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Commentary

## The (sleeping) Beauty in the Beast – a review on the water deer, *Hydropotes inermis*

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### Abstract

The water deer, *Hydropotes inermis* (Cervidae, Mammalia), is a small, solitary cervid. It is native to China and Korea, but some feral populations also live in Europe. In contrast to other deer species, where males are characterized by antlers and small/no upper canines, *H. inermis* lacks antlers, but grows long upper canines. For this phenotype and particularities of its biology, the species holds considerable potential not only for our understanding of cervid biology, but also for important questions about basic developmental and regenerative biology. However, *H. inermis* populations are decreasing, and many of the pressing scientific questions motivated by this peculiar species are still open. Here, we review the most different aspects of the species' biology and discuss scientific publications ranging from the year of the species' first description in 1870 until 2015. We briefly sketch its state of conservation, and we discuss the current understanding of its phylogeny. Lastly, the present overview identifies areas that deserve future research available.

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## Introduction

*Hydropotes inermis*, the water deer, is native to China and the Korean peninsula. It was first described in the scientific literature by Swinhoe (Swinhoe, 1865), who assigned it as a new genus and species to Cervidae (Swinhoe, 1870). Traditionally *H. inermis* is considered to comprise two subspecies, which are distinguished by their geographic distribution and body colour: the Chinese *H. inermis inermis* (Swinhoe, 1870) and the Korean *H. inermis argyropus* (Heude, 1884) (e.g., Allen, 1940; Lee et al., 2011). We address the issue of whether it is indeed justified to distinguish subspecies towards the end of this paper.

*H. inermis* differs from all other deer because males lack antlers; instead they have long, sabre-like canines in the upper jaw (Fig. 1A, B). This peculiar phenotype, which resembles that of non-cervid ruminants, created problems with the systematic classification of *H. inermis* early on. It was repeatedly included with Moschidae, rather than Cervidae (e.g. Gray, 1872; Bubenik, 1983 fig. 17, 1990). Alternatively, it has been classified as a "primitive" cervid sister to antlered deer (Pocock, 1923). More recent molecular analyses generally posit *H. inermis* within Cervidae (e.g., Randi et al., 1998; Hassanin et al., 2012). However, the exact phylogenetic relationships with other deer remain unclear and it cannot be overlooked that there persist considerable discrepancies between phylogenetic hypotheses.

These issues go well beyond the question of the systematic classification of *H. inermis*. Rather, *H. inermis* interests primarily because a

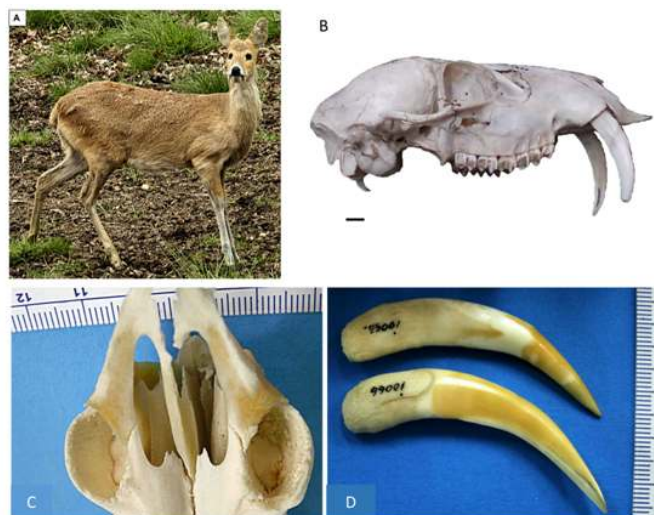
better understanding of the biology of this peculiar small animal holds the potential to yield novel insights into the phylogeny of deer and antler development. Thus, resolution of the systematic position of *H. inermis* is substantial for answering the question whether its lack of antlers is a derived trait or not. In turn, this should eventually allow drawing on *H. inermis* to probe the (phylo-) genetic basis of the origin and development of antlers. A better location of *H. inermis*' phylogenetic position would also be of interest for our understanding of karyotype evolution (Neitzel, 1987; Makunin et al., 2016) and its significance for the diversification of cervids.

From a conservational point of view, a better understanding of water deer biology seems also most desirable. Except for a population of *H. inermis* in France, accurate estimates of the population sizes are not available. However, the Chinese water deer is categorized as "vulnerable" since 2008, according to the IUCN Red List. It is hard to judge whether the situation in Korea is any better, as Korean water deer are classified as being "data deficient" on the IUCN Red List (Lee et al., 2011). Habitat fragmentation and extensive illegal hunt (e.g., Sheng and Lu, 1985b; Ohtaishi and Gao, 1990; Cooke and Farrel, 1998) pose a serious threat to the populations (Harris and Duckworth, 2015), which is supposed to be in steady decline, although dependable data are missing. Ongoing efforts to conserve this species are critically dependent on an in-depth understanding of its biology.

As a contribution towards its status, we set out to summarize and critically review the scientific literature on this extraordinary animal (Fig. 2). While some reviews on this species are available (Allen, 1940; Cooke and Farrel, 1998; Qiong, 2013), these mostly cover selected as-

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**Figure 1** – Morphological characteristics of *Hydropotes inermis*. A: External appearance of a male. Antlers are absent, long upper canines present. The hindlimbs are longer than the forelimbs; the tail is short. Except for the long canines, females have a very similar appearance. Photograph: Nicola S. Heckeberg. B: Skull of male *H. inermis*, with impressive upper canines. Antlers, as well as pedicles, are lacking. Specimen-ID 1977/4438, Zoologische Staatssammlung München. Scale bar: 1 cm. C: Canine alveola of a male *H. inermis*. Ventral view of the snout, rostral pointing to the top. Note the trabecular cushion and the smooth inner alveolar walls. D: Male canine tooth with closed roots. C, D: Specimen il066 from Naturhistorisches Museum Basel. Photographs: Gertrud E. Rössner.

pects of *H. inermis* biology, or regional subgroups of this species. Here, we attempt to integrate this previous work with an extensive search of literature and data of more recent vintage. This review is meant to be a compact but also broad guide for anyone interested in cervid biology.

The rest of this paper is organized as follows: in section 2, we describe aspects of the species' biogeography; section 3 is dedicated to the external and internal morphology. In section 4, we cover aspects of the biology and ecology of *H. inermis*, and we relate them to the fossil record. Section 5 summarizes genetic studies and discusses how genetic data complement or contrast with phylogeography, phylogeny and systematics of the species. Finally, we highlight open questions and issues that need further research.

## Biogeography

As mentioned above, *H. inermis* is native to the Korean peninsula and China, where historically it was found in all territories bordering the Yellow Sea and in wetlands all down China's eastern coast to the South China Sea (Fig. 3A). This is supported both by early descriptions of this species (see Swinhoe, 1865, 1870; Brooke, 1872; Swinhoe, 1873; for an overview, see Ohtaishi and Gao, 1990) and also by the fossil record, although the latter is rather scarce. Well-characterized fossils attributed to *H. inermis* have been found at Anyang (Henan), Choukoutien (Beijing) (Young, 1932; Teihard de Chardin and Young, 1936) and Tangshan (Hebei) (Pei, 1930; Young, 1932). The historical geographic distribution of *H. inermis* that may be reconstructed from these fossils is complemented by finds originating from archaeological excavations, or associated with anthropological remains (Aigner, 1981; Liu et al.,

2010; Wu et al., 2011). Yet, as these are mentioned typically in faunal lists and not described in detail, their identification and association with *H. inermis* is less dependable. Similarly, fauna lists associated with archaeological remains from Misong-ni cave (Pyongyang) and the Haisang cave (Kangwon) in North Korea contain *H. inermis swinhoe* (Henthorn, 1966; Ayres and Rhee, 1984).

Today, the distribution of *H. inermis* in its native lands is much more restricted. In China, remaining animals are found primarily in the eastern half of Guangxi Zhuang autonomous region, and along the eastern Yangtze basin, in the Anhui, Hubei, Jiangsu, Jiangxi, and Zhejiang provinces, and also on the islands at the coast close to the mouth of the Yangtze river Province (Ohtaishi and Gao, 1990). The last available census from 1985 accounted for about 3300 individuals in Zhoushan Islands, the coasts, Poyang Lake and Anhui Province (Ohtaishi and Gao, 1990; Min, 2012). In North Korea, Won and Smith (1999) reported *H. inermis* to be present in the Taebak and Nagrim Mountains, Kangwon Province, and the adjacent South Hamgyong Province. In South Korea, *H. inermis* occurs in all provinces except Seoul and Jeju (Kim and Cho, 2005; Kim et al., 2013b). Kim and Cho (2005) recorded *H. inermis* in the demilitarized zone in Korea, specifically in the forest wetlands and river habitats of the provinces Paju, Yeoncheon, Cheorwon, and in the Donghae coast. For its abundance and damage to crops, the species has been considered a wildlife pest by the Korean Ministry of Environment (Kim et al., 2013a; Kim and Park, 2015). Actual numbers on its prevalence, however, are not available (Kim and Park, 2015).

In the 19<sup>th</sup> century, *H. inermis* was introduced to England. A captive *H. inermis* population was recorded in the London Zoo in 1873. The Duke of Bedford then introduced the species to Woburn Park in 1900, and finally to Whipsnade Zoo in 1929/1930 (Lister, 1984; Hofmann et al., 1988; Corbet and Harris, 1991). Escapes and deliberate releases of the deer resulted in feral populations, which may be found in the Norfolk Broads, Cambridgeshire, Whipsnade, Hertfordshire, Berkshire, and Suffolk (Arnold, 1993; Harris et al., 1995; Wilson, 2003; Ward, 2005) (Fig. 3B). Over time, these feral *H. inermis* seem to have adapted well to the local conditions. In 2004, their population counted approximately 2000 individuals (Battersby, 2005; Macdonald and Burnham, 2011). More recent data are not available because the species is thought to have a low environmental and socio-economic impact (Nentwig et al., 2010; Kumschick et al., 2015); thus, monitoring is limited (Newson et al., 2012).

Lastly, in France, a population of 80–100 animals lives under semi-free conditions in the 12 ha-sized Zoological Park of Branféré (Bretagne). The founders of this population have been introduced in the 1970's from Whipsnade Park, England (Kay, 1987; Axmacher and Hofmann, 1988; Cooke and Farrel, 1998; Dubost et al., 2008). Yet another semi-free ranging population exists in the Haute Touche Zoological Park of Obterre (Centre-Val de Loire) (Bastien Mennecartart, Basel, written notification). A third population ranges around Saint Jean de Ligour (Nouvelle-Aquitaine) and Le Vigen (Occitanie). This population originated from escapes from a local park. Its size is not known, but it is considered as not expanding (Sand and Klein, 1995; Maurin and Gavazzi, 1997).

Given the precarious and endangered status of *H. inermis* in its native habitat, several attempts of conservation are in place. In China, legal hunt is regulated since 1988 (Liang et al., 2011). Further, *H.*

**Table 1** – Aggressive behaviour in *Hydropotes inermis*. Behaviours are ranked from low (first row) to highly aggressive, according to Stadler (1991).

Behaviour	Action
Aggressive approach	Stiff walk towards the opponent, head and neck hold in 90° angle, ritualized.
Parallel walk	Stiff walk side-by-side, ca. 10–20 meters apart, head and neck hold in 90° angle. Stadler (1991) interpreted this behaviour as an ancient, broadside display, because it is found also in other Cervidae, Ruminantia (including Tragulidae), Artiodactyla, Canidae and Rodentia. It is absent in the musk deer. The behaviour might be either interrupted by defecation, territory marking or feeding or extended into a parallel run.
Chase with front-leg-strike	Males chase one another. The dominant male tries to hit the intruder with both front-legs at a time.
Dance	Males are in front of each other, head-to-head or neck-to-neck contact. They try to press to the ground the opponent's neck (Scherpe, 1971). Males jump back and forth, presence of front-leg-strike.

**Table 2** – Reproductive traits of *Hydropotes inermis* compared with those of other cervids and ruminants without cranial appendages. Source: Scherpe (1971); Dubost et al. (2011) and references therein.

Species	GL (days)	LS	AW (weeks)	AM <sub>1</sub> (months)	AM <sub>2</sub> (months)	AM <sub>3</sub> (months)	SM (months) m–f
<b>Non-cervid ruminants</b>							
<i>Tragulus javanicus</i>	140	1	11.5	?	?	?	?–4.5
<i>Tragulus napu</i>	150	1	10	?	?	?	?–5.5
<i>Hyemoschus aquaticus</i>	225	1	12	4	10	20	?–6
<i>Moschus moschiferus</i>	188	1.5	14	?	?	?	?–18
<b>Cervids</b>							
<i>Hydropotes inermis</i>	<b>168.5</b>	<b>2.5</b>	<b>3</b>	<b>2</b>	<b>5</b>	<b>10–12</b>	<b>?–6</b>
<i>Muntiacus reevesi</i>	214.5	1	8	4.75	9.75	23	9–11
<i>Capreolus capreolus</i>	157.5	1.9	12	5	8	16.5	21–13

GL Gestation length  
LS Litter size  
AW Age at weaning  
AM<sub>1</sub> Age at eruption of first lower molar  
AM<sub>2</sub> Age at eruption of second lower molar  
AM<sub>3</sub> Age at eruption of third lower molar  
SM Sexual maturity in males (m) and females (f)

*inermis* is now included in the Category II of the Chinese State Key Protected Wildlife list (Fang and Wan, 2002). This category embraces wildlife under special local protection. Also, attempts to reintroduce populations near Shanghai have been successful (Min, 2013; Yabin, 2013; Chen et al., 2015). A breeding centre exists on the Zhoushan Island, and similar centres have been proposed for the mainland (Hu et al., 2006). In 1994, North and South Korea ratified the Convention on Biological Diversity, which, among others, led to regulation of the hunt of *H. inermis* (Won and Smith, 1999).

## *H. inermis* from head to toe — Aspects of external appearance and morphology

### External appearance

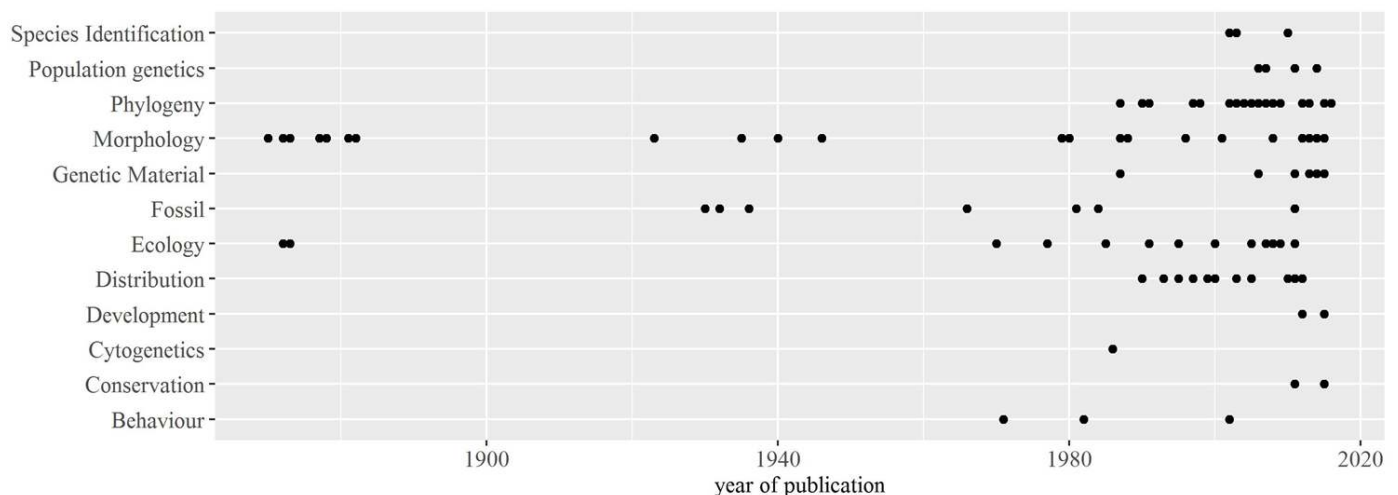
*H. inermis* of both sexes reach approximately 50 cm height at withers (Scherpe, 1971; Cooke and Farrel, 1998) and weigh up to 15 kg (Kay, 1987; Axmacher and Hofmann, 1988; Cooke and Farrel, 1998; Dubost et al., 2008; Hofmann et al., 1988; Zhang, 2000). Both males and females show chestnut-coloured hair tips of the topcoat. The under-fur is black in summer and greyish in winter (Bützler, 1988). The belly and throat are white (Swinhoe, 1870; Garrod, 1877a) or at least paler than

the rest of the body (Cooke and Farrel, 1998). Unlike other deer, *H. inermis* has no white patch on the ventral side of the short tail (Cooke and Farrel, 1998). White coloured patches placed along lines that run from neck to tail (Garrod, 1877a) are characteristic of fawns. These patches are lost around the age of two months and replaced by the adult coat (Cooke and Farrel, 1998). Males are typically dark-coloured around the nose, whereas females are light-coloured around the nose. Males also have thicker necks than females (Cooke and Farrel, 1998).

### The skull

The skull of *H. inermis* has been described and compared to other deer and *Moschus* early on, in studies made at the end of the 19<sup>th</sup> century (Swinhoe, 1870; Brooke, 1872; Swinhoe, 1873; Rüttimeyer, 1881). Generally, females have slightly larger heads than males (Kim et al., 2013c).

Distinctive characters of the *H. inermis* skull noted include small orbits (Rüttimeyer, 1881), small lacrimal fossae confined to the lacrimal bones (Swinhoe, 1870) with two lacrimal ducts, and an ethmoidal gap (Rüttimeyer, 1881). *H. inermis* has no supraorbital ridges. The supra-orbital foramen is in a groove (Swinhoe, 1870). The basioccipital bone is narrow and slightly grooved (Brooke, 1872).



**Figure 2** – Years of publication for scientific papers on *Hydropotes inermis*, published in English, German and French from 1870 to 2015. Each dot in the plot corresponds to one publication. The plot highlights research areas where most research has been performed, i.e. morphology, phylogeny and ecology, as well as areas that are weakly covered. The category “fossil” also includes studies, where *H.inermis* is mentioned in faunal lists. On the China Knowledge Resource Integrated Database more publications (n~80), published in Chinese with an English abstract, are available. The titles and the abstracts of these papers indicate that these are mainly on behaviour, ecology and current species distribution, including fossil findings. We apologize to our Chinese and Korean colleagues that for obvious shortcomings of our language capabilities, we could not appropriately cover their work. Plot made with R (R Core Development Team, 2013) and ggplot2 package (Wickham, 2009).

**Table 3** – Gene sequences available on GenBank for *Hydropotes inermis*. Only few nuclear genes have been sequenced. Mitochondrial sequences sequenced independently and used for phylogenetic analyses are also given in Tab. 4. cds, coding sequence.

Gene name	Sequence	Accession number GenBank	Reference
Mitochondrial genome	Complete	EU315254.1 JN632649.1 KP203884.1 JX254914.2 JF802125.1 NC_018032.1 NC_011821.1	Liu and Huang, direct submission; Hassanine et al. (2012); Yu and Kwak, direct submission; Kim and Park (2015); Kim et al., direct submission
Satellite III	Complete	DQ085265.1	Lin and Li (2006)
Zinc finger protein 238 (ZNF238) gene	Partial cds	GU045457.1	Kim et al. (2010)
ZFX gene	Partial cds, exons 7 and 8	DQ179233.1 FJ866606.1	Han et al. (2005); direct submission Kim et al. (2009); direct submission
SRY gene	Complete cds	EF100132.1	Han et al. (2006), direct submission
Aromatase cytochrome P450 (Cyp19)	Partial, 3' untranslated region	AY122006	Hassanine and Douzery (2003)
Lactoferrin	Promotor region	AY122039	
alpha-lactalbumin	Intron 2	AY122020	
12 microsatellites		GU480080-GU480091	Lee et al. (2011)
Multiple microsatellites		HQ876092-HQ876170	Yu et al. (2011b)

The premaxillae are short and broad (Brooke, 1872) and the median palatal processes of the premaxilla have been described as spindle-shaped (Garrod, 1877b), though they rather impress as slender and equally wide. A rather distinctive feature of *H. inermis* are its large and inflated auditory bullae (Rüttimeyer, 1881; Groves and Grubb, 1987).

The dental formula of *H. inermis* is I 0/3, C 1/1, P 3/3, M 3/3 and thus follows the general pattern present in Cervidae (Putman, 1988) and indeed ruminants, with the notable exception of an upper canine. In the mandible, *H. inermis* has three incisors and one incisiform canine, as typical for ruminants (McKenzie, 1990). The median incisor is larger than the two lateral, equally wide incisors (Swinhoe, 1870; Pocock, 1935; Groves and Grubb, 1987). Boué (1970) noted that the former had the form of a spatula, whereas the latter were lanceolate. Kim et al. (2013b) found that the premolar row in *H. inermis* was shorter than the molar row, both in the mandible and the maxilla.

Clearly, one of the most distinctive characteristics of *H. inermis* is the presence of upper canines (Fig. 1D). In males, these may reach a length of up to six centimetres. In females, they rarely exceed one centimetre length (Aitchison, 1946; Cooke and Farrel, 1998; personal observations). Rüttimeyer (1881) described in detail the shape of the male canine. A convex outer surface and a concave inner one converged posteriorly to a sharp cutting edge and formed a pointed tip, pointing downwards and backwards. In the maxillary alveola, the canine is inserted vertically; of note, the alveola is much larger than the canine root, in both length and breadth, offering space for an extensive, soft-tissue holding apparatus. The alveolar walls are smooth on the inner side, and a cushion of trabecular bone builds up the alveolar roof (Fig. 1C). The canine can move back and forth and from side to side quite extensively (Swinhoe, 1873; Aitchison, 1946). Aitchison (1946) suggested that *H. inermis* could move its canines actively, allowing a successful canine blow and preventing tooth breakage or displacement. Specifically, he proposed that levator muscles in the upper lip, the so-called snarling muscles, controlled the erection of the canines. He noted that when the animals snarled and the muscle contracted, the tusk moved forward; when the muscle relaxed, the tusk returned into its original position. However, it is still unclear whether the canine can really be actively moved and if so, to which extent. Swinhoe (1873) noted that only fully-grown canines were mobile. This correlates with the fact that juvenile *H. inermis* have an open pulp cavity in the upper canines, whereas it is closed in fully developed canines (Brooke, 1872) (Fig. 1D). Yet whether there is causal relationship is not known. With ongoing development, the root of the upper canines also protrudes gradually to the ventral border of the maxilla (Brooke, 1872). An im-

portant physiological consequence of the root closure is that canines are not continuously growing.

In passing, it should be mentioned here that Sasaki et al. (2013) observed a weakly developed tendon of the *M. maxillo-mandibularis* in *H. inermis*. The authors speculated whether this may facilitate wide mouth opening, and thus effective use of the upper canines, as had previously been suggested for Bactrian camels, which also have conspicuous upper canines. These authors studied only female water deer. If their conjecture stands up, one would expect an even weaker *maxillo-mandibularis* tendon in males, which effectively use their much larger canines in fights.

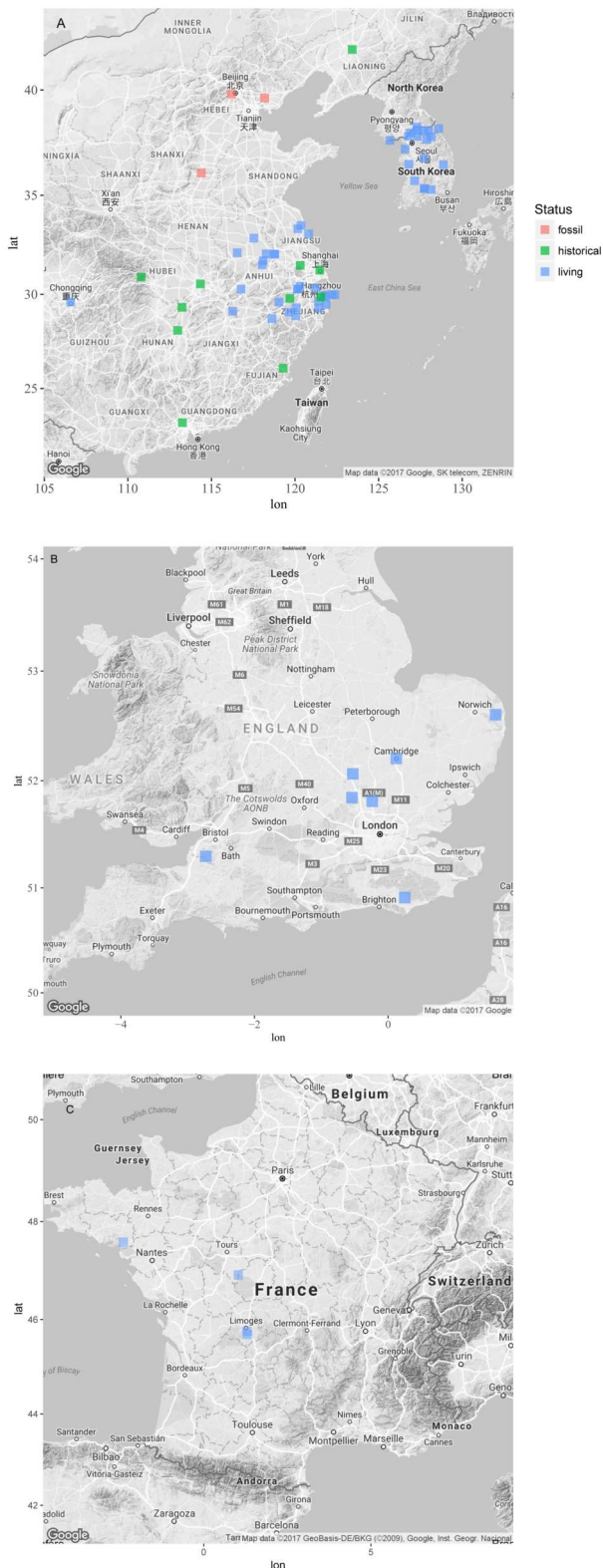
The dental eruption sequence in the lower jaw of *H. inermis* follows that observed in other deer, notably *Axis*, *Odocoileus* and *Capreolus* (Veitschegger and Sánchez-Villagra, 2015). For the upper jaw, the eruption sequence in Cervidae is still unknown.

Besides the upper canines, the complete absence of antlers in both sexes is a diagnostic characteristic of the skull of *H. inermis*. Kim et al. (2013b) pointed out that neither sex showed the slightest tendencies to develop pedicles. This is a clear difference to, e.g., *Capreolus capreolus* and *Muntiacus* species. Thus, even most *Capreolus* females have small outgrowths on the homologous sites of the frontal bones, where males develop pedicles. Female *Muntiacus* have a prolongation of the frontal ridges, although to a lesser extent than males. The absence of antlers also correlates with the structure of the frontoparietal suture. As Li and Suttie (2012) pointed out, in antlered deer the frontal overlaps the parietal bone in the region where antlers develop, whereas in *H. inermis* the parietal overlaps the frontal bone in the homologous region. The brain case of *H. inermis* is long and narrow and its shape is similar to that of *Moschus* (Swinhoe, 1870; Brooke, 1872). It houses a quite convoluted brain (Garrod, 1877b; Forbes, 1882), as typical for Cervidae (Pillay and Manger, 2007), which is considered, though, as small and light (~53 g) compared with body weight (Kruska, 1970).

### Post-cranial Skeleton

The post-cranial axial and appendicular skeleton of *H. inermis* has been studied to a much lesser extent than the skull. Here, we focus on the appendicular skeleton, given its importance for the diagnosis and classification of Ruminantia.

An already externally obvious skeletal characteristic of *H. inermis* is that its hindlimbs are longer than its forelimbs, and that consequently, its back is arched dorsally. In the forelimb, the wrist is composed of seven carpal bones, four in the proximal row (lunate, scaphoid, triquetral, pisiform) and three in the distal row (trapezium, trapezoid-



**Figure 3** – The geographical distribution of free-ranging *Hydropotes inermis*. A: Native habitat in China and Korea. B: *H. inermis* in England. C: *H. inermis* in France. Points approximately mark regions of occurrences. To obtain these, sampling sites and sighting reports were extracted from the literature and transformed into latitudes (lat) and longitudes (lon). Fossils from archaeological sites are only included if a description or drawing of the fossil specimen is available. Literature used: China: Pei (1930); Young (1932); de Chardin and Young (1936); Allen (1940); Ohtaishi and Gao (1990); Sun and Xiao (1995); Sun et al. (2000); Kim and Cho (2005); Rhim and Lee (2007); Xi et al. (2010); Kim and Lee (2011); Min (2012); Kim et al. (2015a); He et al. (2015). England: Arnold (1993); Harris et al. (1995); Wilson (2003); Ward (2005). France: Dubost et al. (2011). All maps made with R and ggmap package (Kahle and Wickham, 2013).

magnum, hamate) (Ahn, 2008). Except for the trapezium, this arrangement is found also in other deer and ruminants (Nickel et al., 1992; Morejohn et al., 2005; Smart, 2009; Hillson, 2016). In the metacarpus, the distal part of the degenerated second and fifth metacarpal bones persist, whereas the proximal part is reduced, a pattern observed also in *Capreolus*, *Alces*, *Rangifer*, and other deer genera known as “Telemetacarpus” (Brooke, 1878) or Capreolinae (Gilbert et al., 2006; Hassanin et al., 2012).

For the hindlimb, it was observed that the median and lateral trochlear ridges of the femur are rather symmetric. This morphology is typical for several small ruminants which share a preference for closed or mixed habitat (like *Hyemoschus aquaticus*, *Muntiacus reevesi*, *Odocoileus hemionus*, *Ourebia ourebi*, *Cephalophus silvicultur*, *Tragelaphus scriptus*, *T. imberbis*, *Antilocapra americana*, *Aepyceros melampus*) and is thought to be the result of convergent evolution (Janis et al., 2012).

The tarsus of *H. inermis* is composed of five bones, as commonly observed in pecoran ruminants. The proximal tarsal row consists of the talus and calcaneus. The second tarsal row consists of the *Os centroquartale* (= *Os naviculocuboideum*), the *Os tarsale I* (= *Os cuneiforme mediale*) and fused *Os tarsale II* and III (= *Os cuneiforme intermediolaterale*) (König and Liebich, 2005; Ahn, 2008; Morlat, 2010).

Finally, it may be noted that the obturator canal in the pelvic girdle of *H. inermis* usually is clearly separated from the foramen obturatorium by a bony bridge or marked bony spines (Tae et al., 2014). Based on the morphology and variability of this characteristic, *H. inermis* may be grouped with Capreolinae, rather than Cervinae (Tae et al., 2014).

### Soft-tissue anatomy

As typical for Cervidae, and indeed Ruminantia, the aortic arch of *H. inermis* gives off a common brachiocephalic trunc, which then branches somewhat variably. Ahn (2008) analysed 23 animals and described the most common (19/23) pattern as follows: the brachiocephalic trunc gives first off the left subclavian artery; then the left common carotid artery; and then it trifurcates into the right common carotid artery, the right costocervical trunk and the right subclavian artery. He also noted that there was no bicarotid trunc. This latter finding in particular is identical to what has been observed in *Axis axis* (3 specimens) and *Ozotoceros bezoarticus* (8 specimens) (Pérez and Erdoğan, 2014). In contrast, a bicarotid trunc seems to be the rule in many domesticated ruminants, *Mazama gouazoubira* (Ahn et al., 2008; Pérez and Erdoğan, 2014) and the Siberian roe deer (Ahn et al., 2014, abstract).

The digestive system of *H. inermis* comprises a quadruplicate omasum, a liver without gall bladder and an intestine wanting the ileocecal gland (Garrod, 1877a; Forbes, 1882). The testis and the accessory reproductive glands are similar to those of other ruminants for shape, location and histology (Sohn and Kimura, 2012). Forbes (1882) described the penis as an “elongated tapering compressed cone, with the urethral opening subterminal” (p. 82). Furthermore, he could not identify a Cowper’s gland in an adult *H. inermis* male.

*H. inermis* lacks a metatarsal gland (Garrod, 1877a), while an interdigital gland in the hind limbs, and inguinal glands are present (Pocock, 1923). The latter glands are specific to *H. inermis* within Cervidae (Pocock, 1923).

## Biology and Ecology

### Habitat

In its native lands, *Hydropotes inermis* is often found in mixed habitats rather than closed forests. It prefers meadows with shrubs to hide (Dubost et al., 2008) or forests interspersed with clearings (Rhim and Lee, 2007). Connectivity and proximity of forest patches seem to be important factors favouring the abundance of *H. inermis* (Jung et al., 2011). From observations made in Korea, it has been concluded that *H. inermis* prefers altitudes below 300 m. However, droppings found on mountain slopes of different degrees indicate that it did not avoid steeper slopes (Kim et al., 2011b). From a Korean sample of four feral animals, the home range of *H. inermis* has recently been estimated to

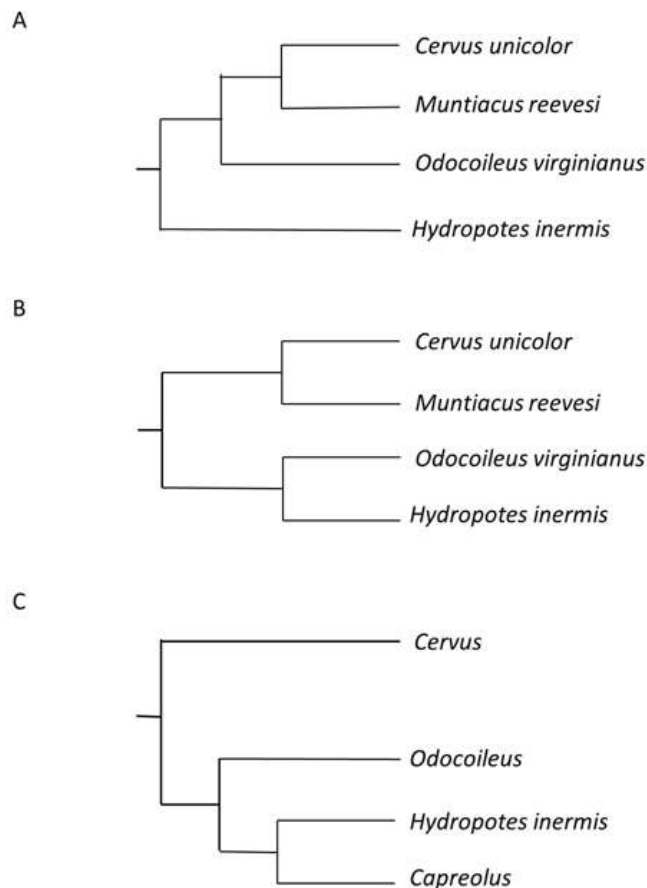
be about two to four km<sup>2</sup> (Kim and Lee, 2011, estimated with the minimum convex polygon (MCP) method). Based on a sample of 10 animals in a reintroduced population in the Nanhui Wildlife Sanctuary near Shanghai, the home range has been estimated to be about 0.7–6.7 km<sup>2</sup> (Chen et al., 2015; MCP method). For this sample, the winter home ranges were reported to be about twice as large as the ranges reported for other seasons (He et al., 2015). In contrast, for the Korean sample, the summer home ranges were found larger (Kim and Lee, 2011). Interpretation of these data is qualified by the small sample sizes and by the fact that the Chinese sample was analysed shortly after reintroduction. Thus, it may not be representative of a truly feral population. In addition, two of the four Korean animals had been wounded before tagging (Kim and Lee, 2011). In England, *H. inermis* has a much more restricted home range (on average: 0.21 km<sup>2</sup>) (Cooke and Farrel, 1998). These observations suggest differences in that home range size may vary with sex, season, and age; however, more data are needed to address these issues.

## Diet

Molecular biological and microhistological analyses of plants extracted from the faeces and feeding signs revealed that in its native lands in China and Korea, *H. inermis* feeds mainly on forbs and woody plants such as Asteraceae, Leguminosae and Fagaceae (Guo and Zhang, 2005; Kim et al., 2011a). Boué (1970) noted that *H. inermis* selected the leaves and twigs to feed on. In England, the stomach contents of *H. inermis* consisted mainly of grasses, sedges and herbs; woody species made up only a small part of the ingested food (Cooke and Farrel, 1998). Clauss et al. (2008) classified individuals from the English Whipsnade population as intermediate feeders, based on the percentage of grass in their natural diet. Yet, as documented by Hofmann et al. (1988), food available to *H. inermis* in Whipsnade might be suboptimal, thus it does not represent their natural choices. Still, it should be stressed that the populations in Whipsnade and in the Bretagne were and are the main resource for studies on the behaviour and ecology of *H. inermis* under (semi-) feral conditions Dubost et al. (2008, 2011).

## Sociality

*Hydropotes inermis* is a rather solitary deer, and especially males range alone. Outside the parturition/early-fawning period, individuals only occasionally form small, transient groups of two, rarely up to five individuals (Stadler, 1991; Sun, 2002). Individuals of both sexes are peaceful, living “unconcerned about the others” (Dubost et al., 2011, p. 196). In a semi-feral population, direct physical interactions were observed to be restricted to the strictly necessary. Adults did not groom each other; rarely licked another and ‘partners’ were not marked (Dubost et al., 2011). In alert situations, groups burst away, each individual in a different direction (Scherpe, 1971). When in danger, *H. inermis* flees in a leaping form (Bützler, 1988; Cooke and Farrel, 1998; Geist, 1998), commensurate to its rather longer hind-legs. Furthermore, *H. inermis* does not tail-flash, as other deer species do, in order to warn each other. More frequent and intensive body contacts among individuals occur during the mating season and the fawning period (Zhang, 2000; Dubost et al., 2011). Mating season lasts from November until January both in Asia and in Europe (Scherpe, 1971; Sheng and Lu, 1985a; Stadler, 1991; Sun and Dai, 1995; Dubost et al., 2008). During the mating season, some males establish and defend territories (Sun and Dai, 1995; Dubost et al., 2011). These territories are based on female distribution (Sun and Xiao, 1995), and female home ranges were observed to overlap with several male territories. Males mark their territories by pawing a hole and filling it with urine or faeces (used in 86.4% of all observations) or by rubbing their forehead, up to several minutes, against an inanimate object (13.6%; Sun and Dai, 1995). A particularly excited male may interrupt forehead rubbing and repeat it several times (Stadler, 1991). Head rubbing of females typically includes also rubbing of the ears and posterior parts of the head and it is considered a comfort, rather than a marking behaviour (Feer, 1982). (Dubost et al., 2011) noted that females and young could travel unhindered through male territories. In contrast, non-territorial males



**Figure 4** – Phylogenetic position of *H. inermis* within Cervidae as described by Kraus and Miyamoto (1991) (A, B) and Douzery and Randi (1997) (C). A: Phylogenetic relationships based on mitochondrial 12S and 16S rRNA genes and considering transversions, transitions and gaps. B: Result obtained considering only transversions. C: Phylogeny based on the cytochrome b sequence. The same phylogeny was obtained regardless of whether transitions or transitions and transversions were considered. Note the basic identity of the cladograms in B and C. *Muntiacus* was not included in the analysis of Douzery and Randi (1997), and Kraus and Miyamoto (1991) did not include *Capreolus*.

usually stayed between the territories, where they lived together peacefully. Moreover, non-territorial males were observed to conquer a territory only rarely, when challenging a territory holder (Stadler, 1991; Dubost et al., 2011).

In a combat for a territory and for females, *H. inermis* males prefer direct attacks (Feer, 1982). Threatening gestures are limited to an aggressive approach (Stadler, 1991, Tab. 1) and to stamping with the forefeet (“Drohstampfen”, Scherpe, 1971). According to Stadler (1991), the fight in *H. inermis* typically consists of well-divided steps. Each step can be associated with a behavioural pattern (Tab. 1) and an increased level of aggressiveness, with the canine blow as last and most aggressive step. Canine-blows can cause serious injuries in captivity (Feer, 1982) and the wild, e.g., “ripped ears, long scars (5–30 centimetres) on virtually all parts of the body, or limping legs” (Stadler, 1991, p. 93). Thus, the canines are very effective weapons, with the potential to kill. For instance, Stadler (1991) reported on a dead male with two holes piercing its heart. The depth of the wound, the shape of each hole and the distance between them matched well with the morphology of water deer canines. In a way, the agonistic fighting behaviour of *H. inermis* finds parallels in that of *Moschus* (described by Zhang et al., 1979; see also: Sathyakumar et al., 2015). In contrast, *Muntiacus* males, which have antlers and canines, use both in intra-specific fights, but with a clear preference for antlers (Barrette, 1977).

## Mating, reproduction, rearing fawns

*H. inermis* is a polygynous species and males herd the females present in their territory (Scherpe, 1971; Stadler, 1991). Only territory holders mate successfully with females. When approaching a female, the

male emits a mating call (Stadler, 1991; Cap et al., 2008; Dubost et al., 2011). It lowers its head, slaps the ears and sniffs either the female or the site where she was lying and then performs flehming to assess her sexual status (Stadler, 1991). Both unreceptive and receptive females withdraw from an approaching male, which follow-up receptive females, until these stop and copulation occurs. Copulation lasts only a couple of seconds (Stadler, 1991; Dubost et al., 2011). The gestation period is about six months (170 days, Dubost et al., 2011) and it is the shortest among cervids (Tab. 2). Most parturitions occur from May to June (Sheng and Lu, 1985a; Stadler, 1991; Dubost et al., 2011) and females do not select isolated places to give birth (Stadler, 1991). In captivity or under semi-free ranging conditions, *H. inermis* has a litter size of two to four, and occasionally up to eight fawns (Dobroruka, 1970; Scherpe, 1971; Sheng and Lu, 1985a; Stadler, 1991; Dubost et al., 2008). This latter number agrees with what has been observed in occasional dissections of pregnant females (Swinhoe, 1870; Hudson, 1872; Hamilton, 1873). Dubost et al. (2008) pointed out that litter sizes in parks in Europe are smaller than the Asian ones, and suggested that, as in other deer, it may vary with overall population density. This comparatively large litter size (see Tab. 2) has been interpreted as a derived condition (Jabbour et al., 1997; Mauget and Mauget, 2009). Thus, an explanation for the high foetus number based on early reports on the one hand and the few new-borns on the other hand, is still missing. Systematic studies that track females (and their foetus) from perception to birth and studies on protected, native populations, which are not exposed to hunting or high-density pressure, might be approaches to find solutions to this bias in *H. inermis* reproductive biology. Females interact with their fawns only for a short period and mother-fawn interaction decreases rapidly with weaning. Occasionally, females help to rear non-filial fawns (Scherpe, 1971; Stadler, 1991; Mauget and Mauget, 2009). Suckling fawns perform the so-called “milk-step” (Scherpe, 1971; Stadler, 1991). Fawns execute the step from bottom-to-top and Scherpe (1971) interpreted the movement to be proportional to the hunger of the fawn. Mothers wean their fawns after only a couple of weeks (Scherpe, 1971; Chaplin, 1977; Dubost et al., 2008). Fawns become independent after three to four months and are loners (Stadler, 1991). At six months, the young reach sexual maturity and at 18 months, they reach adult weight. In the wild, *H. inermis* has been reported to reach an age of eight years (Dubost et al., 2008), in captivity it reaches up to eleven years (Jones, 1977). Dubost et al. (2011) point out that among cervids, *H. inermis* is “the most precocious and the most prolific, even if one takes into account small ruminants like [the dikdik] *Madoqua kirki* or the roe deer *C. capreolus*...”, and they note that for many characters of its reproduction, maturation and life cycle, it is rather reminiscent of large rodents.

## Genetics

Overall, genetic characterization of *H. inermis* is still rather limited. Karyotype analyses revealed that *H. inermis* has 70 chromosomes (2n), comprising 68 autosomes and two sex chromosomes (Hsu and Benirschke, 1973). All chromosomes are acrocentric. Other cervids either have the same or lower numbers of chromosomes (Nietzel et al., 1986; Nietzel, 1987; Dementyeva et al., 2010), which led to the suggestion that the karyotype of *H. inermis* represents an ancestral state (Nietzel, 1987). In 1990, Miyamoto and colleagues published the first mitochondrial gene sequences for *H. inermis*, coding for 12S and 16S ribosomal RNAs. Since then, several authors have published additional mitochondrial sequences, which they used primarily to infer the phylogenetic position of *H. inermis*. Recently, the complete mitochondrial genome of *H. inermis* has been sequenced (Yu et al., 2011a; Hassanin et al., 2012; Liu, Z. and Huang, J., direct submission to GenBank), with sequences available in GenBank (see Tab. 3 for accession numbers). Today, only a handful of nuclear sequences have been published. These include ZNF238, ZFX, ZFY, lactoferrin, and, notably several (micro-) satellite sequences (for additional genes, accession numbers and references, see Tab. 3). In cervids, six satellite DNA families (I–VI) have so far been described (for a review, see Li and Lin, 2011; Hsieh et al., 2014). In *H. inermis* satellite I (Bogenberger et al., 1987;

Lin and Li, 2006), II, III (Lin and Li 2006), and V (Li et al., 2005) families were identified. Satellite families I and II are found in many cervids (see Lin and Li 2006 and references therein). Family III satellite DNA was originally thought to be specific for the roe deer (*Capreolus capreolus*; Buntjer et al., 1998), but subsequently also identified in *H. inermis* (Lin and Li, 2006). The presence of family V satellite DNA, originally identified from the Y-chromosome of Indian muntjac (*Muntiacus muntjak vaginalis*), has been studied so far in only a few cervids and related species. It was found in males of Indian, Formosan and Chinese muntjac (*M. muntjak vaginalis*, *M. reevesi micrurus* and *M. reevesi*, respectively), sambar deer (*Cervus unicolor swinhoei*), and *H. inermis*. Moreover, it was identified in female Indian and Formosan muntjac and in female Chinese water deer. In *H. inermis*, it is found on both the Y and X chromosomes. No satellite V signal was detected in probes from caribou (*Rangifer tarandus caribou*) and black-tailed deer (*Odocoileus hemionus hemionus*) (Li et al., 2005). Finally, family VI satellite DNA was first isolated from chromosome 3+X of the Indian muntjac. In this species, the X-chromosome fused with the autosome 3 (Hartmann and Scherthan, 2004). Thus, females have 2n=6 (chromosome pairs 1, 2, 3+x) and males have 2n=7 (chromosome pairs 1, 2, unfused 3 and 3+X and Y) (?Li et al., 2005). Satellite VI was then also found in the Formosan sambar deer (*Rusa unicolor swinhoei*), in Formosan sika deer (*Cervus nippon taioanus*) and the Formosan muntjac. In contrast, this satellite was not detectable in black-tailed deer, caribou, water deer, roe deer, bull and goat (Hsieh et al., 2014). Given the role attributed to microsatellites for centromere function (see, e.g., Lin and Li, 2006; Ferguson-Smith and Trifonov, 2007; Makunin et al., 2016), it will be interesting to see whether, and how these data may be integrated with karyotype variability in cervids.

Besides application in phylogenetic studies (see the following section), genetic approaches have been used for species identification, forensic science, food safety (e.g., Fang and Wan, 2002; Wan and Fang, 2003; Kim et al., 2010), population genetics, and management (e.g., Hu et al., 2006, 2007; Kim et al., 2014; Shi et al., 2014). Thus, analyses of microsatellites (Hu et al., 2007; Shi et al., 2014) and the mitochondrial control region (Hu et al., 2006) led the authors to conclude that *H. inermis inermis* in China “has a relatively high-genetic diversity” when compared to other rare cervid species, such as the Chinese sika deer (*Cervus nippon*), Eld’s deer (*Cervus eldi*), the black muntjac (*Muntiacus crinifrons*) (Hu et al., 2006), the forest musk deer (*Moschus berezovskii*), and the North American wapiti, (*Cervus elaphus*) (Shi et al., 2014). As expected, intraspecific genetic diversity was higher in feral populations living in mainland China and three islands of the Zhoushan archipelago than in zoo populations (Hu et al., 2007). Similarly, mainland populations had a greater haplotype diversity than island populations (Hu et al., 2006). The authors disagree whether there is no inbreeding (Shi et al. 2014), some inbreeding (Hu et al., 2006) or severe inbreeding (Hu et al., 2007) levels in populations from the Zhoushan Archipelago. The genetic diversity of a population of *H. inermis argyropus* living in South Korea was found to be lower than that of the Chinese populations of *H. inermis inermis* (Kim et al., 2014).

## Passing the buck — Phylogenetic considerations Morphological evidence

The resolution of the phylogenetic position of *H. inermis* is of considerable interest, arguably less for systematics than for the insight into fundamental biological processes, such as karyotype evolution (Nietzel, 1987; Ferguson-Smith and Trifonov, 2007; Makunin et al., 2016) and antlerogenesis evolution (DeMiguel et al., 2014; Ceacero, 2016; Heckeborg, 2017). Furthermore, antlerogenesis is considered a prime model for mammalian regenerative biology, and indeed medicine (Price et al., 2005a; Kierdorf et al., 2009). Its conspicuous cranial morphology, and in particular its tusk-like upper canines, long and narrow brain case and the absence of supraorbital ridges led Gray (1872) to classify *H. inermis* with Moschidae. However, early on, differences with *Moschus* were noted: Brooke (1872) pointed out that, among others, the premaxilla is shorter and broader and the basioccipital bone is narrower in *H. inermis* than in *Moschus*. He and Rüttimeyer (1881), also

stressed that *H. inermis* had smaller orbits than *Moschus*, a lacrimal fossa and an ethmoidal gap. In a detailed study on *H. inermis*' internal organ anatomy (Garrod, 1877a) contrasted *H. inermis* with *Moschus moschiferus*, identifying the lack of a gall bladder and an ileocecal gland, the quadruplicate psalterium (duplicuplicate in *M. moschiferus*), differences in the numbers of colic coils (2.5 vs. 3.5, respectively), and finally, the considerably more convoluted brain of *H. inermis*. He summarised his observations sharply, stating, "In other words, *Hydropotes* is typically Cervine, whilst *Moschus* is anything but so", concluding

"To what group of the Cervidae *Hydropotes* is most allied there is still considerable uncertainty" (Garrod, 1877a, p. 891). Further morphological studies done since then (see, e.g., Brooke, 1878; Forbes, 1882; Pocock, 1923; Heintz, 1963; Meunier, 1963; Leinders, 1979; Leinders and Heintz, 1980; Groves and Grubb, 1987; Scott and Janis, 1987; Bouvrain et al., 1989) have not really solved this conundrum. More recent studies suggest that additional anatomical structures such as the vascular branching pattern of the aorta (Ahn et al., 2008; Clauss, 2014) or the obturator canal (Tae et al., 2014) may hold significant phylogenetic

**Table 4** – Overview of molecular studies concerning the phylogenetic position of *Hydropotes inermis*. Results are discussed in the text. Sequences sequenced for the first time in the studies listed are highlighted in bold.

Number in text	Reference	Research aim	Approaches	Material sequenced and/or analysed
1	Kraus and Miyamoto (1991)	Relationships among pecoran ruminants	Two step tree construction: Step 1: MP on transitions, transversions, gaps; Step 2: MP on transversions only; Indels included (=gaps)	<b>mtDNA; 12S, 16S rRNA and flanking regions 2.7 kilo kbp</b>
2	Douzery and Randi (1997)	Test for the postulated basal position of the antlerless Hydropotinae within Cervidae and for affinities between Odocoileinae and Hydropotinae	Two step tree construction: MP; all indels excluded; ML; NJ	<b>MtDNA; control region (1099 bp)</b>
3	Randi et al. (1998)	Phylogenetic position of <i>H. inermis</i>	MP; ML, quartet puzzling; NJ	<b>MtDNA; cytochrome b (1140 bp)</b>
4	Hassanin and Douzery (2003)	Phylogeny of ruminants, with special emphasis on the position of <i>Moschus</i>	MP, equal weights and differential weights; ML, standard and partitioned; NJ	MtDNA: 12S, 16S rRNA, cytochrome b, complete sequences; <b>nDNA: cytochrome oxidase P450 (193bp), lactoferrin promotor (325 bp), alpha-lactalbumin intron 2; k-casein exon 4 (401 bp)</b>
5	Pitra et al. (2004)	Phylogeny of Cervinae	MP, equally weighted; ML, quartet puzzling; NJ; BI	MtDNA: cytochrome b
6	Kuznetsova et al. (2005)	Phylogeny of Cervidae	MP, equally weighted; ML	MtDNA: 12S, 16S rRNA (2445 bp)
7	Hernández Fernández and Vrba (2005)	Phylogeny of Ruminantia	Supertree, Matrix representation parsimony	Combination of trees based on morphology, genetics, behaviour, physiology
8	Price et al. (2005b)	Phylogeny of Cetartiodactyla	Supertree, Matrix representation parsimony	Combination of different trees based on morphology, genetics, behaviour
9	Gilbert et al. (2006)	Phylogeny of Cervidae	ML; Bayesian	MtDNA: cytochrome b (1140bp), <b>CO2</b> ; nDNA: alpha-lactalbumin, <b>PRKC1</b>
10	Lin and Li (2006)	Tracing rare cervid satellites in <i>H. inermis</i>		nDNA: Satellite DNA
11	Cap et al. (2002)	Phylogeny of Cervidae	MP, unweighted characters	Behavioural traits: resting, survey, type of locomotion, postures, feeding activities, interactions with the non-social environment, grooming activities, agonistic and affiliative acts, and play
12	Cap et al. (2008)	Phylogenetic coherence of behaviour with molecular data	MP	Male vocal behaviour
13	Marcot (2007)	Phylogeny of terrestrial artiodactyls	Super matrix	mtDNA: cytochrome b, 12S, 16S rRNA, alpha-lactalbumin, CYP19, lactoferrin
14	Agnarsson and May-Collado (2008)	Phylogeny of Artiodactyla	Bayesian analysis	MtDNA: cytochrome b
15	Zhang and Zhang (2012)	Phylogeny of Cervidae	NJ; Bayesian analysis	MtDNA: whole genome
16	Hassanin et al. (2012)	Phylogeny of Artiodactyla	ML	<b>MtDNA: whole genome</b>
17	Wang and Yang (2013)	Phylogeny of Cetartiodactyla	ML; Bayesian analysis	MtDNA: whole genome

MtDNA Mitochondrial DNA  
nDNA Nuclear DNA  
MP Maximum parsimony  
ML Maximum likelihood  
NJ Neighbourhood joining



signals. However, the variability of these traits (see also Pérez and Erdoğan, 2014; Ahn et al., 2014 (abstract)) and the relatively low numbers of specimens analysed so far, precluded its assessment.

Before the advent of molecular analysis, Pocock's idea that *H. inermis* is "the most primitive of all existing Cervidae" (Pocock, 1923), p. 195), which implies that the lineage leading to *H. inermis* split off from all other cervids before antlers have evolved, seems to have been the predominant, but not uncontested view. For instance, Simpson (1945) and Ellerman and Morrison-Scott (1951) presented alternatives to Pocock's "primitive deer hypothesis", without, however, arguing their point. Simpson (1945) stressed, "the classification of the deer presents many difficult, and in large part unsolved, problems" (p. 266) — which sounds like an echo of Garrod's (1877a) conclusion cited above. A concise overview of the status and problems of the phylogenetic classification of *H. inermis* before molecular data became available is given by Bouvrain et al. (1989). For these authors, it is clear that *H. inermis* belongs to Cervidae, but less so whether it may be grouped with Odocoileinae or Cervinae, or whether it defines a sister group to both of these clades. On the weight of the morphological data available at that time, they favour the view that *H. inermis* either is a member of Odocoileinae or constitutes a sister group to them, and that Cervinae are a sister group to the lineage formed by *H. inermis* and Odocoileinae together. They also note, though, that this is not "satisfying" to them ("L'hypothèse (...) est, à notre avis, la plus vraisemblable, bien qu'elle ne soit pas vraiment satisfaisante", p. 89).

Considering our current molecular-based perspective of *H. inermis* phylogeny (see below, following section) it seems ironic that Pocock formulated his hypothesis focussing on differences between *Hydropotes* and *Capreolus*, notably the lacking antler and presence of tusks, preorbital and inguinal glands, and the absence of the metatarsal gland in *Hydropotes*. This focus on differences between the two species rapidly overshadowed the potential close relatedness of *H. inermis* and *Capreolus*, which was suggested by a set of morphological criteria, as pointed out early on, like skull morphology (Rütimeyer, 1881) and soft-tissue peculiarities, such as the brain, the absence of Cowper's glands, and the glans penis (Forbes, 1882), the latter being long, slender, cylindrical and with a subterminal opening in *C. capreolus* (Garrod, 1877b).

### Molecular, genetic, and behavioural evidence

More recently, behavioural and molecular characters were increasingly used to probe the phylogeny of *H. inermis*. In behavioural studies, it was noted that the scent-marking behaviour in *H. inermis*, which uses urine or head rubbing resembles more that of antlered deer than that of other ruminants lacking cranial appendages like *Moschus*, which use their musk and caudal glands (Green, 1987; Green and Kattel, 1997), or *Tragulus napu*, which uses its intermandibular glands (Kalina and Adams, 1984). While it was noted that the forehead rubbing of *H. inermis* was reminiscent to that observed in *Capreolus capreolus* (Johansson and Liberg, 1996), yet another analysis, based on locomotion, feeding and non-social and social interactions did not allow resolving the phylogenetic relationships between *H. inermis* and antlered Cervidae (Cap et al., 2002) (Tab. 4, #11). Specifically, in that study, the bootstrap support for a clade encompassing *H. inermis* and *C. capreolus* remained underneath the 50% threshold of acceptance. In contrast, in a maximum parsimony analysis of male vocal behaviour, *H. inermis* and *C. capreolus* did cluster together (Cap et al., 2008) (Tab. 4, #12).

The era of DNA-based, molecular analysis of cervid phylogeny was heralded by Miyamoto et al. (1990), who sequenced the ribosomal RNA from the mitochondria to study the evolutionary relationship of antlered deer. In that study, the authors used *H. inermis* as outgroup. In subsequent studies, authors used additional mitochondrial DNA, different sample compositions and statistical methods to probe the phylogenetic position of *H. inermis*. This might have resulted in conflicting conclusions (Kraus and Miyamoto, 1991; Douzery and Randi, 1997; Randi et al., 1998) (Fig. 4).

The importance of methodology is impressively documented already in the first study providing molecular phylogenetic trees of *H. inermis*

(Kraus and Miyamoto, 1991). Using Maximum parsimony (MP) analyses of a ~2.7 kbp DNA fragment encompassing the mitochondrial 12S and 16S rRNA genes (Tab. 4, #1), these analyses placed *H. inermis* as a sister group to Cervidae when point mutations, i.e. transitions and transversions, and gaps in the sequence were considered. In contrast, when only transversions were considered, *H. inermis* was placed within Cervidae, specifically Odocoileinae/ Capreolinae, as sister to *Odocoileus virginianus*. Further, Douzery and Randi (1997) pointed out that use of a maximum likelihood method with the data of Kraus and Miyamoto (1991) "strongly favours the grouping of *Hydropotes* with *Odocoileus*" (p. 1163). In the same study, Douzery and Randi (1997) also provide an example how the influence of methodology on phylogenetic inference may depend on the particular sequence analysed. Thus, in contrast to the data used by Kraus and Miyamoto (1991), analysis of the phylogenetic signal in the mitochondrial control region (~1kbp) consistently placed *H. inermis* within Odocoileinae, irrespective of whether transitions or conversions and transitions were considered (Tab. 4, #2). Importantly, it should be mentioned that the study of Douzery and Randi (1997) was the first to provide molecular support for a close relationship between *H. inermis* and *C. capreolus*, which had been suggested in older, but rather neglected, morphological studies (see above, and in particular Bouvrain et al., 1989). Subsequent analyses using additional mitochondrial and nuclear sequences, either from *H. inermis* or other cervids (Douzery and Randi, 1997; Randi et al., 1998; Pitra et al., 2004; Kuznetsova et al., 2005; Gilbert et al., 2006; Hassanin et al., 2012) (Tab. 4, #2,#3, #5, #6, #9, #16) concur to support the placement of *Hydropotes* in Capreolinae, and indeed as a sister to *Capreolus*. Furthermore, although the (statistical) support for this interpretation of the data predictably varies with the genes analysed and exact methods used, this is currently the most accepted interpretation of available data. We would also like to point out that even in the cytochrome b-based study by Agnarsson and May-Collado (2008), which placed *Capreolus* and *Hydropotes* in a clade closer to Muntiacinae and Cervinae than to Odocoileinae, the close association of *Hydropotes* with *Capreolus* was not questioned (Tab. 4, #14). Furthermore, in Heckeberg et al. (2016), *Hydropotes* and *Capreolus* species are placed in an unresolved trichotomy. Lastly, the fact that *H. inermis* and *C. capreolus* are the only cervids sharing family III satellite DNA III also supports a close relationship between these two genera (Lin and Li, 2006) (Tab. 4, #10).

### Combined assessment of morphological, genetic and other evidence

Some of the studies just cited already combined information from more than one gene, or even genetic and morphological/paleontological information. For instance, Hassanin and Douzery (2003) (Tab. 4, #4) and Gilbert et al. (2006) (Tab. 4, #9) both analyzed several concatenated mitochondrial and nuclear genes together. Pitra et al. (2004) (Tab. 4, #5) present a cytochrome b-based phylogram that was fossil-constrained. Finally, Cap et al. (2008) combined molecular and behavioural data. A formalized technique that allows to combine different data types is the supertree approach (for reviews, see Sanderson et al., 1998; Bininda-Emonds et al., 2002). Key to this methodology is that instead of individual characters, topologies of phylogenetic trees constructed based on such characters are interpreted as phylogenetic evidence. Tree topologies are encoded as matrices, which then may be combined using a variety of algorithms. In a supertree analysis of Artiodactyla, Price et al. (2005b) found that *H. inermis* grouped with antlered deer, in agreement with the molecular genetic studies discussed above (Tab. 4, #8). This analysis employed a variant of the supertree approach referred to as matrix representation with parsimony (MRP). It was obtained by integrating 201 source trees from 141 publications. In contrast, Hernández Fernández and Vrba (2005) (Tab. 4, #7) applied this methodology to a set of 124 phylogenetic trees for Ruminantia from 158 publications, 67 of these publications overlapped with those used by Price et al. (2005b). They also used a MRP-based approach, which, however, seemed to differ in several aspects from the that used by Price et al. (2005b). Their results suggested that *H. inermis* does not belong to

antlered deer, but is sister group to the latter. Yet their data also show that the support for this conclusion, as measured by the Bremer decay index, remained low. Their significance of our understanding of Artiodactyla and Ruminantia phylogeny, notwithstanding these analyses, do not help to resolve the issue of the phylogenetic position of *H. inermis*. Their conflicting conclusions may be due to differences in the database or exact methodology used in these studies. Of note, both research groups point out a lack of data for lineages in the phylogeny that is particularly relevant to derive the position of *H. inermis*. Thus, Price et al. (2005b, p. 455) indicate that their analysis “highlights areas in need of further phylogenetic research and data collection (...) especially on (...) Cervidae (...), where very little phylogenetic information is currently available”. And Hernández Fernández and Vrba (2005, p. 291) stress that “the most serious gaps in our knowledge concern the basal relationships of Odocoileini (...). This situation must be recognized and remedied...”, which is supported by a recent study on Cervidae (Heckeberg et al., 2016). Hernández Fernández and Vrba (2005) also repeatedly point out the significant role of fossil evidence for reconstructing a dependable phylogeny. Indeed, the presence of fossils in a phylogenetic tree can change the topology, compared with analyses where only extant species are used (Gauthier et al., 1988; Axsmith et al., 1998). Among others, Scott and Janis (1987) and Gentry and Hooker (1988) already included ruminant fossils in cladistic analyses, while Lister et al. (2005) combined morphological and molecular approaches to determine the phylogenetic position of the giant deer, *Megaloceros giganteus*.

## The rocky road of *Hydropotes inermis* — Fossil evidence

Overall, the fossil record that so far could be linked to *H. inermis* is exceedingly scarce. Specimens interpreted as possible direct predecessor to *H. inermis* or intermediate forms between *H. inermis* and other cervids (or ruminants) are still unknown. The rather short list of where *H. inermis*-related fossils have so far been found was already given above (see section “Biogeography”). The better diagnosed ones from Tangshan (Hebei), Choukoutien (Beijing) and Anyang (Henan province) include some upper canines and other teeth, lower jaws, one juvenile skull, and limb bones (Young, 1932; de Chardin and Young, 1936). The most ancient findings are those from Tangshan and Choukoutien, which are dated back to the Lower Pleistocene (de Chardin and Young, 1936). To the best of our knowledge, *H. inermis* fossils from Korea have not been described yet. To date, this age estimate seems the only evidence that may be linked with the genetic record. Considering that fossils available closely resemble contemporary animals — although, as noted by Young (1932), extinct *H. inermis* might have been somewhat larger than contemporary forms — it seems reasonable to speculate that the species originated well before the period for which fossils are available. Unfortunately, this rather vague estimate is not informative with respect to the affinity of *H. inermis*, as it does not allow to relate the fossil appearance of the species with any of the critical splits of the phylogenetic tree within Cervidae (see e.g., Pitra et al., 2004, fig. 3; Gilbert et al., 2006, fig. 4). No fossils are known that might be interpreted as transitional forms between *H. inermis* and its purported relatives.

## From past to future

If what we know about the past of *H. inermis* is rather limited, what may we say about its future? As documented above (see section “Biogeography”), numbers of free living *H. inermis* are not really known, but rather small, and probably in decline (Harris and Duckworth, 2015). On the other hand, breeding under semi-feral conditions and in captivity seems rather straightforward, and conservation programs are under way, notably in China (Hu et al., 2006; Min, 2013; Yabin, 2013). Still, recommendations whether combine (Shi et al., 2014) or not combine (Hu et al., 2006, 2007) distinct Chinese subpopulations are conflicting, which reflects a deeper lack of scientific understanding of the internal structure of the species *H. inermis* and its subpopulations. Any

conservation effort must confront and address these issues, which have been around since the early years of *H. inermis* description. We did not find active conservation programs for *H. inermis* in Korea. Traditionally, two subspecies of *H. inermis* are recognized: *H. i. inermis* occurs in China, and *H. i. argyropus* occurs in Korea. Today, these populations must be designated as allopatric due to habitat fragmentation; up to about hundred years ago, they were parapatric (Ohtaishi and Gao, 1990, fig. 4; Xu et al., 1997). The two subspecies are said to differ by pelage colour. This is so far the only criterion on which the diagnosis is based on, although information on pelage colour is still conflicting (Heude, 1884; Kori, 1922; Tate, 1947). Kori (1922) described differences regarding canines and the skull. However, he had access to only a single Korean specimen and some Chinese specimens. A more recent study aimed to investigate the geographical variation in the *Hydropotes* skull and test the validity of the traditional subspecies classification (Kim et al., 2015b). This study was based on a much larger sample size for both subspecies. It did not reveal any differences between the two allopatric populations. So far, both mitochondrial DNA and (nuclear) microsatellites have been used to study the population structure of *H. inermis* (e.g., Koh et al., 2009; Yu et al., 2011b; Kim et al., 2014, 2015a). While these studies yielded valuable insight in the genetic diversity of various populations both in China and in Korea (see above, section “Genetics”), they generally do not support the notion that Korean and Chinese populations of *H. inermis* might be genetically distinct. A notable exception is the microsatellite study described by Yu et al. (2011b), where it was found that allele sizes at three microsatellite loci were well separated in Chinese and Korean water deer gene pools. However, the authors also caution that “further studies using larger numbers of Korean water deer should be performed” (p. 6) before this lead might be sensibly interpreted. While the origin of species is ultimately due to a genetic process, just how much or which genetic changes allow to define a novel species is contentious, or plainly unknown. As Zachos (2016a) pointed out, species ranking is an arbitrary decision, as nature has fuzzy boundaries and we humans try to fit it into a binary system (for a detailed discussion of this issue, see, e.g., Zachos et al., 2013; Zachos, 2016a). What is clear, though, is that, genetic data available for *H. inermis* are far too few to seriously probe whether the two allopatric populations may be considered subspecies, or even different species, as has also been suggested (Heude, 1884; Tate, 1947). Zachos et al. (2013) proposed potential guidelines how to recognize species when few data are available. Accordingly, it would be best to “compare them to data from the same marker in better-studied closely related pairs of sister species... If no such data exist, then the single genetic finding maybe formulated as a two-species hypothesis that needs further testing” (Zachos et al., 2013, p. 4). Besides the two (sub-) species under investigation, there are no further sister species and therefore, it might be reasonable to apply the second criterion. We do not know whether the Korean and Chinese (or European) populations of *H. inermis* may or can crossbreed. At least we are not aware of any published studies addressing this issue. Thus, we cannot even test one of the more prominent species concepts, referred to as the Biological Species Concept, which posits that we may distinguish two species if these are reproductively isolated “due to intrinsic isolation mechanisms, not due to extrinsic factors such as a geographical barrier” (Zachos, 2016a, p. 110). Since most of the genetic data is based on mitochondrial sequences, mitochondrial introgression may pose a further problem blurring phylogenetic relationships “up to the point that in some populations most or even all animals carry mtDNA from a closely related but different species (“mitochondrial capture”)” (p. 4, Zachos et al., 2013, see also: Bradley and Baker, 2001; Baker and Bradley, 2006). Therefore, for the time being, the question whether *Hydropotes* is monospecific cannot be answered. Clearly, there is an urgent need for more data before the population structure, and the subspecies structure, of *H. inermis* may be sensibly discussed. Recently, a taxonomic revision of the species has been proposed (Groves, 2016). An integrative approach, using both molecular and morphometric data, allowed to successfully identify squirrel species (Wauters et al., 2017) and thus, such an approach might help to clarify the taxonomic status

of the water deer. The species concept in taxonomy is currently under debate (Gippoliti and Groves, 2013; Zachos et al., 2013); a (new) taxonomic assignment to *H. inermis* allopatric populations will likely have impacts on rational efforts of conservation and wildlife management and therefore, these questions are also of eminent practical importance (see e.g., Gippoliti and Groves, 2013; Zachos, 2016b). Currently, protection seems to be biased towards the Chinese population of *H. inermis*.

## Conclusions

In this review, we summarize the to-date available information on the biology of the water deer, *Hydropotes inermis* and highlight the potential for future research involving this species. Morphological studies mostly focused on the skull, while the skeleton and soft-tissues have been rather neglected. A deeper knowledge on its morphology, biology, ecology and genetics are required in order to manage and conserve the species. This also requires a more intense international collaboration between scientists and managing institutions from countries hosting the species. The weight of genetic evidence favours the placing of *Hydropotes* within Capreolinae/Odocoileinae, and indeed as closest relative to *Capreolus*. However, in the light of the limited raw material available and phylogenetic methods performed, the factual basis is still restricted, and its interpretation somewhat variable. Phylogenetic studies on ruminants and artiodactyls generally include *H. inermis* in the sample, but its phylogenetic positioning appears to be a by-product, rather than a principal research aim. Moreover, none of the genetic traits characterized so far are to the antlerless state of male *H. inermis*, or their prominent canines, i.e. the morphological characters defining their contested phylogenetic classification. The focus on mitochondrial genetic markers, i.e. the matrilineage, also limits our understanding of the population structure and dynamics of these animals. Moreover, the absence of described fossils of *Hydropotes* in Korea as well as the absence of diagnostic phenotypic traits between allopatric populations combined with their genetic and morphological conformity, question the conventional (sub-) species rank of *H. inermis*. The scarcity of fossil remains, and the complete lack of what may be considered transitory forms between *H. inermis* and its relatives, does not allow us to complement, and test results from molecular phylogenetic analyses. Yet, while the access to additional fossils can hardly be planned, further genetic studies might profit from genes involved in dental and bone development and antler induction. While for the latter process, genes are still to be discovered, genes involved in tooth growth might eventually be informative also for other mammals with excessive upper canines. ☞

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## Supplemental information

- After acceptance of this Manuscript, the following relevant papers were published:
- Menecart B., DeMiguel D., Bibi F., Rössner G.E., Métais G., Neenan J.M., Wang S., Schulz G., Müller B., Costeur L., 2017. Bony labyrinth morphology clarifies the origin and evolution of deer. *Sci. Rep.* 7(1): 13176.
  - Chen Y.J., Liu K.H., Chu W.L., 2016. New Record of Water Deer (*Hydropotes inermis*) from Iron Age Archeological Sites in Central Taiwan. *Collect. Res.* 29: 31–39.