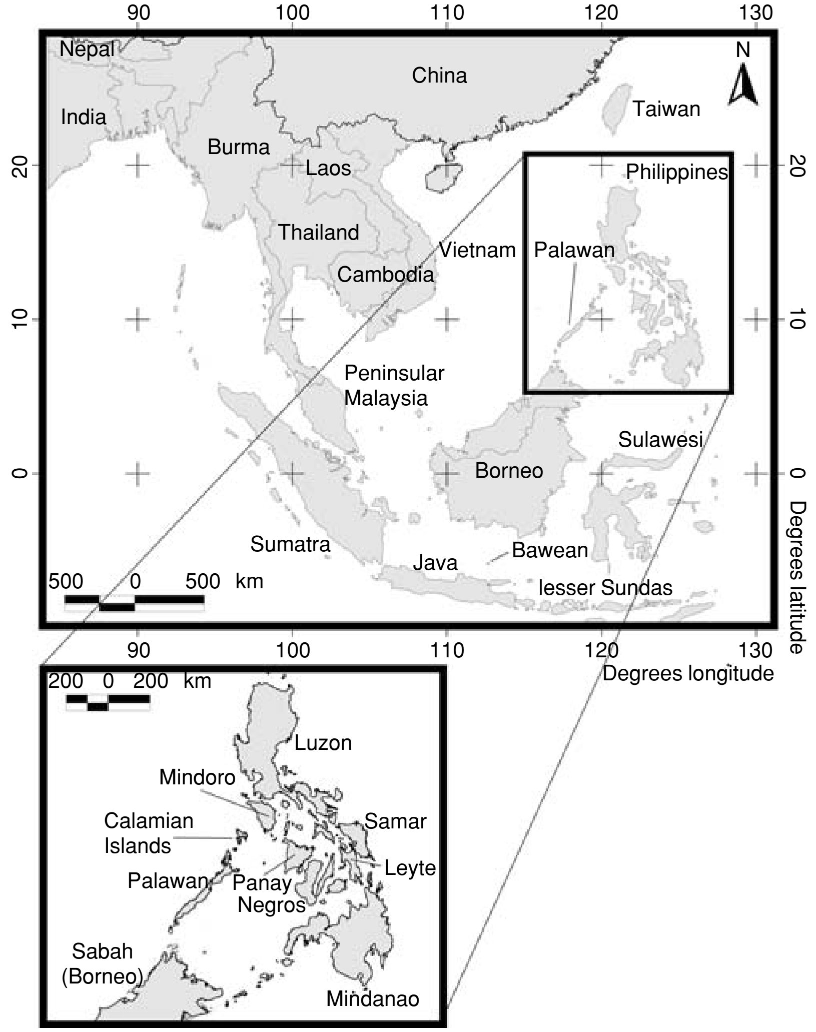

Fig. 1. Map of the areas mentioned in the text.

(GTL); condylobasal length (CBL); basal length (BL); palate length (PL); distance between prosthion and the alveoli of the second premolars (Pros); nose depth 1 (minimum depth between the inter-nasal/frontal suture at the proximal end of the premaxillae and the inter-maxillary suture) (N1); nose depth 2 (between the inter-nasal suture and the inter-maxillary/palatine suture) (N2); palate depth (minimum depth between the staphylion and the inter-frontal suture) (PD); condylar breadth (CBR); rostrum length (RL); nasal length (NL); bi-orbital breadth (BOB); maximum breadth of nasals (NB); premaxilla length (PML); minimum breadth across maxilla (MM); inter-orbital breadth (IO); and braincase breadth (BR). All measurements were made with an accuracy of 0.1 mm with a pair of Vernier callipers (precision 0.05 mm).

To investigate measuring differences between EM and CG, the individual measurements of 4 skulls that had been measured by both workers were compared. The differences were negligible for all measurements except PML, N2 and NL, of which the latter especially had been measured differently by EM and CG. Measurements by CG for these 3 characters were therefore excluded from the analysis to ensure that specimens could be meaningfully compared.

For all skulls, the age class was determined as follows: adult (A1) = M^3 erupted and basilar suture (= spheno-occipital synchondrosis, which fuses with increasing age) fused; between young adult and adult (A2) = M^3 erupted and basilar suture fusing; young adult (A3) = M^3 erupted and basilar suture open; juveniles = M^3 not yet erupted.

Sex ratios of the specimens within each of the species varied considerably (see Table 1), and therefore the differences between males and females within each of the species were investigated using a 1-way ANOVA of all the variables to determine whether sexual dimorphism would mask interspecific variation.

The measurements were analysed using multivariate statistical software (SPSS 11.0). Principal component analyses (PCA) were used to determine whether deer species were craniometrically distinct, and how these species grouped together into species groups. A PCA is often used in data reduction to identify a small number of factors that explain most of the variance observed in a much larger number of variables. Following this, discriminant analyses (DA) were used to determine the nature of the differences between species or species groups. A discriminant analysis is useful for building a predictive model of group membership based on the observed characteristics of each case. The procedure generates a set of discriminant functions based on linear combinations of the predictor variables that provide the best discrimination between the groups.

As the taxa examined in this study differed in size, the raw variables were log transformed, and the analysis run on both transformed and untransformed datasets. No difference in the results appeared.

The similarities between the fossil specimens of *A. lydekkeri* and the 2 subgenera *Axis* and *Hyelaphus* were also investigated. Multivariate statistics were only used in 1 analysis because of the limited number of measurements that it was possible to take per fossil specimen; only CBR and BR could be measured on a substantial number of specimens, and in 1 specimen these measurements could be combined with N2, IO and NB. A bivariate analysis was used to investigate further the morphometric affiliation of the fossil specimens.

Finally, the phenetic relationships between different species were analysed using MEGA 2.1 software (Kumar *et al.*, 2001). Unstandardized canonical discriminant functions evaluated at group centroids were obtained, which provided the input in a dissimilarity matrix based on the squared Euclidean distance between species. These data were used to generate species trees based on craniometric similarities. The phenetic relationships between the Cervini were analysed by neighbour-joining (NJ) analysis using the group centroids for 5 discriminant functions. This technique produces an unrooted tree, because it does not require the assumption of a constant rate of evolution, but the tree can be rooted anywhere.

The degree to which phylogenetic information may be encoded in morphometric relationships is assessed in the Discussion.

RESULTS

All species (apart from *schomburgki* for which only males were measured) showed sexual dimorphism with males being larger in most variables than females. Thus combining the sexes could mask any interspecific differences. It was, however, decided to investigate the level of separation between species first using multivariate statistics, and then to combine or separate the sexes based on the outcome.

A PCA of the mature skulls (age classes A1, A2, A3; both sexes) showed that most skulls in the genera *Axis* and *Cervus* grouped together, but that *Elaphurus* separated as a distinct group close to *Cervus* but very far from *Axis* (Fig. 2). The component matrix (Table 2) of this analysis showed that the genera are primarily differentiated by size, because of the high positive values of the correlation factor between the variables and the first component. *Elaphurus* was differentiated from the others by the high value of the first component and the relatively low value of the second component; Table 2 shows that the low values of the second component were primarily caused by a small palate depth and wide nasals (but note that the second component only represented 2.7% of the total variance). Because of its distinctness, it was decided initially to leave out *Elaphurus* from the rest of our analysis and concentrate on the differences between the remaining species.

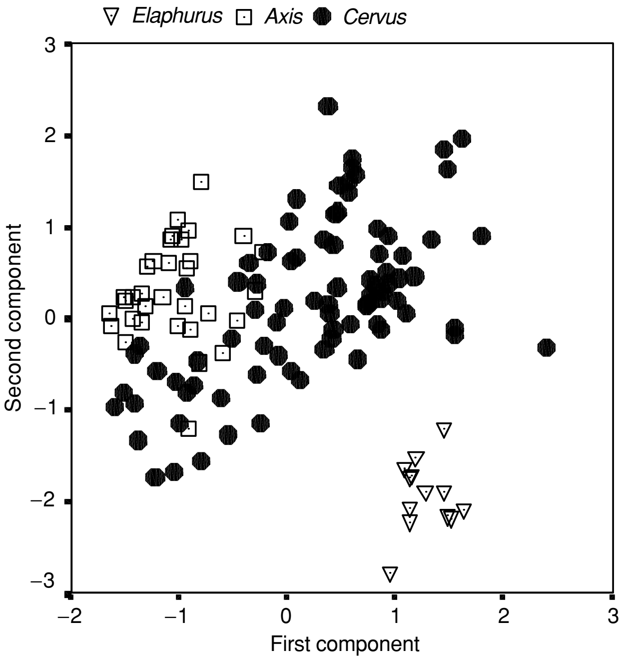

Fig. 2. Principal component analysis of all mature Cervini skulls.

Table 2. Correlation matrix of a principal component analysis for mature Cervinae specimens (see Fig. 2)

	Component	
	1	2
GTL	0.99	−0.09
CBL	0.99	−0.09
BL	0.99	−0.10
PL	0.97	−0.14
Pros	0.94	−0.02
N1	0.91	0.09
N2	0.96	0.13
PD	0.89	0.36
CBR	0.94	0.14
RL	0.96	−0.22
BOB	0.99	0.02
NB	0.87	−0.33
MM	0.96	0.09
IO	0.95	0.13
BR	0.98	0.05
Eigenvalue	13.6	0.4
Percentage of variance	90.7	2.7

A subsequent PCA showed that the remaining mature cervines split into three or four groups (Fig. 3), which were separated by visual inspection of the PCA graph. The

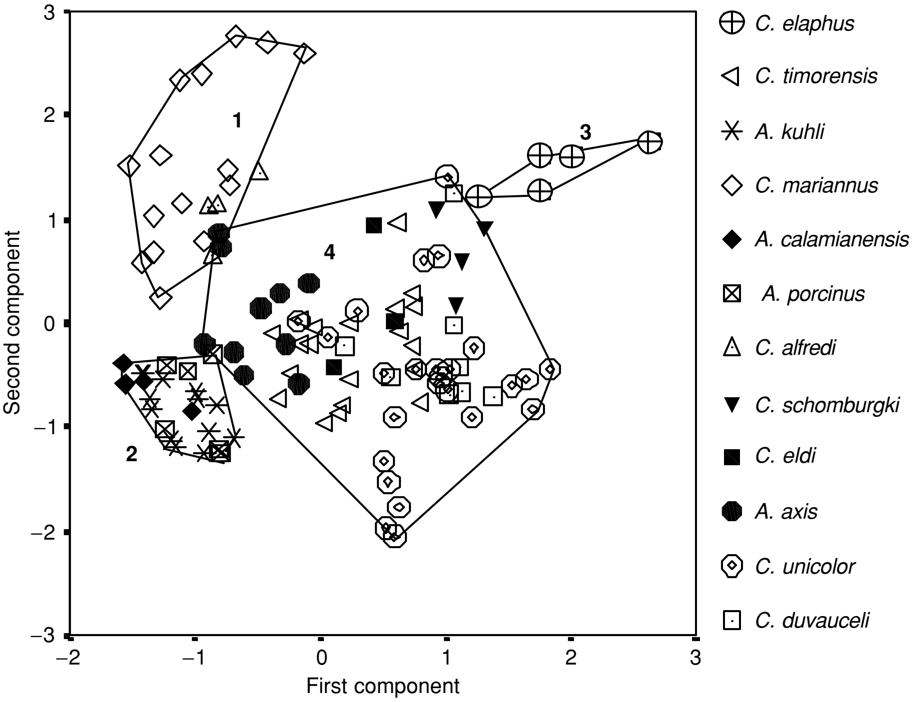

Fig. 3. Principal component analysis for mature specimens of *Cervus* and *Axis*. For group numbers 1–4, see text.

Table 3. Correlation matrix of a principal component analysis for mature specimens of *Cervus* and *Axis* (see Fig. 3)

	Component	
	1	2
GTL	0.99	– 0.05
CBL	0.99	– 0.04
BL	0.99	– 0.03
PL	0.98	– 0.07
Pros	0.93	0.01
N1	0.90	– 0.06
N2	0.96	– 0.16
PD	0.92	– 0.17
CBR	0.96	0.05
RL	0.97	– 0.01
BOB	0.98	– 0.01
NB	0.85	0.51
MM	0.97	0.05
IO	0.94	0.02
BR	0.98	0.01
Eigenvalue	13.6	0.3
Percentage of variance	91.0	2.2

numbers in Fig. 3 refer to the following group numbers: (1) *C. alfredi* and *C. mariannus* specimens; (2) *A. kuhli*, *A. calamianensis* and *A. porcinus*; (3) *C. elaphus*; (4) a mixed group containing the remaining *Cervus* species, and *A. axis* as a distinct subset. Again, the groups were primarily differentiated along the first component axis (91% of total variance), which was mostly determined by overall size (Table 3).

To investigate the nature of the differences between the four groups found in the PCA further, a discriminant analysis was conducted (DA) (Fig. 4). We excluded *Elaphurus* and *C. elaphus* because these had appeared as outlying groups in the PCAs, and also because there were too many missing values for *C. elaphus*. For this analysis CBL, BL, PL, PD and CB were excluded because of the many missing values in these characters. This analysis resulted in an 82.4% accurate classification of the originally grouped cases. In a plot of the first and second function values, the small species *A. porcinus*, *A. kuhli* and *A. calamianensis* again grouped together, with *A. calamianensis* somewhat separated from the other two. *Axis axis* seemed to be intermediate between the *C. mariannus* and *C. alfredi* group (overlapping completely with *C. alfredi*, but very little with *C. mariannus*) and the group containing all other *Cervus* specimens. The *C. eldi* specimens were differentiated from all others, primarily because of the low value of N1, IO and MM (see Table 4, Appendix). A plot of the first and third component did not show further differentiation between species.

Because of the suggestions by Emerson & Tate (1993) and Randi, Mucci, Claro-Hergueta *et al.* (2001) that *Cervus* may be paraphyletic, the differences within the *Cervus* group and *Elaphurus* were investigated next. Craniometrically, *Elaphurus* is distinct from all other members of *Cervus* (showing no overlap with other groups) with high values for the first and low values for the second function (Fig. 5). High values for function 1 correlate primarily with length measurements (PML, GTL, RL), and to a lesser extent also with the widths (BOB, MM, IO) and nose depths (N1, N2) (see Table 5). Especially, the ratio between GTL and N1 seems to

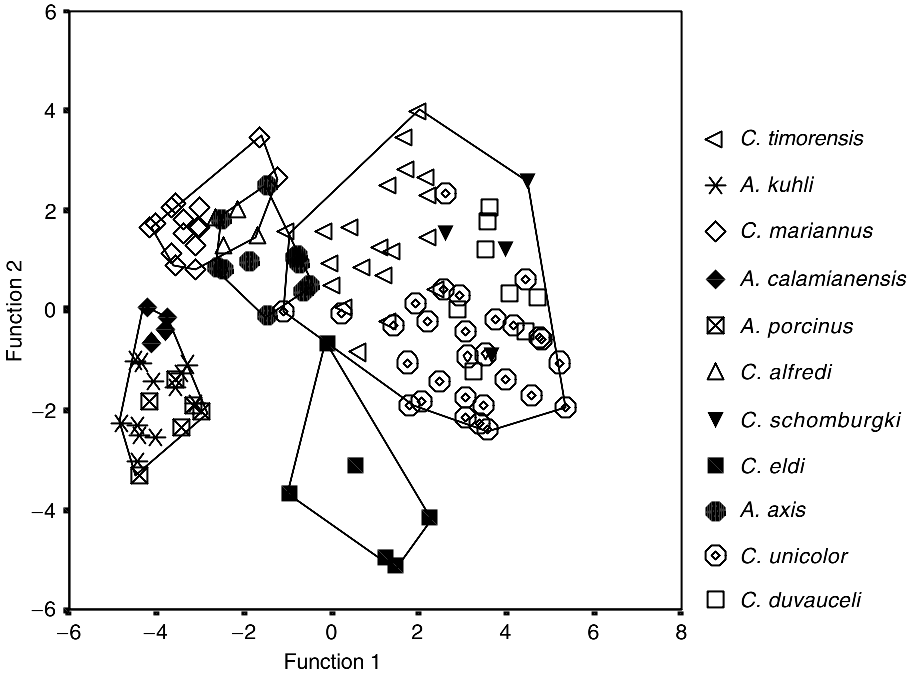

Fig. 4. Discriminant analysis for mature Cervinae specimens (excluding *C. elaphus*).

Table 4. Structure matrix of the principal component analysis of all mature specimens of *Cervus* and *Axis* (see Fig. 4)

	Function	
	1	2
GTL	0.89	0.26
RL	0.85	0.19
BOB	0.68	0.46
N1	0.62	0.71
IO	0.51	0.64
MM	0.53	0.57
Pros	0.58	0.30
Eigenvalue	8.35	2.51
Percentage of variation	65.0	19.5

Table 5. Structure matrix of a discriminant analysis of all mature specimens of *Cervus* and *Elaphurus* (see Fig. 5)

	Function	
	1	2
PML	0.88	– 0.25
Pros	0.71	– 0.37
GTL	0.70	– 0.21
RL	0.69	– 0.04
NL	0.63	0.19
N1	0.44	– 0.17
N2	0.42	– 0.33
MM	0.34	– 0.26
BOB	0.48	– 0.19
NB	0.29	0.14
IO	0.32	– 0.21
BR	0.42	– 0.21
Eigenvalue	14.42	4.72
Percentage of variation	63.6	20.8

Table 6. Correlation matrix of a principal component analysis for mature specimens of the *Hyelaphus* and *Axis* subgenera and one fossil specimen of *A. lydekkeri* (see Fig. 7)

	Function	
	1	2
N2	0.82	0.56
CBR	0.94	– 0.08
IO	0.95	0.00
NB	0.90	– 0.35
BR	0.96	– 0.08
Eigenvalue	4.18	0.44
Percentage of variation	83.6	8.9

separate *E. davidianus* from all other species (Fig. 6), although in this it shows similarities to *A. porcinus* and *A. kuhli*. The relatively low values for nose depths in *Elaphurus* also become clear from the data in Appendix. Low values for function 2 correlate primarily with low values for IO, MM, BOB and N1. The group containing *C. alfredi* and *C. mariannus* is again distinct from the other *Cervus* species, primarily because of their smaller length measurements. *Cervus elaphus* also formed a craniometrically distinct group, primarily because of high values for lengths (PML, GTL, RL) and high values for IO, MM and N1.

A PCA for one fossil specimen of *A. lydekkeri* on which several measurements were taken and the *Axis* and *Hyelaphus* specimens suggested that the fossil *A. lydekkeri* specimen grouped with *Hyelaphus* (Fig. 7). Table 6 shows that the difference between *Axis* and *Hyelaphus* is primarily related to overall size (see high, positive correlation coefficients of the first component); the *A. lydekkeri* and two *A. porcinus* specimens were

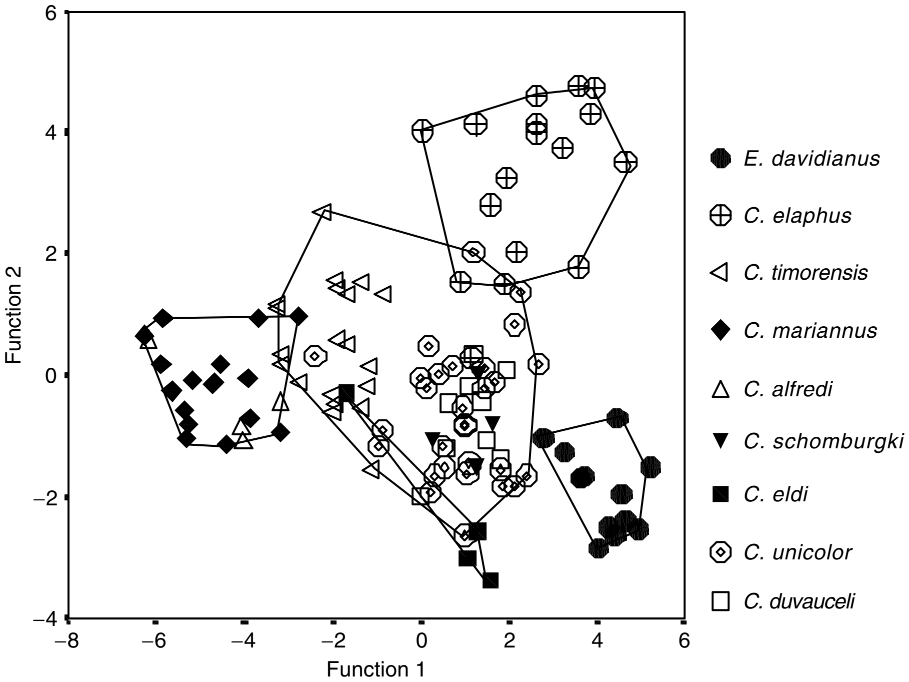

Fig. 5. Discriminant analysis for mature specimens of the genera *Cervus* and *Elaphurus*.

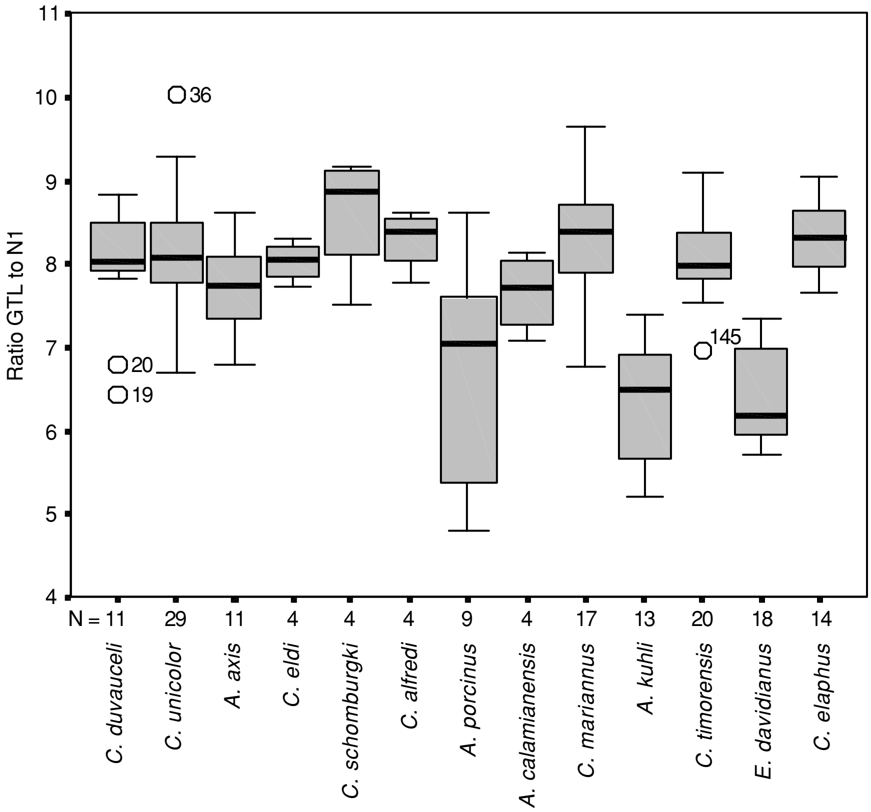

Fig. 6. Ratio between GTL and N1 for each of the Cervini species in this research. Number of specimens per species, *x*-axis; dark, horizontal lines in boxes, median value; boxes, interquartile ranges; thin lines on either sides of boxes, outliers; extreme individual variables, numbered circles.

primarily differentiated by their high values for N2 and low values for NB. The grouping of the *A. lydekkeri* in a bivariate plot for CBR and BR (Fig. 8), resulted in most *A. lydekkeri* specimens falling within the range of *Hyelaphus*, being especially close to *A. kuhli*, but two *A. lydekkeri* specimens together with one *A. kuhli* were

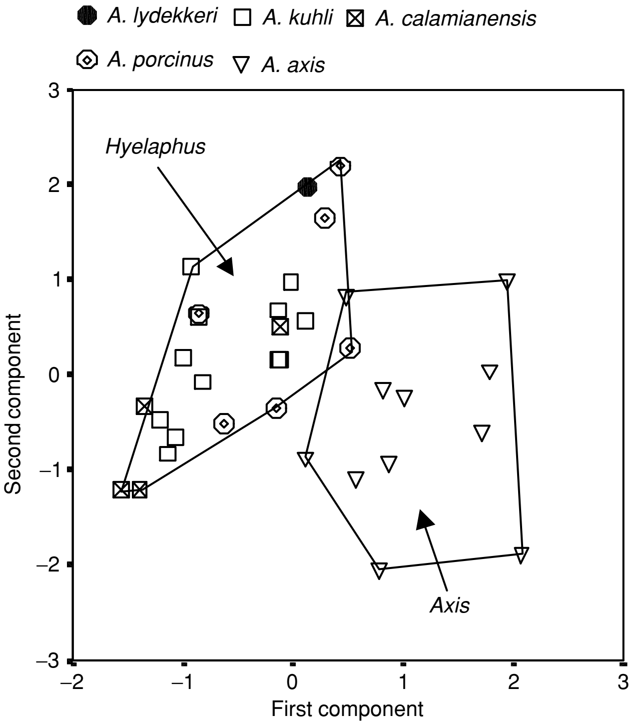

Fig. 7. Principal component analysis of the *Axis* and *Hyelaphus* subgenera in relation to one fossil specimen of *A. lydekkeri*.

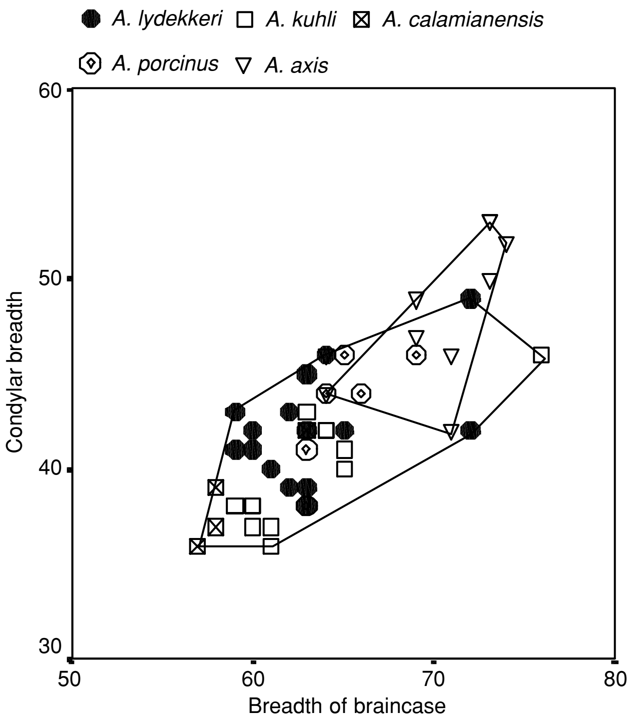

Fig. 8. Bivariate plot of the BR *vs* CBR in five species of *Axis* (including one fossil species).

clearly closer to *A. axis*. This separation depends on size, not proportional differences.

The PCA and DA diagrams have evolutionary directionality; this much is indicated by the consistent closeness of species not otherwise related (*C. mariannus* and *alfredi*, *A. axis*) towards the upper left side of the diagrams. The NJ dendrogram represents these relationships very well, and highlights the fact that some species really do retain primitive skull features, as many of the branches are very short; in a NJ tree, the length of the branches are proportional to phenetic difference. The NJ analysis of all the species in this research rooted at the split between *Axis* and *Cervus* (including *Elaphurus*) resulted in a species tree that grouped together all species in *Axis* (*axis*, *kuhli*, *calamianensis* and *porcinus*); the *Cervus* species grouped closely together, except that *C. mariannus* joined the clade with only a very short branch, with *E. davidianus* taking a position close to *C. elaphus* (Fig. 9).

DISCUSSION

One of the problems in our study was that our multivariate analyses of deer species resulted in groupings that were predominantly determined by overall skull size (see the high, positive correlation factors for most of the variables in the first functions used in this research). Deer show a large range in body sizes, from the small *A. kuhli* that weighs < 50 kg (Kurt, 1990) to 300 kg or more for *C. elaphus* (Wemmer, 1983). This plasticity in size obscured cranial similarities between species. The different strengths of the correlation on the first component and first function, however, did denote some degree of shape difference, and the second component and second function were not size correlated at all. Proportional differences between taxa, such as those revealed by multivariate analysis, are generally used in a phenetic sense only, but here we argue that they have phylogenetic significance. Taxa that are not otherwise related, yet are close together in a PCA or DA plot, have a similar skull shape, and this suggests a primitive retention, giving polarity to the diagram.

Thus, our results suggest the following:

(1) *Elaphurus* is morphologically distinct from all other Cervini, and most similar to the *Rucervus* group and to *C. unicolor*, whilst also showing some similarity to *C. elaphus* (Figs 2 & 5), but note that, on the size-independent axis (Fig. 5, function 2), it is very distant from *C. elaphus*.

(2) *Axis porcinus*, *A. calamianensis* and *A. kuhli* are morphologically similar, and distinct from *A. axis* (Figs 3, 4 & 7);

(3) *Cervus mariannus* is morphologically similar to *C. alfredi*, and both species are distinct from the other *Rusa* deer (*C. timorensis* and *C. unicolor*), while showing some similarity to *A. axis* (Figs 3 & 4);

(4) *Cervus elaphus* is a distinct group (Figs 3 & 5). Furthermore, there seems to be limited craniometric similarity between *C. unicolor* and *C. timorensis*, two species that have traditionally been regarded as closely related species (e.g. van Bemmel, 1949), and *C. timorensis* seems to be equally similar to *A. axis* and

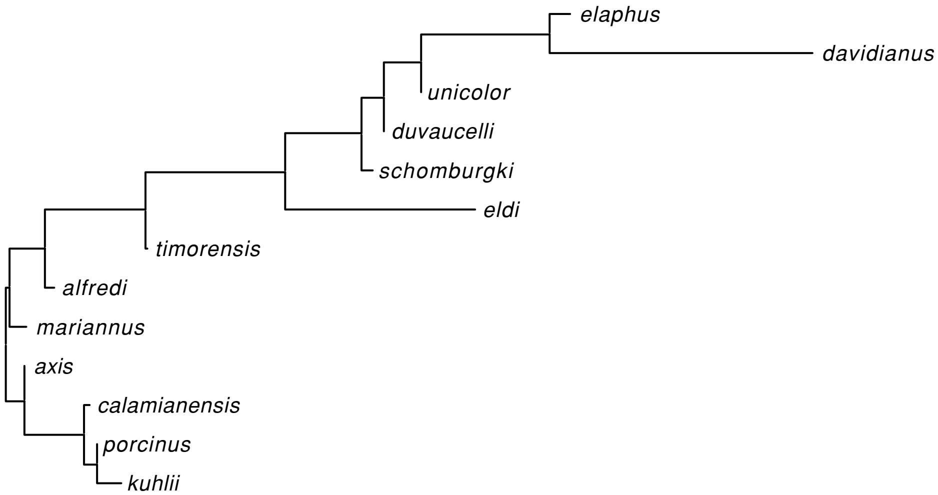

Fig. 9. Neighbour-joining species tree for Cervini based on craniometric similarities.

C. unicolor. We have argued (above) that a multivariate plot has an inherent polarity.

The phylogenetic position of *Elaphurus*

Wemmer (1983), paraphrasing R. I. Pocock, stated that 'there is no stag whose systematic position has troubled zoologists as much as *Elaphurus*'. Wemmer (1983) compared several traits of *Elaphurus* with those of *C. elaphus* and *C. unicolor*, and concluded that *Elaphurus* bears no strong superficial resemblance to either of them. Still, the karyotype of *Elaphurus* is essentially the same as that of *C. elaphus* (Hsu & Benirschke, 1969), while in several phylogenetic studies *Elaphurus* nested within *Cervus* (Emerson & Tate, 1993; Randi, Mucci, Claro-Hergueta *et al.*, 2001), suggesting that it is phylogenetically close to this genus. In addition to these studies, Geist (1998) reported that in its social behaviour *Elaphurus* shows some parallels with cervine (i.e. *Cervus* (*Cervus*) *sensu stricto*) deer while retaining a primitive rusine element (see Table 7 for an overview list of the putative affinities of *Elaphurus* with other deer).

Our data indicate that *Elaphurus* is craniometrically most closely related to the subgenus *Rucervus*, as did the mtDNA studies by Randi, Mucci, Claro-Hergueta *et al.* (2001) and X.-H. Liu *et al.* (2003). On the other hand, the lack of inflation of the auditory bullae (Groves & Grubb, 1987) suggests that it is not closely related to this subgenus, unless the uninflated condition arose more than once within the Cervini. Geist (1998) concluded that *Elaphurus* is an early derivative of three-pronged deer (which include *Axis* and *Cervus* (*Rusa*)), which convergently acquired some features similar to those of other lineages that penetrated into cool climates. *Elaphurus* seems to share derived characters with several taxa (see Table 7), which raises the possibility that *Elaphurus* is a lineage – there are several extinct species of *Elaphurus* (e.g. Ji, 1985) – of hybrid origin. Hybridization between deer species occurs (e.g. Goodman *et al.*, 1999), although it is unclear whether it happens under natural conditions, and hybridization can lead to the formation of new species (for a review see Barton, 2001). An example of this was given by Hirai *et al.* (2003) who hypothesized that hybridization between two gibbon species (*Hylobates agilis* and *H. muelleri*) and the subsequent isolation of the hybrid population had resulted in the formation of a new species, *H. albibarbis*. *Elaphurus* readily hybridizes with *C. elaphus* under controlled conditions in captivity, and male and female F1 *Elaphurus* × *C. elaphus* hybrids were fertile and produced over 300 viable backcross hybrids in matings with *C. elaphus* (Tate *et al.*, 1997). *Cervus elaphus* and *C. unicolor*, however, did not produce fertile offspring in 440 artificial inseminations, and only one female calf was born alive (Muir *et al.*, 1997). This suggests that *Elaphurus* and *C. elaphus* are more closely related than *Elaphurus* and *C. unicolor*, although it may also reflect the retention of the same karyotype, facilitating meiosis (P. Grubb, pers. comm.). If the *Elaphurus* clade is of hybrid origin, then perhaps early in the evolution, a species of the *Rucervus* group hybridized with a species of the subgenus *Cervus*, after which the hybrid population became isolated and evolved into a distinct lineage. *Elaphurus* probably arose in eastern Asia during the Late Pliocene (Taru & Hasegawa, 2002), and northern or eastern China or Japan would be likely areas for this hypothetical hybridization event to have taken place.

Another possibility is that *Elaphurus* diverged from a *Cervus* (*Rucervus*)-like ancestor, as suggested by the mtDNA-based phylogenies of Randi, Mucci, Claro-Hergueta *et al.* (2001) and X.-H. Liu *et al.* (2003), and our craniometric data, after which it convergently acquired characteristics that link it to *C. elaphus* or *C.* (*Rusa*). Further genetic work should be able to test these hypotheses.

Thus, while the exact relationship between *Elaphurus* and the other Cervini remains unresolved, it seems clear that *Cervus* is paraphyletic in relation to *Elaphurus* and that the latter should be referred to the genus *Cervus* (*Cervus* has priority over *Elaphurus*), or that *Cervus* should be partitioned into several genera.

Table 7. Resemblances of *Elaphurus* to other species of Cervini reported in the literature and possibly suggesting phylogenetic affinity

Character of *Elaphurus*	Suggested close relationship	References[a] + remarks
Incisiform teeth uniformly broad	Synapomorphic character with most *Cervus* species, except *C.* (*Rusa*) *mariannus* and *C.* (*Cervus*) *nippon*	1 This character could have arisen more than once within the Cervini
Lack of inflation of auditory bullae	Synapomorphic character with most *Cervus* species, except *C*. (*Rucervus*) and *C*. (*C*.) *nippon*	1 Lack of inflation is a derived character-state, but not necessarily a synapomorphic condition
Craniometrics	much changed and specialized branch of *Cervus* (*Rusa*)	2
Karyotype	Symplesiomorphic character with *C*. (*C*.) *elaphus*	3
Long facial aspect	Intermediate between *C*. (*Rusa*) *unicolor* and *C*. (*C*.) *elaphus*	4 Only 3 species compared
Hook-like sphenoid process	*C*. (*Rusa*) *unicolor*	5 Only 3 species compared
Double channel in pedicle	Present in *C*. (*Rucervus*) *schomburgki* (but not other *C*. (*Rucervus*))	6
Crouched female urination position has been lost	Also lost in *C*. (*C*.) *elaphus* and *Dama*	6
Females do not vocalize in a submissive posture upon the approach of the courting stag	Neither do females of *C*. (*C*.) *elaphus* and *C*. (*C*.) *nippon*	6
During courtship, the stag initially approaches in a deep low-stretch	Also in *C*. (*Rusa*) *unicolor*, *Axis axis* and *C*. (*Rucervus*) *duvauceli*	6
mtDNA sequences	*C*. (*Rucervus*) *eldi* (90% bootstrap support)	7 No *C*. (*Rucervus*) *duvauceli* in research
Electrophoretic patterns of 22 proteins	*C*. (*C*.) *elaphus* and *C*. (*C*.) *nippon*	8 *C*. (*Rucervus*) not in research
K-casein DNA sequences	*C*. (*C*.) *elaphus* and *C*. (*C*.) *nippon* (70% bootstrap support)	9 *C*. (*Rucervus*) *eldi* not in research
Cytochrome *b* sequences	*C*. (*Rucervus*) *eldi* (73% bootstrap support)	10

[a] 1, Groves & Grubb (1987); 2, Flerov (1952); 3, Benirschke (1983); 4, Wemmer (1983); 5, Bubenik (1966; 1975 in Wemmer (1983); 6, Geist (1998); 7, Randi, Mucci, Claro-Hergueta *et al.* (2001); 8, Emerson & Tate (1993); 9, Cronin *et al.* (1996); 10, X.-H. Liu *et al.* (2003).

Relationships of *Rusa*

In their discussion of the deer of the Philippines, Grubb & Groves (1983) concluded that *C. alfredi* and *C. mariannus* were distinct species, with especially the latter species being morphologically similar (apart from overall size) to *C. unicolor brookei* (the subspecies from Borneo). *Cervus mariannus* shared certain characteristics with *C. alfredi* which implied an early separation from the *unicolor* stock. Our data indicate that although *C. alfredi* and *C. mariannus* are morphologically distinct from other *Rusa*, this is mostly based on the smaller size of the Philippine forms. Interestingly though, Fig. 4 (in which the first function is, unusually, not based on size) could suggest that the two Philippine species are more similar to *A. axis* than to *C. timorensis* and *C. unicolor*; our preferred interpretation is that the similar skull shape of the two Philippine species and *A. axis* may indicate that the three species retain primitive skull characteristics, and that *C. timorensis* and *C. unicolor* are more derived forms. That hypothesis is somewhat supported by Randi, Mucci, Claro-Hergueta *et al.*'s (2001) data, which indicate an early divergence of both *C. alfredi* and *A. axis*.

Data by Randi, Mucci, Claro-Hergueta *et al.* (2001) do not support the monophyly of the subgenus *Rusa*, although considering the low number of specimens per species and the relatively low bootstrap value for the node splitting off *timorensis* and *unicolor*, that result may turn out to be flawed. Our own data are inconclusive; either *alfredi* and *mariannus* derived from a *unicolor* or *timorensis*-like ancestor, or else their similarity to each other and to the otherwise unrelated *A. axis* is plesiomorphic, in which case *C. unicolor* and *timorensis* are derived from the same stock, *timorensis* retaining a more plesiomorphic skull form.

Geist (1998) suggested that within this group, the Indian Sambar *C. unicolor unicolor* is possibly the most derived, judging from its low diploid number of $2n = 60$, compared with closely related taxa from island South-east Asia (*C. mariannus* $2n = 65$) or from Indochina (*C. u. cambojensis* $2n = 62$). Lower chromosome numbers have been reported, however: *C. u. malaccensis* (from peninsular Malaysia), $2n = 56$; *C. unicolor niger* (from northern India), $2n = 58$ (Benirschke, 2002), and *C. timorensis* also has a diploid number of $2n = 60$ (G. Semiadi, pers. comm.). Thus, the exact branching sequence within *Rusa* remains unclear, and the question remains whether an ancestral species gave rise to the Philippine deer which then split into two lineages and to the Sundaland deer which split into *timorensis* and *unicolor*, or whether the divergence of the Philippine deer came much earlier and *timorensis* and *unicolor* diverged from another group. Further phylogenetic work is needed to resolve this issue.

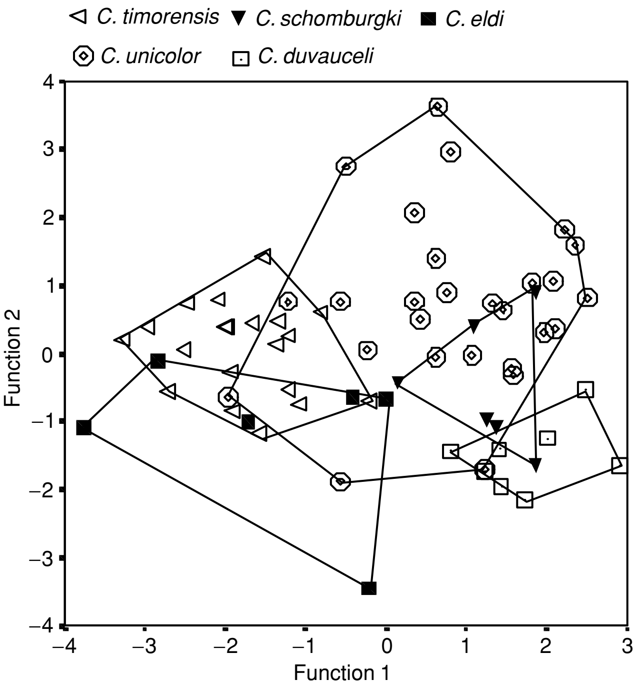

Fig. 10. Discriminant analysis for mature specimens of *eldi*, *duvauceli*, *schomburgki*, *timorensis*, and *unicolor*.

Relationships of *Rucervus*

The close relationships within the subgenus *Rucervus* have been established based on the basis of the branching of the trez tine (Pocock, 1943), which is unique among the Cervini. They also share a more flexed skull and more hypsodont teeth and smaller canines (Groves & Grubb, 1987). Groves & Grubb (1987) pointed out, however, that in other respects *C. eldi* and *C. duvauceli* show different affinities. Thus, the antlers in *C. eldi* are more like *A. axis* than *C. unicolor*, while *C. eldi* differs from *duvauceli* in having a deep lachrymal pit, like *Rusa*. Our results indicate that the *Rucervus* specimens seem to largely overlap in skull shape with *C. timorensis* and *C. unicolor* (but not *C. elaphus*). A more detailed analysis of *eldi*, *duvauceli*, *schomburgki*, *timorensis* and *unicolor* (Fig. 10) suggested that there may be considerable similarities in skull shape between *timorensis* and *eldi*, whereas *duvauceli* and *schomburgki* closely resembled each other. Our data may therefore indicate that both *timorensis* and *eldi* have retained primitive skull features, and that *unicolor*, *duvauceli* and *schomburgki* are more derived forms. A close relationship between *schomburgki* and *duvauceli* and their distinctness from *eldi* had already been noticed by Gray, who restricted the former two to *Rucervus* and the latter to a new genus *Panolia* (see Pocock, 1943: 553). We therefore hypothesize that *eldi* is on a different evolutionary line than *duvauceli* and *schomburgki*, which would leave *Rucervus* paraphyletic.

Craniometric relationships within the genus *Axis*

Van Bemmel (1944) pointed out the similarities between *A. kuhli* and *A. porcinus*, and suggested that 'in case the subgenus *Hyelaphus* is accepted *C. kuhlii* (sic) should be referred to it', owing to the characters of the antlers, the low build and the plain not dappled colour of the hide. Van Bemmel also suggested that *A. calamianensis* may prove to be closely related to this group. Our results confirm the close craniometric similarities between *A. kuhli*, *A. porcinus* and *A. calamianensis* (Figs 3 & 4), and clearly show the morphometric differences between *Hyelaphus* and *Axis* (Figs 3, 4 & 7). We tentatively conclude that the fossil specimens of *A. lydekkeri* from Pleistocene Java were more similar to the *Hyelaphus* group than to *Axis*, but our analysis did not clearly indicate the specific relationships of *A. lydekkeri* within the *Hyelaphus* subgenus. For now we recommend maintaining the specific status of *A. lydekkeri*, as *A.* (*Hyelaphus*) *lydekkeri*, which, according to Zaim *et al.* (in press), is a senior synonym for *C. zwaani*. The latter species was found in the Bumi Aju Fauna indicating that the subgenus *Hyelaphus* arrived on Java in the Early–Middle Pleistocene. Furthermore, van Bemmel (1944) suggested that the fossil species *C. oppenoorthii* V. Koenigswald, 1933 from Late Pleistocene Java, should be classified as a fossil subspecies of *A. kuhli*, and that the Bawean (see Fig. 1) population of *A. kuhli* is a relict of a previously much larger distribution range (including Java). On the other hand, Zaim *et al.* (in press) suggested that *C. oppenoorthii* may be more closely related to the subgenus *Rusa*. Still, *A. kuhli* probably occurred in East Java until the Holocene, as suggested by fossil finds described by van den Brink (1982), which suggests that from Early/Middle Pleistocene to the Holocene, *Hyelaphus* was present on Java. The dispersal of *Hyelaphus* to the Calamian Islands probably occurred via Borneo and Palawan, which is supported by Fox (1979), who considered the extinct deer of Palawan to belong to *Axis*. *Axis calamianensis* could have been introduced or spread naturally to the Calamianes quite recently, perhaps from Palawan, where they later became extinct, as suggested by Hoogstraal (1951).

The evolution of the Cervinae in a palaeogeographical context

The first antlered deer were Old World forms, which originated in the Middle to Late Tertiary and radiated repeatedly from tropical into cold climates during the Pleistocene (Geist, 1998). Douzery & Randi (1997) estimated that the Cervinae (as represented by *Cervus* and *Dama*) diverged from the American deer between 14.4 and 10.6 million years ago (Ma), the genus *Cervus* (represented by *C. nippon* and *C. elaphus*) between 10.2 and 6.8 Ma, and subspecies within *C. elaphus* between 2.5 and 0.4 Ma. In a later paper, Randi, Mucci, Pierpaoli *et al.* (1998) estimated the split between the Muntiacinae and Cervinae at 16.7–15.0 Ma. These estimates were based on the divergence of antlered deer by about 20 Ma, a date derived from work by Ginsberg (1988 in Douzery & Randi, 1997) and Ginsburg & Azanza (1991) who stated that the earliest known cervids occur in the

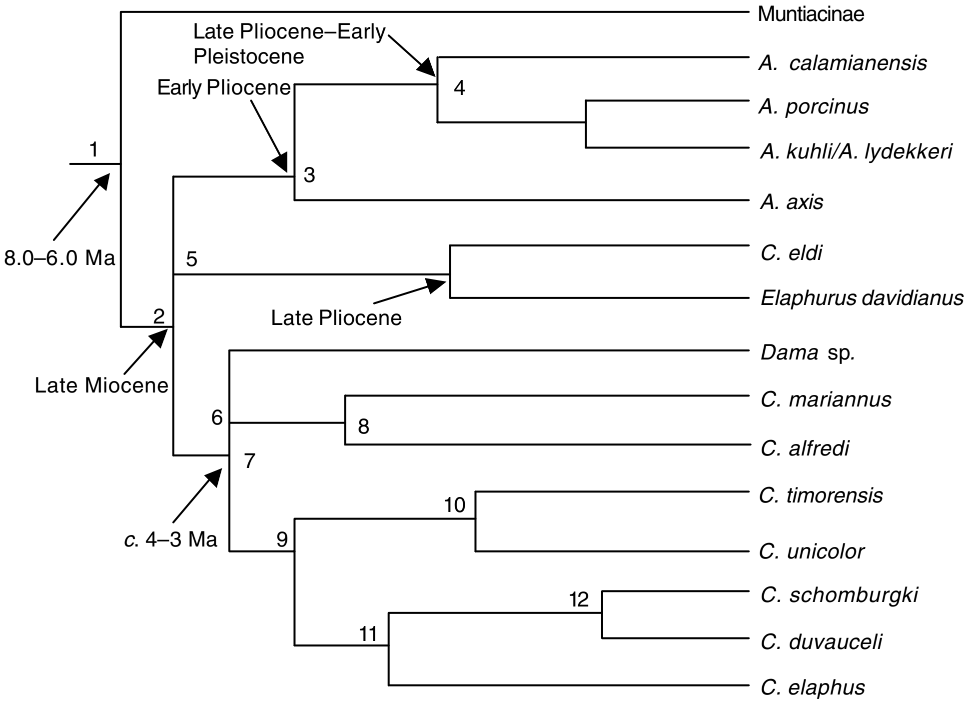

Fig. 11. Phylogenetic tree of the Cervinae based on our craniometrics and data by Randi, Mucci, Claro-Hergueta *et al.* (2001), and rescaled after data by Miyamoto, Kraus & Ryder (1990). For explanations of nodes 1–12 see Table 8.

middle part of the Early Miocene of Europe. Thenius (1969), however, stated that primitive two-pronged cervids radiated shortly after they evolved in the Middle Miocene, and that the modern descendants of this group included *Muntiacus* (muntjaks) and *Elaphodus* (tufted deer). The next radiation led to the three-pronged deer of southern Asia (*Axis*, *Rusa*, *Rucervus*) (Geist, 1998). It thus seems that the Early Miocene cervids discussed by Ginsburg and colleagues included the ancestors of *Muntiacus* and *Elaphodus*. The estimated origin of the Cervini by Douzery & Randi, who did not include *Muntiacus* or *Elaphodus* in their research, may therefore be incorrect, especially because the branching pattern between the Muntiacinae, Cervinae, Hydropotinae, and Odocoileinae remains unresolved (e.g. Geist, 1998). Randi, Mucci, Claro-Hergueta *et al.* (2001) repeated their earlier (i.e. Randi, Mucci, Pierpaoli *et al.*, 1998) statements about a Middle–Late Miocene origin of *Axis*, *Dama*, and *Cervus* (respectively estimated at 12.5–9.5 Ma, 11.6–8.9 Ma, and 10.5–7.9 Ma). They considered these divergence time estimates to be congruent with the fossil record, because 'Plio-Pleistocenic *Axis*, *Dama* and *Rucervus* are widespread among the Eurasian fossils'. One could as easily argue that the divergence estimates by Randi, Mucci, Claro-Hergueta *et al.* (2001) precede the Plio-Pleistocene (which started *c.* 5 Ma) by several million years, and that these genera originated considerably later than suggested by the mtDNA data of Randi and his colleagues. In fact, the earliest fossils of *Rucervus* date back to 2.9 Ma (Azzaroli *et al.*, 1988), and those of *Elaphurus* to the Late Pliocene (*c.* 3–2 Ma) (Taru & Hasegawa, 2002), which is considerably later than 10.5–7.9 Ma, the date estimated by Randi, Mucci, Claro-Hergueta *et al.* (2001). Also, *C. nippon* fossils were first found in Late Pliocene deposits of Europe (Thenius & Hofer, 1960 in Geist, 1998), 1 or 2 Ma later than suggested by the mtDNA data of Randi *et al.* As opposed to Randi and his colleagues, Miyamoto, Kraus & Ryder (1990) suggested that the Cervini split from the Muntiacini between 8 and 6 Ma, rather than between 16.7 and 15.6 Ma as suggested by Randi, Mucci, Claro-Hergueta *et al.* (2001). Also, Bubenik (1990) stated that the Muntiacidae appeared in the Late Miocene (11.1–5.3 Ma), while Di Stefano & Petronio (2002) named the Late Miocene *Cervocerus novorosiae* as the most primitive member of the Cervini; it thus seems that Miyamoto *et al.* provided a more accurate estimate of the evolutionary start of Cervini.

Based on the information above, we developed a phylogenetic scenario for the Cervini (Fig. 11). We assumed that Miyamoto *et al.*'s (1990) estimate is the more accurate of the two and initially applied it to Randi, Mucci, Claro-Hergueta *et al.*'s (2001) phylogram, which we combined with our own findings and those by Emerson & Tate (1993), Cronin *et al.* (1996), X.-H. Liu *et al.* (2003) and Di Stefano & Petronio (2002). In addition:

(1) we added *A. calamianensis*, and *A. kuhli*, and using our craniometric data we hypothesized that *A. calamianensis* is sister species to the group containing *kuhli* and *porcinus*;

(2) we added *C. mariannus* as sister species of *C. alfredi*. We consider this an ancient group, not directly related to *C. timorensis* and *C. unicolor*, as also implied by the mtDNA data of Randi, Mucci, Claro-Hergueta *et al.* (2001);

Table 8. Explanations of nodes 1–12 in Fig. 11

1	Late Miocene divergence between Muntiacinae and Cervinae (see text).
2	Divergence between *Axis*, *C. eldi* and *Elaphurus* lineage from other Cervini (following Di Stefano & Petronio (2002) and Randi, Mucci, Claro-Hergueta *et al*. (2001)).
3	Divergence between the *Hyelaphus* and *Axis* subgenera (following Di Stefano & Petronio (2002) and Randi, Mucci, Claro-Hergueta *et al*. (2001)).
4	Relationships within *Hyelaphus* are based on Fig. 10.
5	A close relationship between *Axis* and *C. eldi/Elaphurus* was suggested by Di Stefano & Petronio (2002), but the latter lineage might also represent an early divergence from the lineage leading to the *Cervus* and *Rusa* subgenera. Randi, Mucci, Claro-Hergueta *et al*. (2001) suggest a close relationship between *eldi* and *Elaphurus*; others suggest a closer proximity of *Elaphurus* to *elaphus*. *Elaphurus* may also have resulted from a hybridization event as argued in the text.
6	Divergence of *Dama* from others (following Randi, Mucci, Claro-Hergueta *et al*., 2001); divergence sequence between *Axis*, *Dama*, and *Cervus* is poorly understood and may have occurred rapidly. Emerson & Tate (1993) suggest a close relationship between *Dama* and *A. axis*, whereas Di Stefano & Petronio (2002) suggest that *Dama* split from the lineage leading to the *Rusa* and possibly *Cervus* subgenera in the Early Pliocene, and then split from a *Rusa*-like lineage (*Pseudodama*) as late as the Pleistocene.
7	The basal position of the Philippine *Cervus* deer within the group containing the *Cervus* and *Rusa* subgenera is supported by Randi, Mucci, Claro-Hergueta *et al*. (2001) with 82% bootstrap support, and our craniometric data.
8	This could either be the result of one dispersal event to the Philippine islands, or there might have been two (or more) separate events.
9	This clade was supported by Randi, Mucci, Claro-Hergueta *et al*. (2001) with 69% bootstrap support and by X.-H. Liu *et al*. (2003), although the latter included *A. porcinus* in a well-supported clade with *C. unicolor*.
10	Randi, Mucci, Claro-Hergueta *et al*. (2001) found strong support for a clade containing *C. unicolor* and *C. timorensis*, although our craniometric data suggest that *timorensis* is similar to *Axis* (Fig. 10), and not *unicolor*.
11	The phylogenetic position of *elaphus* remains unclear. Cronin *et al*. (1996) link it to *Elaphurus* and *nippon* to the exclusion of *duvauceli* and *unicolor*; Randi, Mucci, Claro-Hergueta *et al*. (2001) associate it with *unicolor*, *timorensis* and *nippon* to the exclusion of *alfredi*, *eldi* and *Elaphurus*; Emerson & Tate (1993) link it to *nippon* and *Elaphurus*, to the exclusion of *timorensis* and *unicolor*; our craniometric data suggest similarities to *unicolor* and *Elaphurus*. The *elaphus* lineage probably also contains *C. nippon* and *C. albirostris* (X.-H. Liu *et al*., 2003).
12	Our craniometric data support phenetic similarities between *schomburgki* and *duvauceli*; their phylogenetic proximity, to the exclusion of *elaphus* and *Elaphurus* is supported by Cronin *et al*. (1996).

(3) we followed Di Stefano & Petronio's (2002) interpretation of the phylogenetic position of fallow deer *Dama* sp. as a member of the *Pseudodama* lineage that diverged from the *Rusa* lineage in the Early Pliocene. Based on craniometric analysis of fossil and recent material, Pfeiffer (1999) found as much support for a sister group relationship between *Axis* and *Dama* as for a sister group relationship between *Cervus* and *Axis*. This may indicate that these three genera diverged rapidly, probably sometime in the Late Miocene–Early Pliocene;

(4) we added *C. eldi*, which, based on our craniometric data seems to be closely related to *C. timorensis*, but which both Randi, Mucci, Claro-Hergueta *et al*. (2001) and X.-H. Liu *et al*. (2003) found to be closely related to *Elaphurus*;

(5) we added *C. duvauveli* and *C. schomburgki*.

Figure 11 seems to fit the fossil record: Dong (1993) reported that *Axis* appeared in northern China at the end of the Miocene, while the subgenus *Rusa* first appeared in Late Pliocene. Also, our reconstruction seems to be in line with the phylogenetic data provided by Li, Wang *et al*. (1999), who estimated the divergence between *Rucervus* (represented by *C. eldi*) and *Cervus* at 2.8–2.4 Ma (10.5–7.9 Ma according to Randi, Mucci, Claro-Hergueta *et al*. (2001); 4.4–3.7 Ma according to our rescaled model). Also, Li, Sheng *et al*. (1998) estimated that the Cervini and Muntiacinae diverged before 6 Ma, which fits our estimate.

To hypothesize on dispersal or isolation events that led to allopatric speciation within the Cervini, Fig. 11 is combined with palaeogeographic reconstructions by Meijaard (2003*a*). Before doing this, the ecological affinities of the species need to be established. *Hyelaphus* species are small deer of tall grassland, although *A. kuhli* is more a species of hill forest, not marshy, low-lying grasslands (Blouch & Almosoedirdjo, 1982). *Axis axis* has features typical of ungulates that dwell in open terrain in large herds, and seems to be adapted to regularly burned grassy areas (Geist, 1998); it also occurs in forest edge areas, where it grazes and feeds on fallen fruit (Grubb, 1990). *Rusa* species are specialized for solitary life in thickets, apart from *C. timorensis*, which lives gregariously in savannahs (Geist, 1998). *Rucervus* species are deer of open woodland and the tall grass of flood plains; they are specialized graminivores with uniquely folded cheek teeth (Grubb, 1990).

Above we suggested that *Axis*, *Cervus* and *Dama* diverged rapidly in the Late Miocene–Early Pliocene. At this time there was a change from the generally humid and warm climate of the Miocene to drier, cooler conditions in the Pliocene. On the Indian Peninsula and in Indochina and southern China this led to the gradual replacement of evergreen tropical rainforest by deciduous forests (for an overview see Morley, 2000). Between 7.4–7.0 Ma and 5 Ma, a vegetation mosaic of grasslands and forest was probably present in the Himalayan foothills (Awasthi, 1992 in Quade, Cerling & Bowman, 1989; Morley, 2000), and after 5 Ma grasses dominated the vegetation, possibly interspersed with riparian habitats in which some C_3 trees and shrubs grew. Such conditions would have initially favoured the evolution of deer of forest edge and open forest types, such as the *Axis* species. As the vegetation structure became increasingly open and grasslands more common, grazing deer may have started to replace browsing species, as suggested by Quade *et al*. (1989). The Early Pliocene cooling event (see Wang, 1994) was followed by a Middle Pliocene warmer period (*c*. 3.5–3.0 Ma). Reconstructions of the climate and vegetation indicate that there was a considerable expansion of evergreen forest in southern China, whereas Indochina was mostly covered by rainforest, possibly with patches of deciduous forest in the area of present-day Burma (Dowsett *et al*., 1994). It would be interesting to check whether this could have led to isolation of grassland-dependent species in areas where such vegetation remained. If indeed *Elaphurus* is a hybrid species, as suggested above, it may also have been at this time when a *Rucervus*-like deer population mixed with the ancestral *Cervus elaphus/nippon* lineage, possibly in the swamps of the major Chinese rivers.

Another factor that may have influenced deer evolution in South-east Asia is the split between the Indochinese and Sundaic faunistic subregions. Woodruff (2003) hypothesized that this occurred during the Early Pliocene when high sea levels created one of two wide sea ways cutting the Thai/Malay Peninsula in two and separating two faunas for as much as 1 Ma. Meijaard (2003*a*) found further evidence that these conditions may have occurred again later in the Pliocene. If this scenario is proven to be true, it could have been a factor behind the divergence of the *Hyelaphus* group, if indeed it is of Sundaic affinity.

The Middle Pliocene warm period was followed by a severe cooling period at the Pliocene–Pleistocene transition (2.4–1.8 Ma). According to D. Liu & Ding (1984), Indochina and southern China were still covered by humid rainforest at the Pliocene–Pleistocene boundary, but this rainforest zone was progressively pushed south during the Pleistocene until no rainforest remained in China. By the Middle Pleistocene, the subtropical and tropical zones had shifted south- and eastward, and by the Late Pleistocene, these zones had migrated even farther southward and were considerably reduced in area (Jablonski & Whitfort, 1999). Evidence for grasslands in Indochina is limited through most of the Pliocene, but subsequently shows a marked increase, together with charred grass cuticle, during the Early Pleistocene, indicating the expansion of savannah vegetation, which was subject to burning (Morley, 1999). Several fossil species of *Axis* have been found in China, including *A. speciosus*, *A. shansius* and *A. rugosus*, with *A. shansius* appearing in the Late Pliocene (3.3–1.8 Ma) (but see Di Stefano & Petronio (2002) for an older age of that species) and *A. rugosus* in the Early Pleistocene (1.8–0.8 Ma) (Dong, 1993). Di Stefano & Petronio (2002) hypothesized that the *Hyelaphus* lineage diverged from the *Axis* lineage in the Early Pliocene (*c*. 4.5 Ma), with *A. speciosus* as the most ancestral species of the *Hyelaphus* lineage. The Plio-Pleistocene may have been the time of the evolution of *A. axis*-like species that specialized on short sprouting grass.

Axis first appeared in the fossil record on Java in the Early to Middle Pleistocene, probably as a species of the subgenus *Hyelaphus*. At that time, Java was probably connected to the Malay Peninsula via a land bridge, which also connected it to Borneo, and possibly to Sumatra (Meijaard, 2003*a*). Presumably, this led to the evolution of *A. lydekkeri*/*A. kuhli* on Java, which became extinct on the island after the last Pleistocene glacial, leaving only the remnant population of *A. kuhli* on Bawean Island. Our data suggested that *A. calamianensis* separated from the *A. porcinus*/*A. kuhli* clade before these two species split, which presumably happened when the Javan population became separated from the rest of South-east Asia in the late Middle Pleistocene. It is unclear when *A. calamianensis* dispersed to Palawan and the Calamianes. Heaney (1985) suggested that there was a connection from Borneo to Palawan until the Middle Pleistocene, so presumably *A. calamianensis* dispersed to Palawan before or during that time. The Pliocene to Middle Pleistocene incursion of *Hyelaphus* into the South-east Asian tropics (including Borneo) suggests that vegetation types were more open than they are now, possibly consisting of deciduous forests and open grasslands (the habitats of *A. kuhli*, *A. porcinus*, and *A. calamianensis*; Wemmer, 1998). Such conditions would only have existed in the tropics during a severe glacial (Meijaard, 2003*a*). The palaeoenvironments of that time are not known, but if we assume that conditions were similar to the equally severe last glacial maximum, then a band of more open vegetation types may have occurred in southern and eastern Borneo (see Meijaard, 2003*b*), possibly providing a dispersal route for *Hyelaphus* to Palawan. There is only one known deer fossil from Borneo (see Busk, 1869), but this was a species larger than *C. timorensis*, and probably not closely related to *Hyelaphus*. Relatively open environmental conditions would also explain how *Axis javanicus* (renamed as *A. sunda* by Kretzoi, 1947 in Grubb, 2000), which is similar to, if not the same as *A. axis*, dispersed from mainland Asia to Java during the Late Pleistocene. This species generally occurs in a mixture of forest and more open grass–shrub associations (Moe & Wegge, 1994), and such vegetation types may have existed in the area of the present-day Java Sea and the area east of the Malay Peninsula (Meijaard, 2003*b*). We tentatively suggest that both *A. sunda* and *A. kuhli*/*A. lydekkeri* became extinct on Java because of increased competition from *C. timorensis* in open areas and *Muntiacus muntjak* in forest areas after the climate on Java became wetter during the Holocene, although there were probably additional factors involved in that process.

Van Mourik & Stelmasiak (1986) suggested that *C. timorensis* evolved together with other *Rusa* species in the Szechuan region of China during the Late Pliocene, from where it dispersed west to continental Europe, east to Taiwan, and south-east to Java. Di Stefano & Petronio (2002) hypothesized that the Asian and European *Rusa* lineages split much earlier, in the Early Pliocene (*c*. 4 Ma).

At the end of the Pliocene most of China was still covered by tropical, subtropical and warm temperate forests (e.g. Jablonksi & Whitfort, 1999), and presumably the first *Rusa* species would have been species adapted to quite dense habitats of forest with some open grass and scrub vegetation. In northern India, a *Rusa*-like deer (*Cervus punjabensis*) with hypsodont dentition (being indicative of grassland habitat) appeared about 2.5 Ma. It was part of an intrusion of east Asian deer species that occurred at a time of climatic deterioration (Geist, 1998). *Rusa*-like deer were also described from the upper Pliocene of Europe and west Asia (e.g. Schaub, 1941; Yanovskaya, 1954; Czyewska, 1959). However, Schaub (1941) and Heintz (1970) pointed out that, although Pliocene deer of Europe, such as *C. philisi* and *C. perrieri*, showed some similarities with *Rusa* (and *Axis*), they were more likely to be an early (Middle Pliocene) lineage from either of these two groups that became extinct during the Pleistocene. Czyewska (1959) came to a similar conclusion, which suggests that the present subgenus *Rusa* may never have occurred in Europe. It would be interesting to test whether members of this early *Rusa* lineage show similarities to the white-faced Tibetan deer *Przewalskium albirostris*; Flerov (1952) suggested that *Przewalskium* diverged from *Rusa* in the Late Pliocene (but X.-H. Liu *et al.*'s (2003) data link it to *C. nippon*). Several other *Rusa*-like species, *C. (R.)* cf. *elegans*, *C. (R.) microtus*, *C. (R.) stehlini*, *C. (R.) timorensis*, *C. (R.) unicolor*, and *C. (R.) yunnanensis* occurred in the Early–Late Pleistocene of China, with *C. (R.) unicolor* first appearing in Middle Pleistocene deposits (Zong, 1987; Dong, 1993). As mentioned above, during the Pleistocene, the subtropical forest zone in China moved south and tropical vegetation almost completely disappeared. It is likely that this process eventually led to the disappearance of *Rusa*-like deer from most of China, while possibly being a factor in the evolution of species such as *C. elaphus* and *C. nippon*.

CONCLUSION

Attempting to elucidate the relationships among extant deer species in Asia in this study has led to some important new insights. Our results suggest that elements of skull shape as determined by morphometrics can be used as phylogenetic characters and depict phylogenetic relationships among Cervini deer species that is not far removed from the picture given by molecular studies and other characters. Based on this, a new evolutionary model has been developed that suggests that a taxonomic revision may be needed for the Cervini. Deer evolution in Asia, however, has been a complicated process and it seems that the data to understand how and when lineages diverged are still lacking. A thorough cladistic analysis of all available fossil material would be a considerable step forward in unravelling how the different groups are related to each other, while also providing a historic account on changing distribution ranges of individual species. The possibility that hybridization may have played a role in deer evolution has been raised, and this could be investigated by analysing different sections of the genome, for instance as has recently been carried out for the primate genus *Macaca* (see Tosi, Morales & Melnick, 2000). Finally, once the divergence sequence of deer taxa has been analysed in more detail this could be linked to the continuously improving palaeoenvironmental models for the region, which would hopefully result in a causal relationship between palaeoenvironmental and palaeogeographical changes and deer evolution.

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Appendix. Means and standard deviations

		GTL	CBL	BL	PL	Pros	PML	N1	N2	PD
E. davidianus	Mean	418.9	399.1	377.8	258.8	131.1	136.3	50.5	85.7	85.0
	n	14	15	15	15	14	15	15	15	15
	SD	15.7	14.3	14.3	8.0	6.2	6.8	2.9	3.5	6.5
C. duvauceli	Mean	377.7	347.5	329.0	220.3	125.7	108.6	46.9	80.6	90.3
	n	20	8	8	8	17	9	11	9	8
	SD	17.9	21.2	21.6	14.0	8.4	21.7	6.4	8.4	7.3
C. unicolor	Mean	357.5	340.5	318.6	212.0	114.6	103.1	44.5	81.4	87.6
	n	30	27	29	29	30	29	30	29	29
	SD	35.0	35.3	33.0	22.5	12.3	11.6	6.5	11.3	10.0
C. eldi	Mean	305.3	280.0	261.8	175.7	98.2	89.0	37.7	69.7	80.7
	n	6	5	5	6	6	6	6	6	6
	SD	44.5	37.8	36.3	24.7	15.7	16.0	6.4	14.6	12.8
C. schomburgki	Mean	374.2	351.5	333.2	220.0	127.0	112.3	43.8	84.0	93.8
	n	6	6	5	5	6	6	4	4	4
	SD	10.8	11.3	13.5	5.7	9.6	7.9	4.3	3.4	2.6
C. alfredi	Mean	244.3	235.0	218.8	139.3	72.0	55.3	29.4	52.8	65.6
	n	4	4	4	4	4	4	5	5	5
	SD	16.5	15.2	12.0	9.5	4.3	5.7	1.5	5.3	3.0
C. mariannus	Mean	230.3	219.4	203.6	131.5	66.7	51.4	28.1	48.6	61.5
	n	18	16	16	18	18	16	19	19	21
	SD	25.7	24.8	23.3	13.7	7.6	7.8	4.3	7.6	6.3
C. timorensis	Mean	311.3	297.5	276.6	178.9	99.3	90.0	38.7	71.6	83.3
	n	20	20	20	20	20	20	20	20	20
	SD	22.6	22.7	21.6	11.8	7.5	9.9	3.8	7.2	8.5
C. elaphus	Mean	409.1	385.5	358.2	236.3	140.2		65.9		89.7
	n	22	17	11	8	19		20		6
	SD	35.0	33.2	27.2	19.8	30.6		8.3		6.2
A. axis	Mean	259.0	248.5	231.9	149.8	78.9	70.7	33.7	57.7	69.5
	n	11	11	11	10	11	11	11	11	11
	SD	17.3	17.0	18.0	10.7	7.7	3.9	3.0	4.2	8.0
A. porcinus	Mean	227.6	220.1	205.2	133.0	67.2	61.7	35.1	56.0	65.3
	n	9	9	9	9	6	6	9	6	6
	SD	11.6	11.1	11.3	5.5	3.7	2.6	8.4	5.5	3.6
A. calamianensis	Mean	203.3	190.5	177.0	116.3	59.5	58.5	26.8	46.5	59.0
	n	4	4	4	4	4	4	4	4	4
	SD	16.1	15.8	15.0	8.1	4.7	4.4	3.6	5.4	4.1
A. kuhli	Mean	213.2	204.5	190.7	122.5	65.2	57.3	34.1	52.1	66.2
	n	13	13	13	13	13	12	13	12	13
	SD	12.8	13.1	11.6	8.9	4.2	4.6	4.9	3.9	4.9

Appendix. *Continued*

		CB	RL	NL	BOB	NB	MM	IO	BR
E. davidianus	Mean	64.5	257.2	140.3	158.0	55.9	55.5	98.4	92.7
	n	14	15	15	15	15	15	15	15
	SD	2.4	7.5	6.1	7.0	5.4	3.5	4.6	5.0
C. duvauceli	Mean	63.5	211.9	99.9	146.5	42.4	52.6	97.2	86.9
	n	11	18	9	20	8	20	20	20
	SD	4.2	11.1	10.1	10.3	6.6	4.4	9.6	5.1
C. unicolor	Mean	65.4	199.1	104.7	139.4	39.4	51.4	88.9	86.7
	n	27	30	30	30	30	30	30	30
	SD	7.1	26.7	14.7	14.8	7.4	7.0	13.5	7.5
C. eldi	Mean	53.2	166.5	77.5	118.2	36.7	45.8	50.5	76.7
	n	5	6	6	6	6	6	6	6
	SD	4.8	25.6	14.2	17.1	12.3	8.1	14.8	4.8
C. schomburgki	Mean	68.7	211.0	101.8	146.4	49.7	56.3	96.7	88.3
	n	6	6	6	5	6	6	6	6
	SD	2.5	8.5	7.7	3.6	3.7	2.0	4.1	1.6
C. alfredi	Mean	47.8	131.5	72.8	94.2	34.0	36.4	53.6	64.2
	n	5	4	5	5	5	5	5	5
	SD	1.5	11.9	9.9	6.2	4.7	9.0	5.6	2.4
C. mariannus	Mean	46.7	122.2	64.8	96.1	34.4	31.9	54.8	64.7
	n	19	18	18	21	21	19	21	21
	SD	5.7	14.5	8.8	12.1	7.0	5.5	9.9	5.1
C. timorensis	Mean	58.5	169.7	87.3	125.1	35.1	48.0	86.7	78.4
	n	20	20	20	20	20	20	20	20
	SD	7.8	12.1	8.8	12.0	5.3	5.8	14.1	6.1
C. elaphus	Mean	72.8	239.3		169.2	55.7	71.7	125.1	99.4
	n	9	20		24	24	20	20	9
	SD	5.8	22.7		16.8	10.8	8.6	13.0	5.3
A. axis	Mean	48.0	139.6	66.0	105.7	29.5	36.5	67.5	69.5
	n	11	11	11	11	11	11	11	11
	SD	3.7	11.0	7.2	12.0	3.5	4.1	8.4	3.9
A. porcinus	Mean	43.2	118.9	61.3	100.6	22.2	33.8	53.8	67.0
	n	6	9	6	9	9	9	9	9
	SD	3.1	6.0	4.5	6.9	2.8	4.3	6.7	3.9
A. calamianensis	Mean	38.5	103.5	53.5	86.5	17.8	27.5	47.5	59.0
	n	4	4	4	4	4	4	4	4
	SD	2.6	9.7	4.8	9.3	1.7	2.6	9.1	2.7
A. kuhli	Mean	39.7	108.8	61.7	93.7	20.3	30.2	50.3	62.8
	n	13	13	12	13	13	13	13	13
	SD	2.9	7.3	6.6	7.7	2.0	2.9	6.8	4.5