REVIEW

Colin Groves

The genus *Cervus* in eastern Eurasia

Abstract In 2004, Christian Pitra and co-workers published the first molecular phylogeny of Old World deer which advanced our understanding of the Cervinae immeasurably by demonstrating the non-monophyletic status of the red deer/wapiti group, the chital/hog deer group and the swamp deer/Eld's deer group. Therefore, many conspicuous external features—antler complexity, mane and rump-patch development—turned out to be related not to phylogeny as much as to climatic-related lifestyle factors. At a lower level, molecular genetics has reinforced some conclusions drawn on the basis of morphology or behaviour. Striking examples are the divisions between mainland and Japanese sika and between northern and southern forms of Japanese sika. In this paper, I will look at the species living in what Pitra et al. (Evolution and phylogeny of old world deer. Mol Phylogenet Evol 33:880–895, 2004) identified as the heartland of cervine evolution: eastern Eurasia. I will consider the two species groups in this region that seem to crystallize both the problems of cervine classification and the ways in which the new sources of evidence have opened up new avenues of inquiry.

Keywords Deer · Molecular phylogeny · Morphology · Sika

Introduction

The main outlines of the phylogeny of the Cervini, the "true deer" of the Old World, seemed to be clear ever since the classic work of Brooke (1878), through Lydekker (1915), Ellerman and Morrison-Scott (1951), Flerov (1952) and Groves and Grubb (1987), to Geist (1998). The groupings of species—usually regarded as genera, subgenera or a mixture of both, by different authors—would be as follows:

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Dama (common fallow deer *D. dama*, Persian fallow deer *D. mesopotamica*), *Axis* (chital or spotted deer *A. axis*, hog deer *A. porcinus*, Bawean deer *A. kuhlii*, Calamian deer *A. calamianensis*), *Cervus* (red deer *C. elaphus*—including the wapiti *C. canadensis*, sika *C. nippon*—sometimes placed in a separate subgenus *Sika*), *Rusa* (sambar *R. unicolor*, rusa *R. timorensis*, Philippine deer *R. mariannus*, Prince Alfred's deer *R. alfredi*), *Rucervus* (swamp deer *R. duvauceli*, Schomburgk's deer *R. schomburgki*—sometimes placed in a separate subgenus *Thaocervus*, Eld's deer *R. eldii*—sometimes placed in a separate subgenus *Panolia*), *Przewalskium* (white-lipped deer *P. albirostris*) and *Elaphurus* (Père David's deer *E. davidianus*). However, a complete turnabout in understanding came with the comparison of the mitochondrial cytochrome *b* (cyt *b*) sequences of an almost complete set of Cervini (Pitra et al. 2004). The major findings were that the genera/subgenera *Axis*, *Rucervus* and *Rusa* and the species *C. elaphus* are non-monophyletic and that *Elaphurus* is part of *Cervus*. In detail:

1. Of the species referred to *Axis*, one (*A. axis*) is only distantly related to other Cervini; the other (*A. porcinus*) is the sister species to *R. timorensis*.
2. Of the species referred to *Rucervus*, two (*R. duvauceli* and *R. schomburgki*) form a clade which is only remotely related to other Cervini but may be distantly linked to *A. axis*, while the third (*R. eldii*) is closely related to *Cervus* and linked to *Elaphurus*.
3. The species referred to *Rusa* do form a clade which also includes *A. porcinus*.
4. The subspecies ascribed to *C. elaphus* form two quite distinct groups: the western subspecies form a rather divergent clade, while the eastern ones (*C. canadensis*) form a clade which is closely linked to *C. nippon* and *C. albirostris*.
5. *Elaphurus* may be of ancient hybrid origin; the female parent was related to *Cervus eldii*, the male to *C. canadensis*. The question of whether other cervine lineages may also be of hybrid origin was left open.
6. Employing the time/rank equation of Goodman et al. (1998), four genera can be recognized: *Rucervus*

(containing only *R. duvauceli* and *R. schomburgki*), *Axis* (containing only *A. axis*), *Dama* and *Cervus*.

7. The ancestral cervine lived in woodland or open country, probably in eastern Eurasia.
8. Characters such as antler complexity (including development of a bez tine), large size, neck manes and white rump patches, formerly used as evidence for relatedness, are probably parallel developments in different lineages that entered open, temperate habitats.

Figure 1 shows the phylogeny of the genus *Cervus* broadly, as depicted by Pitra et al. (2004), except that all clades with <90% support are reduced to polytomies.

These new conclusions deserve fuller examination. Factors involved in speciation in the Cervini need to be elucidated. I take a species to be a population or series of populations that is diagnosable, which means that they have one or more fixed heritable differences from all other populations [Phylogenetic Species Concept (PSC)]. This concept is fully compatible with the idea that some species are ultimately of hybrid origin. In this paper, I will look at the species living in what Pitra et al. (2004) identified as the heartland of cervin evolution: eastern Eurasia, a zone that includes East Asia (China, Japan, Korea and Mongolia) and eastern Siberia. I will consider the two species groups in this region that seem to crystallize both the problems of cervine classification (with a brief glance at a third) and the ways in which the new sources of evidence have opened up new avenues of inquiry. If from time to time I criticize some of my valued colleagues for making what seem to be untested assumptions, it acknowledges that molecular phylogenetic studies are in their infancy, in a stage of explosive development, and much bridging remains to be done with traditional, but vital, sources of evidence.

Materials and methods

I have examined material of cervids in the following collections: NHM, Natural History Museum, London [formerly British Museum (Natural History)]; MNHP, Musée National d'Histoire Naturelle, Paris; RNHL, Naturalis (formerly Rijksmuseum van Naturlijk Historie),
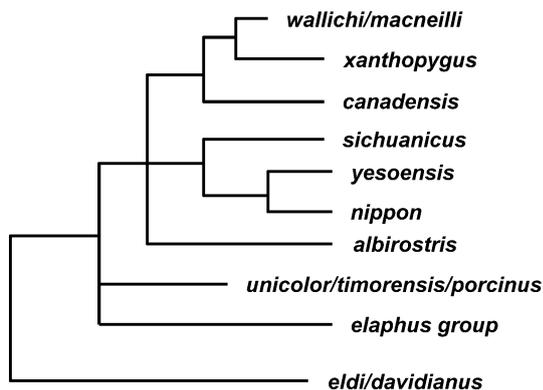

Fig. 1 Simplified tree of genus *Cervus* modified after Pitra et al. (2004)

Leiden; ZMB, Museum für Naturkunde (formerly Zoologisches Museum Berlin); ZSI, Zoological Survey of India, Calcutta; BNHM, Beijing Natural History Museum; SMST, Shanghai Museum of Science and Technology (formerly Shanghai Natural History Museum). The following measurements were taken:

1. Cranial measurements: greatest length, nasal length, condylobasal length, nasal length, maximum nasal breadth, rostrum length, palate length, maxillary breadth, bio-orbital breadth, inter-orbital breadth, brain-case breadth.
2. Antler measurements: total length, burr to brow tine distance, brow to bez tine, bez to trez tine, length of brow tine, length of bez tine, length from terminal fork to tip of beam, length of posterior tine.

In examining skins, particular attention was paid to the following aspects: development of mane, colour of limbs, colour and extent of rump patch and tail. All these features were compared with published measurements, descriptions and photographs.

Results and discussion

Sambar, Eld's deer, Père David's deer and white-lipped deer

Chinese sambar have, even at subspecific level, not been separated from Indo-Malayan *Cervus* (cf. *unicolor*) *equinus* despite karyotype differences (see Groves and Grubb 1987). Specimens in Chinese zoos differ from those from mainland South Asia and Southeast Asia, e.g. by the pale limbs contrasting with the dark body.

The rare and unusual Eld's deer (*C. eldii*) was referred to the genus *Rucervus* by Thomas (1918), thereby aligning it to the swamp deer (*Cervus* or *R. duvauceli*). Pocock (1943) revived the generic name *Panolia* for it; however, a taxonomic separation of these two species is clearly warranted as they appear in quite different parts of the cervine cluster (Pitra et al. 2004). Thomas (1918) recognized three species in the group: *R. eldii* from Manipur, *Rucervus thamin* from Burma and *Rucervus platyceros* from Thailand, Indochina and Hainan (this last species, incidentally, should actually be called *Rucervus siamensis*, not *R. platyceros*), while Pocock (1943) preferred to combine all three into a single species. Without preempting a formal study, I noted that the three taxa are extremely different; the difference between *R. siamensis* and the other two is conspicuous, and I predict distinctness. Using mtDNA, Balakrishnan et al. (2003) found that *R. siamensis* indeed forms a clade separate from the other taxa, but unexpectedly, the single specimen of *R. eldii* fell within the *R. thamin* clade. In China, Eld's deer are found only on Hainan and described as subspecies *R. hainanus*, but they are generally similar to *R. siamensis*. While the two specimens from Hainan formed part of the *R. siamensis* clade, they were separate from those from Thailand (Balakrishnan et al. 2003).

Père David's deer, commonly dubbed *E. davidianus*, may be a species of ancient hybrid origin (Meijaard and Groves 2004). Its maternal ancestry is proto-*R. eldii*, from which stems its mtDNA separated in the Middle Pliocene, according to Pitra et al. (2004); its paternal ancestry would then be the species ancestral to the rest of the genus *Cervus*. Studies of Y-chromosome DNA would test this hypothesis in the future.

The white-lipped deer (*C. albirostris*) was sister to all wapiti (including shou) and *Sika* in Polziehn and Strobeck's (2002) consensus analysis of the control region, but clustered with *Sika* in the maximum likelihood analysis. It also clustered with *Sika* in Liu et al.'s (2003) partial cyt *b* sequence analyses, but was sister to both *Sika* and wapiti groups (but with weak support) in their whole sequence analysis.

Wapiti group

Despite similarities (e.g. the presence of a bez tine, except in small-sized individuals of some Mediterranean red deer), members of the wapiti group can be distinguished from members of the red deer group (*C. elaphus*, *Cervus maral*, *Cervus yarkandensis*) by clear and consistent features:

1. The rump patch. In the wapiti group, it flares out laterally on the upper rump then contracts to be confined just to the inner margins of the upper thighs; in the red deer group, it does not flare on the upper rump and is more nearly parallel-sided to about half-way down the backs of the thighs.

2. Antlers. They are pale hued; P3 is posterior to A3, not mesial to it as in the red deer group, and the distal part of the antler is flattened.

Within the wapiti group, we can distinguish two subgroups, "true wapiti" and "shou". The differences are summarized in Table 1. No longer being seen as subspecies of *C. elaphus*, the question arises: should they be united in that species' eastern successor, *C. canadensis*, or be split among two or more species?

The two populations of undoubted wapiti in the Old World are distinguished as subspecies by Dolan (1988; but not by Flerov 1952): *C. canadensis songaricus* from the Tienshan system and *C. canadensis sibiricus* from the Altai system. According to Dolan (1988), they differ mainly in the colour and border of the rump patch. However, neither of these differences is consistent; the same holds true for those of the North American wapiti. If differences are not upheld, there is no problem to retain them in one species.

Shou are very different and more diverse. They are wapiti-like, but retain many features of build, colour, rump patch, moult pattern, gait and voice that characterized the primitive basal stock of the entire red deer/wapiti/sika/rusa group. Like several other plesiomorphic mammal groups, shou have survived in suitable areas of the southern and western margins of the Tibetan or Xizang–Qinghai Plateau. There are at least two shou taxa which should be distinguished at full species level: (a) *Cervus wallichi* and (b) *Cervus macneilli*.

(a) *C. wallichi* was rediscovered in the Lhasa zoo (Dolan and Killmar 1988, Dolan 1988). Dolan and Killmar (1988) noted a "broad anterior portion of the face [which] re-

Table 1 External differences in major taxa of *Cervus canadensis* group

	C. canadensis	*C. wallichi*	*C. macneilli* group	*C. xanthopygus*
Colour: winter	Grey-brown or buff	Yellowish brown	Stags creamy grey with reddish tones and reddish dorsal stripe; hinds redder	Creamy fawn, with dorsal stripe
Colour: summer	Darker brown	Dark grey-brown	Darker, redder	Light yellow-red; dorsal stripe more marked
Rump-patch colour	Creamy	White	White	Darker red
Rump-patch shape	Expansive	Extends well up onto the croup, often divided by a dark line	Less extensive; divided by a black line which may extend onto upper tail surface	Wapiti-like
Dark border to rump patch	Confined to lower part of margin (on thighs)	Poorly marked	Black; dorsally expanded into a broad black patch extending up onto the croup	Black-brown
Rump-patch size	Very large	Usually small	Medium	Large
Tail	Very short	Very short	Longer	Very short
Moult	Twice a year (spring and autumn)	Only once (July/August)	?	?
Antler structure	Complex	Simple	Usually simple	Complex
Beam	Curved	Angulated at middle of beam	Somewhat angulated	Somewhat curved

sembles *Rangifer*"; this presumably reflects the enlarged nasal cavity of an animal adapted to high altitudes. The type specimen of *C. wallichi* Cuvier, 1823 is a deer from the Barrackpore Menagerie (the old Calcutta zoo) said to be from Muktinath in Nepal, close to the Tibetan border. It was likely not captured there, but rather brought across from Tibet and later purchased for Barrackpore. Another *C. wallichi* specimen was later brought to the London Zoo [figured and described by Pocock (1912) and later by Dolan and Killmar (1988)]. This animal came from the upper Tsangpo (Zangbo), near Lake Mansarowar. Both (Calcutta and London) stags had very large rump patches, unmarked by any line and extending well over the croup. Hodgson (1841) described a similar deer as *C. affinis* (he later redescribed the same species under two more names); however, all his specimens had much smaller rump patches than *C. wallichi*, generally (not invariably) divided by a weak dark line which did not, however, extend onto the tail. Probably all of Hodgson's specimens came from the Chumbi valley (Fig. 2), ~650 km east of Muktinath and 850 km east of Lake Mansarowar. Thus, are *C. wallichi* and *C. affinis* truly different? New evidence, combined with a study of the NHM sample, indicates that they are not. The animals described and figured by Dolan and Killmar (1988) (from the Yarlung Zangbo, south of Lhasa, ~200 km north-east of the Chumbi, Fig. 2) had rump patches of varying size, more or less spanning the gap between the two described taxa.

The NHM has two skins from the Chumbi and two from Sikkim. They are all pale grey, with yellow hair on the feet; the rump patch has a strongly marked median dark line in one, a weakly marked line in two others, but no line in the fourth. The skin of the London Zoo stag from Mansarowar, which died in 1926, is also in the NHM collection. It is light fawn rather than grey, but has the same yellow feet. The enormous rump patch contrasts strongly in its extent with the Chumbi/Sikkim skins, although a close examination shows that there is in fact—contra Pocock (1912)—a very vaguely marked median line. The sixth NHM skin has the *C. wallichi* rump-patch type, but comes from the Tsari

district (Fig. 2), further east than any other known specimen. Thus, specimens from the outermost ends of the range are more similar to each other than with those from localities in-between.

Most likely, the findings of Dolan and Killmar (1988) are right: Hodgson's name *C. affinis* is really a junior synonym of *C. affinis*, and the size and pattern of the rump patch are unexpectedly variable.

(b) *C. macneilli* is the prior available name for the pale red-grey deer of the eastern margins of the Tibetan plateau. Dolan (1988), and as confirmed from museum specimens and examination of photos in Engelmann (1938), describes the colour as variably red-toned creamy grey with a reddish dorsal stripe, hinds are darker and redder, especially in summer, the rump patch is divided by a black line which may extend onto the tail and has a strong black border which dorsally expands as a broad black patch extending onto the croup, more conspicuously in females than in many males. This black croup zone is the most striking characteristic of the species. Lydekker (1909) originally described a speckled light-grey fawn female from "Sze-chuan" (i.e. Sichuan). It appears (Table 2) that these deer are smaller in the males, but not so much in the females; the nasal bones are less shortened, and the antlers average larger. Dolan (1988) and Dolan and Killmar (1988) recognized a subspecies *C.e. kansuensis*; in winter, the male is "bright steel grey" with black underparts, the female being lighter; in summer, both sexes are uniform rufous; the black border to the rump patch and the dark croup patch are still more conspicuous. In contrast, the original description (Pocock 1912), based on a female from Tao-chow, Gansu, at 3,300 m, stated that while it resembled *C. macneilli* in having a large black-brown patch above the tail root, reaching nearly or quite to the summit of the croup, it was predominantly brown rather than grey in colour (in March) and had less black on the upper side of the tail. It should be emphasized that taxonomy cannot be assumed; we should first look at specimens of known locality, and only then could we assign them to taxa. To my knowledge, since the original descriptions of *C. macneilli* and *C. kansuensis*, specimens

Fig. 2 Localities for *Cervus wallichi* and the *Cervus macneilli* group (for explanation, see text)
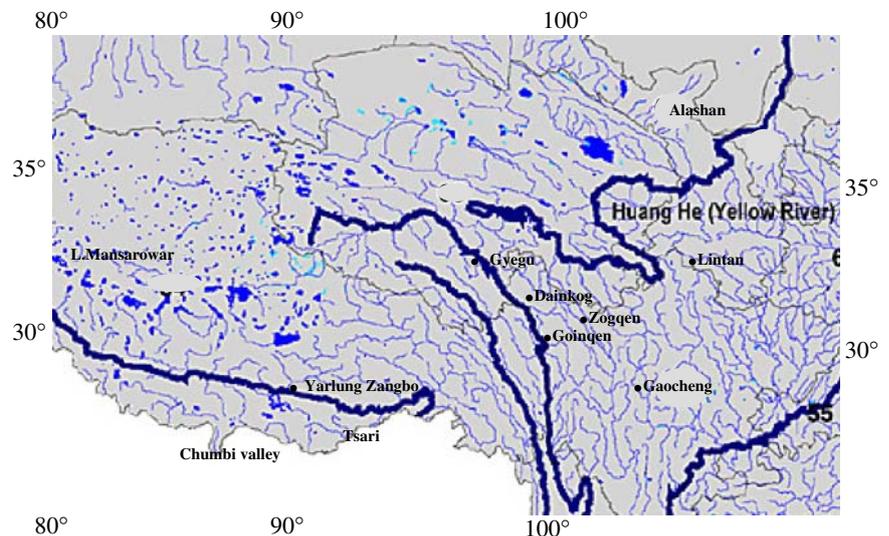
Table 2 Skull measurements of the Chinese members of the *C. canadensis* group from NHM (London), MNHP (Paris) and ZSI (Calcutta) specimens and Allen ([1940])

	Greatest skull length		Nasal length		Antler length
	Male	Female	Male	Female	
C. wallichi	445–481 (9)	361–411 (2)	153–183 (7)	140 (1)	800–1040 (8)
C. macneilli	ca. 400[a](1)	ca. 377[a] (1)	145 (1)	147 (1)	Average 910, maximum 1150
C. kansuensis type		385 (1)		140 (1)	
C. kansuensis Shanxi	405–418 (2)	375–387 (2)			
C. xanthopygus	–	380–415 (3)	–	135–155 (2)	

[a]Calculated from condylobasal length as given by Allen ([1940])

of known origin have been described in detail only by Engelmann ([1938]) and Allen ([1940]).

Engelmann ([1938]) stated that the distribution of *Cervus macneili* [sic] reaches from the type locality, Tatsienlu (now Lucheng, 30°03′N, 102°25′E) in the west, across the parallel north–south gorges of the Yalung, Yangtse and Mekong, to Yunnan in the south, usually above 3,600 m, in heavy rhododendron forest; Schäfer collected the specimens from which he based his description near the following localities (Fig. 2): Litang (now Gaocheng, 30°00′N, 100°16′E), Derge (now Goinqen, 31°49′N, 98°40′E), Denko (now Dainkog, 32°27′N, 97°54′E), Dzogchengompa (now Zogqen, 32°08′N, 98°51′E) and west and south-west of Jekundo (now Gyegu, 33°01′N, 96°43′E). He described the species as 120–140 cm in height, with a speckled grey winter colour, varying from brownish or reddish to silvery white; belly and sides of the head are more or less pure white, and the very small rump patch is pure white, bisected by a dark line, with a dark border and a thick blackish brown upper edging. At the moult, the females become brownish, with a dorsal stripe. Allen ([1940]) concurred with this description. Under the name *C. kansuensis*, Allen ([1940]) described females from northern Shansi (Shanxi) as being drab grey, with some buffy tones dorsally on the rump patch, and the dark stripe fading dorsally but extending across above the rump patch as a dark patch, which varies in extent and darkness; they are also less brown than in specimens of the same form from Gansu, with the rump patch less white (and greyer than *Cervus xanthopygus*, with the rump patch paler).

As noted by Dolan and Killmar ([1988]), the two forms of deer exhibited in several Chinese zoos as *C. macneilli* and *C. kansuensis* are quite distinct, the winter pelage being especially different: *C. macneilli* stags are very light, creamy grey, while *C. kansuensis* stags are deep steel grey. The black on the croup occurs in both, but is much more conspicuous in *C. kansuensis*. The *C. kansuensis* type is the skin of a female in the Natural History Museum, London, from Tao-chow (now Lintan or Xincheng, 34°42′N, 103°21′E: Fig. 2). Despite wide black bands on the hair, it is predominantly lighter in colour than most of the living females in Chinese zoos displayed as *C. kansuensis*. The locality is not very far from north-east of those where Schäfer collected undoubted *C. macneilli* (see above).

The name *C. canadensis alashanicus* Bobrinskii and Flerov, 1935 was given to a form of deer from the Alashan (Hola Shan) Ridge in Ningxia (Fig. 2). It was described by Flerov ([1952]) as being grey-brown with a large wapiti-sized rump patch, divided by a broad but indistinct line, and with almost no dark edging. For Dolan ([1988]), the name *C. canadensis alashanicus* is a synonym of *C.e. kansuensis*. The locality is geographically in-between the type locality of *C. kansuensis* and the specimens assigned to the latter by Allen ([1940]).

Using cyt *b* (partial sequences, many individuals), Liu et al. ([2003]) found that what they called *C. kansuensis* and *C. macneilli* were joined in a weakly supported clade, with *C. wallichi* as their sister group, whereas using complete cyt *b* sequences (fewer individuals) led to a link between *C. macneilli* and *C. wallichi*, with *C. kansuensis* as their sister group.

In short, while there is no doubt on the validity of a large-antlered deer (smaller than *C. wallichi*, with black-bordered rump patch and lives on the eastern plateau margins), I think the evidence for the difference of the two species needs to be re-examined. What we need to know is where the deer displayed as *C. macneilli* and *C. kansuensis* in Chinese zoos come from. A number of possibilities are presented: Are they perhaps not from different geographic areas at all, but morphs, which have been kept separate for presentation purposes? If they are geographically different, do the so-called *C. kansuensis* come from around the type locality of that taxon (they do not seem to resemble the type specimen)? If they do not come from the type locality of *C. kansuensis*, do they actually represent *C. canadensis alashanicus*? For the moment, I recommend the recognition of *C. macneilli* as a species, but that of *C. kansuensis* and *C. canadensis alashanicus* be put off for further studies.

There is one taxon that does not fall readily into either the "true" wapiti or shou group: *C. (cf. canadensis) xanthopygus*, a light reddish-toned deer with a characteristically fox-red rump patch with a clear black-brown border. It does not bugle like a wapiti. Its range extends from the former Manchuria to somewhere in northern Mongolia. In their cyt *b* study, Liu et al. ([2003]) found that *C. xanthopygus* was linked not to true wapiti, but to the shou clade, with the Asian wapiti (*C. canadensis sibiricus* and *C. canadensis songaricus*) forming a sister clade to them. Polziehn and

Strobeck (2002) linked "Manchurian" to North American wapiti; this clusters to *C. canadensis sibiricus*, then to *C. canadensis alashanicus* and, finally, to *C. kansuensis* and *C. macneilli*. Ludt et al. (2004) linked *C. xanthopygus* to *C. canadensis alashanicus*, the two forming a sister group to shou + wapiti. Are these differences real, or do they result from sequencing inadequately sourced specimens under the names that were supplied? It must be stressed that localities are paramount; the identification of subspecies and other closely related taxa must never be accepted as given, and such taxa must be discovered, not assumed. Localities are facts; taxa are hypotheses.

Sika group

Banwell (1999), unaware of the DNA phylogenetic evidence, noted a similarity of the rutting call of sika (*C. nippon*) to that of wapiti. The sika group affinities towards wapiti make sense, as shown by Pitra et al. (2004). There is a deep and consistent division between sika from Japan and those from the mainland and Taiwan. They differ in colour pattern, voice and colour of the antler velvet (Banwell 1999). Randi et al. (2001), using the control region, also found a deep and consistent split between Japanese and mainland/Taiwan sika (with the exception of two specimens, one of unknown origin, identified as *C. nippon nippon*, the other identified as *C. nippon dybowskii*; they

plausibly consider these two to be incorrectly identified). In contrast, Cook et al. (1999) had previously found in their cyt *b* study that what they called *Cervus hortulorum* (=mainland sika) aligned with northern Japanese sika, in contrast to *Cervus pseudaxis* and *Cervus taiouanus*. This again emphasizes the need for papers reporting molecular analyses to describe (in detail, if necessary) the reason for the identification of the animal that yielded a given sample and any available information on the locality of origin of the individual.

Japanese sika

They have black antler velvet, tend to be dark and always have a pale facial chevron. They differ in their vocalizations with those from mainland sika (Banwell 1999); during the rut, males utter at night a bray call like a donkey's hee-haw. Japanese sika are very diverse; many of the small islands of Japan have their own taxon, but Groves and Smeenk (1978) found the most basic split between northern and southern forms. The split is not between islands, but on Honshu, at about Biwa Ko (Fig. 3). This is the molecular finding, too. Goodman et al. (2001), examining micro-satellites from a number of populations, found a northern and a southern clade, except that a sample from Hyogo (just south-west of Biwa Ko) was "northern", as was one from Nagasaki (introduced?). All animals from

Fig. 3 Approximate distribution of the species and subspecies of sika from the Japanese islands
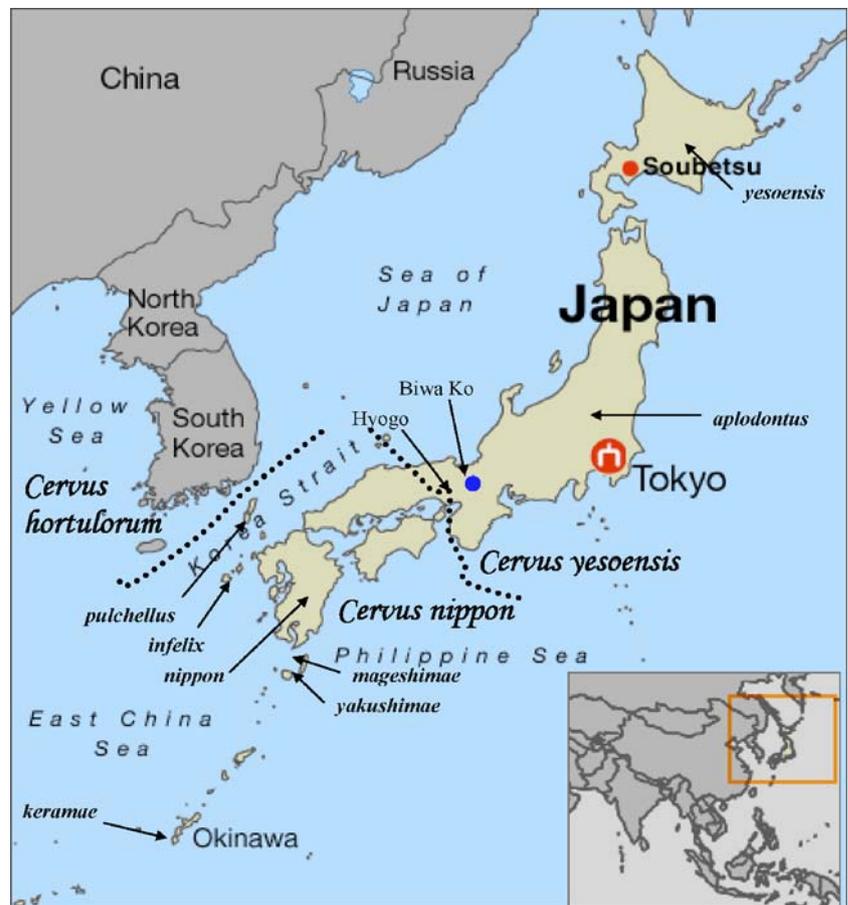
England and Scotland proved to be of northern origin. Pitra et al. (2004) likewise corroborated a northern vs a southern split, the small insular populations being southern. In studies by Nagata et al. (1999, using the D-loop) and Cook et al. (1999, using cyt *b*), sika from China, northern Japan and southern Japan actually form three equal branches. Northern forms of Japanese sika are much larger than southern forms; their sizes barely overlap (condylobasal length is >260 mm in northern, <267 mm in southern). Northern forms have spots that are more prominent in summer; southern forms have a clearly marked dorsal stripe, especially in summer. Given the evidence, I propose to separate them as two distinct species (Table 3).

(a) *Cervus yesoensis* Heude, 1884—the northern species. Several names applicable to this species appeared in Heude's (1884) paper; Imaizumi (1960), by using *C. yesoensis* as the name for a distinct taxon, in effect selected it to have priority over the other names. These other early names include *C. aplodontus* (Heude, 1884); this was used as the name for a valid taxon by Groves and Smeenk (1978) in place of the more generally used but much later name *C. centralis* Kishida, 1936. There would be two subspecies: *C. yesoensis yesoensis* (Heude 1884) in Hokkaido and *C. yesoensis aplodontus* (Heude, 1884) in northern and central Honshu (Fig. 3). They are well described and illustrated in Banwell (1999).

(b) *C. nippon* Temminck, 1838. Groves and Smeenk (1978) synonymized all sika from the southern Japanese islands, but Banwell (1999) showed (at least) four good subspecies: *C. nippon nippon* Temminck, 1838, from southern Honshu, Shikoku and Kyushu; *C. nippon mageshimae* Kuroda and Okada, 1951, from Mageshima and Tanegashima; *C. nippon yakushimae* Kuroda and Okada, 1951, from Yakushima; and *C. nippon keramae* Kuroda, 1924, from Kerama Is. in the

Riukius. On the evidence of Imaizumi (1970), the Tsushima *C. nippon pulchellus* is also recognizable. The Goto Is. Sika is notable, especially for its very small antlers as shown by the large series in the BNHM and SMST (listed by Braun et al. 2001); the prior available name is *C. nippon infelix* (Heude 1884). The distributions of these putative subspecies are shown in Fig. 3.

Mainland and Taiwan sika

They have red velvet. The rutting call, a single descending tone (Banwell 1999), is made in daylight only, except in the Vietnam sika. They are also very diverse, but some of this diversity has probably been lost because of the mixing of different stocks, historically in the Summer Palace gardens (whence some of the type specimens came) and, more recently, in north Chinese deer farms. The Taiwan sika is diagnosably distinct from mainland forms and should be ranked as species *C. taiouanus* Blyth, 1860. The earliest name for the mainland species is *C. hortulorum* Swinhoe, 1864.

(a) *C. hortulorum* Swinhoe, 1864. The antlers are eight-pointed. Among the northern mainland sika, both Dobroruka (1959, 1960) and Banwell (1999) recognized four subspecies: *C. hortulorum hortulorum* (Dybowski's deer), from the Russian Far East, northeastern Heilongjiang and the northern part of North Korea; *C. hortulorum mantchuricus*, from most of Korea (including Cheju Do), south-western Heilongjiang, Jilin and northern Liaoning; *C. hortulorum grassianus*, perhaps extinct, formerly occurring in Shanxi; and *C. hortulorum mandarinus*, also probably extinct, formerly living in Hebei and Shandong. Banwell (1999) recognized three southern subspecies: *C. hortulorum sichuanicus*, from restricted areas in

Table 3 Measurements of the sika group (males) from Heude (1884), Allen (1940), Heptner et al. (1961), Imaizumi (1960, 1970), Groves and Smeenk (1978), Guo et al. (1978), Matsumoto et al. (1984), Dao (1985) and Banwell (1999)

	Condylobasal length (mm)	Nasal length (mm)	Antler length (mm)	Height, male (cm)	Weight, male (kg)
C. nippon yesoensis	285–305	105–118	718–818	100–150	80–120
C. nippon aplodontus	260–293	83–105	348–718	90–95	49–80
C. nippon nippon	233–243	75–87	349–660	80–85	39–55
C. nippon pulchellus	251–267	83–87	456		
C. nippon infelix	220–254	68–80	270–350	66–67	
C. nippon mageshimae	239–260	77–82	377–460	80	59–77
C. nippon yakushimae	209–224	76	260–330	70–75	45–69
C. nippon keramae			260–300	65–70	30
C. taiouanus	280–291	88–106	450–860	100–110	42–110
C.h. hortulorum	270–320	110	650–930	100–112	104–131
C. hortulorum mantchuricus			650–760	95–100	120
C. hortulorum mandarinus	289	104	650–760	95–100	110
C. hortulorum grassianus	322	125	500–710	90–107	85–100
C. hortulorum sichuanicus	246–293	86–114	500–880	89–110	110–150
C. hortulorum kopschi	250–258	96	500–710	85–110	85
C. hortulorum pseudaxis	245		500–760	90	90

Sichuan and Gansu, is close to the northern forms (and perhaps one of the sources of the Summer palace deer?); *C. hortulorum kopschi*, from southern Anhui, Jiangsu, Jiangxi and perhaps elsewhere; and *C. hortulorum pseudaxis*, from northernmost Vietnam. In terms of geographic variation in mainland sika, Groves and Grubb (1987) noted that the type descriptions of both *C. hortulorum hortulorum* and *C. hortulorum mandarinus* recall southern subspecies more than northern ones. Until the applicability of these names (particularly *C. hortulorum hortulorum*, the earliest available name for the species as a whole) is sorted out, no convincing revision is possible. There are large series of mainland sika in the BNHM and SMST, as catalogued in Braun et al. (2001).

(b) *C. taiouanus* Blyth, 1860. It is clearly spotted in winter on both sexes, unlike most of the mainland sika; strongly maned in the male; and with antlers rather weak, but ten-pointed (Dobroruka 1959). Banwell (1999) stressed the bright chestnut tones of the summer pelage and the prominent dorsal stripe; he also noted a long-bodied habitus compared with other sika.

Conclusions

Molecular phylogenetic studies, culminating with that of Pitra et al. (2004), have shown a new world of possibilities. Combining them with the PSC has advanced our understanding of the Cervinae immeasurably during the last decade. Mainly interrelationships among different species groups were completely reorganized; the non-monophyletic origins of the red deer/wapiti group, the chital/hog deer group and the swamp deer/Eld's deer group are prime examples. Many conspicuous external features—antler complexity, mane and rump-patch development—have turned out to be related not to phylogeny as much as to climatic-related lifestyle factors. At a lower level, the impact of molecular phylogenetics has been different. Instead of a total reorganization, molecular genetics has both emphasized that there are deeper divisions than were often suspected and reinforced some conclusions that had been drawn based on morphology or behaviour. Striking examples of this are the divisions between mainland and Japanese sika and between northern and southern forms of Japanese sika. There is a need for greater cooperation between taxonomists and molecular phylogeneticists. Non-taxonomists commonly take a classification (a taxonomic schema) as a "given"; actually, it is a working hypothesis. Like other hypotheses in science, it is subject to continual testing and, if the need arises, it will be subjected to modification. This includes the lowest levels—both subspecies and allopatric species. A subspecies is a concept tied to a geographic locale (and, in essence, this also holds true for many allopatric species); in this sense, the location of a specimen, including the DNA sample it yields, is much more important than the subspecies classification. As a matter of principle, the locality of origin of all samples— those used as controls as well as those central to the paper —should always be stated clearly in a low-level molecular phylogenetics publication (i.e. one in which relationships between population groups, a.k.a. subspecies, are being investigated). If the locality is not known—if it is a zoo animal, for example—then any relevant information should be given; a photograph would be especially useful.

We are at an exciting juncture in our understanding of phylogenetics; a two-way process has begun when molecular workers and those using "traditional" methods, such as morphology or behaviour, are beginning genuinely to interact and make a difference.

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