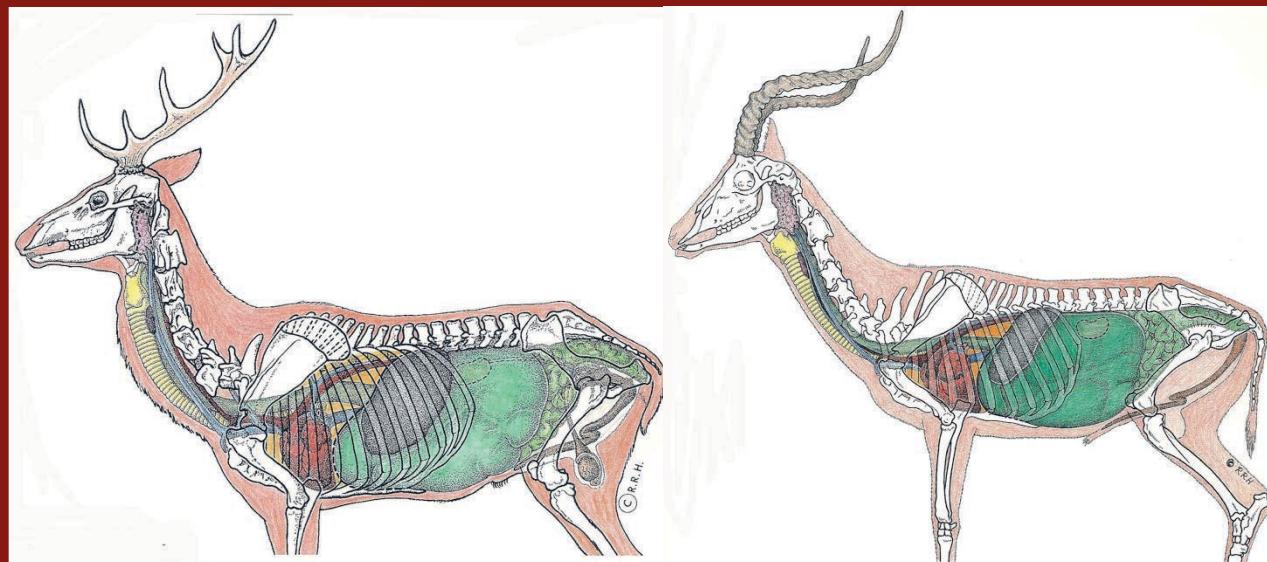




Soft tissue biology



Marcus Clauss

Clinic of Zoo Animals, Exotic Pets and Wildlife, University of Zurich



University of Zurich
Vetsuisse Faculty



Clinic
of Zoo Animals, Exotic Pets and Wildlife

graphics from Hofmann (2006)



International Conference on
Ruminant Phylogenetics Munich 2015

The first principle of paleobiology



The first principle of paleobiology

Christine Janis thought of it already
(and most likely before you were born).





International Conference on
Ruminant Phylogenetics March 2015

AMERICAN MUSEUM *Novitates*

The Interrelationships of Higher Ruminant Families with Special Emphasis on the Members of the Cervoidea

CHRISTINE M. JANIS¹ AND KATHLEEN M. SCOTT²

FEATURES OF THE SOFT ANATOMY

Cervids have been noted to have a number of features of soft anatomy which are specialized over the general pecoran condition. These are: the absence of a gall bladder (Flower, 1875); the possession of a placenta with few cotyledons (as opposed to many cotyledons as is typical of other pecorans) (Brooke, 1878); the absence of an ileocecal gland; and 2½ (as opposed to 3½) colic coils (Garrod, 1877) (character suite 34). These specialized features are shared by *Hydropotes* (Forbes, 1882; Garrod, 1877), clearly indicating that this genus belongs in the Cervidae.



Notes on the Visceral Anatomy and Osteology of the Ruminants, with a Suggestion regarding a Method of expressing the Relations of Species by means of Formulae.

By A. H. GARROD, M.A., Prosector to the Society.

I. Name.	II. Gall-bladder.	III. Caudate Lobe.	IV. Spigelian Lobe.	V. Depth of Umbilical Fissure.	VI. Length of Caecum and Sex of specimen.	VII. Intestinal lengths.	VIII. Papillæ of Rumen.	IX. Cells of Reticulum.	X. Præterium.
<i>Cervus elaphus</i>	Absent.	Lateral in young, small in adult.	Absent.	Almost nil.	1 ft. ♀, adult.	S.I. 42 ft. L.I. 30 $\frac{1}{2}$ ft.	Cylindroid, elongate, flattened.	Not deep.	Quadruplicate, 13.
— <i>cushmeirianus</i>	Absent.	Almost nil.	Absent.	+	♂, adult.	Cylindroid, except longest (1 in.), flattened and expanded.	Quadruplicate, 10.
— <i>dama</i>	Absent.	Cylindroid.	Broad-walled.	Quadruplicate, 10.
— <i>aristotelis</i>	Absent.	Square.	Oviform in one, rusiform in another.	+	♂, nearly adult.	Cylindroid, slightly flattened.	Broad-walled.	Quinquiplicate, 12.
— <i>swinhonis</i>	Absent	Large, square.	Rusiform.	+	1 $\frac{1}{2}$ ft. ♂, adult.	S.I. 48 $\frac{1}{2}$ ft. L.I. 25 $\frac{1}{2}$ ft.	Cylindroid, slightly flattened.	Quadruplicate, 9.
— <i>kuhlii</i>	Absent.	Square.	Absent.	5 in. ♂, adult.	S.I. 29 $\frac{1}{2}$ ft. L.I. 10 ft.	Cylindroid, slightly flattened.	Quadruplicate, 10.
— <i>malaccensis</i>	Absent.	Squarish.	Oviform.	+	1 $\frac{1}{2}$ in. ♂, new-born.	S.I. 14 $\frac{1}{2}$ ft. L.I. 8 $\frac{1}{2}$ ft.	Quadruplicate, 10.
— <i>mariannae</i>	Absent.	Square.	Absent.	+	10 in. ♀, adult.	S.I. 39 $\frac{1}{2}$ ft. L.I. 15 ft.	Quadruplicate, 10.
— <i>ducucensis</i>	Absent.	Square.	Rusiform.	+	1 ft. ♀, aged.	S.I. 45 ft. L.I. 25 $\frac{1}{2}$ ft.	Quadruplicate, 10.
— <i>porcinus</i>	Absent.	Lateral.	An oviform rudiment.	+	7 in. ♂, a year old.	S.I. 26 $\frac{1}{2}$ ft. L.I. 13 $\frac{1}{2}$ ft.	Cylindroid and tongue-shaped.	Deep, $\frac{1}{4}$ inch.	Quadruplicate.
— <i>alfredi</i>	Absent.	Large, square.	Oviform, small (juv.).	+	10 in. ♂, adult.	S.I. 34 ft. L.I. 18 ft.	Slender, small, cylindroid.	Broad-walled.	Quadruplicate.
— <i>capreolus</i>	Absent.	Lateral.	Oviform and everted.	+	10 in. ♂, adult.	S.I. 31 $\frac{1}{2}$ ft. L.I. 15 $\frac{1}{2}$ ft.	Some large and tongue-shaped.	Fairly deep.	Quadruplicate, 10.
<i>Cervulus muntjao</i>	Absent.	Lateral.	Rudimentary.	7 in. ♂, adult.	S.I. 18 $\frac{1}{2}$ ft. L.I. 8 $\frac{1}{2}$ ft.	Cylindrical.	Quadruplicate.
— <i>taeniatus</i>	Absent.	Oviform rudiment.	9 $\frac{1}{2}$ in. ♂, not adult.	S.I. 23 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	Very shallow.	Triplicate, 10.
<i>Elaphodus cephalophorus</i>	Absent.	Lateral.	Absent.
<i>Cervus puda</i>	Absent.	Lateral.	Absent or rudimentary.	Nil.	6 in. ♂.	S.I. 24 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	Cylindroid and slightly flattened.	Very shallow.	Triplicate, 10.
— <i>campestris</i>	Absent.	Absent.	11 in. ♀, adult.	S.I. 28 $\frac{1}{2}$ ft. L.I. 16 $\frac{1}{2}$ ft.	Cylindroid.	Quadruplicate, 9.
— <i>rufus</i>	Absent.	Squarish.	Absent, or rudimentary.	+	5 $\frac{1}{2}$ in. ♂.	S.I. 26 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	Short, flattened.	Very shallow.	Quadruplicate, 11.
— <i>mexicanus</i>	Absent.	Lateral.	Quadruplicate, 18.
<i>Camelopardalis giraffa</i>	Absent.	Absent.	+	2 $\frac{1}{2}$ ft. ♀, adult.	S.I. 196 ft. L.I. 75 ft.	Duplicate, 19.
<i>Moschus moschiferus</i>	In fossa.	Small, lateral.	Large, rusiform.	Quinquiplicate, 9.
<i>Antilocapra americana</i>	In fossa.	Very small, lateral.	Rusiform.	1 $\frac{1}{2}$ ft. ♀, adult.
<i>Ovis canadensis</i>	Very elongate.	Lateral.	Oviform.
<i>Cupra picta</i>	Very elongate.	Short, lateral.	Oviform.	+	1 $\frac{1}{2}$ ft. ♂, adult.	S.I. 45 $\frac{1}{2}$ ft. L.I. 19 ft.
— <i>jemuica</i>	Very elongate.	Short, lateral.	Oviform.	+	1 $\frac{1}{2}$ ft. ♂, adult.	S.I. 45 $\frac{1}{2}$ ft. L.I. 19 ft.
<i>Gazella dorcas</i>	In fossa.	Small, lateral.	Absent.	+	8 $\frac{1}{2}$ in. ♀.	S.I. 42 $\frac{1}{2}$ ft. L.I. 16 $\frac{1}{2}$ ft.
— <i>granti</i>	In fossa.	Small, lateral.	Small, rusiform.	+	8 $\frac{1}{2}$ in. ♂.	S.I. 36 $\frac{1}{2}$ in. L.I. 11 $\frac{1}{2}$ ft.
— <i>subgutturosa</i>	In fossa.	Small, lateral.	Oviform, or absent.	+
— <i>muelleri</i>	In fossa.	Small, lateral.	Absent.	+	5 $\frac{1}{2}$ in. ♂.	S.I. 19 ft. L.I. 9 $\frac{1}{2}$ ft.
— <i>rufifrons</i>	In fossa.	Small, lateral.	Rudimentary.	+	Fair depth.	Triplicate.
— <i>arabica</i>	In fossa.	Small, lateral.	Oviform.	+
<i>Nanotragus nigricaudatus</i>	Present.	Rudimentary.	Modified, rusiform.	+	7 in. ♂.	S.I. 16 $\frac{1}{2}$ ft. L.I. 11 ft.	Mostly cylindroid, some tongue-shaped.	Fair depth.	Duplicate, 9.
<i>Cephalophus maxwelli</i>	Absent.	Short.	Modified, rusiform.	+	8 in. ♂.	S.I. 21 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	Cylindrical and short.	Duplicate, 10.
— <i>pygmaeus</i>	Absent.	Short.	Modified, or absent.	+	6 in. ♂, adult.	S.I. 20 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	Cylindrical and short.	Fair depth.	Triplicate, 10.
<i>Tetracerus subquadricornutus</i>	Present, as is cystic fissure.	Absent.	Absent.	+	6 in. ♀.	S.I. 20 $\frac{1}{2}$ ft. L.I. 9 $\frac{1}{2}$ ft.	All flattened.	Shallow.	Triplicate, 10.
<i>Strepsiceros kudu</i>	Elongate.	Lateral.	Rudimentary.	+	2 $\frac{1}{2}$ ft. ♂, adult.	S.I. 106 ft. L.I. 78 ft.	Quadruplicate, 9.
<i>Oreamnos canadensis</i>	Present.	Oviform.	+	8 in. ♂, adult.	S.I. 20 $\frac{1}{2}$ ft. L.I. 16 ft.	Quadruplicate, 15.
<i>Tragelaphus scriptus</i>	Elongate.	Lateral.	Absent.	+
<i>Damaliscus pygargus</i>	Present.	Small, lateral.	Enormous, rusiform.	+	10 in. ♀.	S.I. 42 $\frac{1}{2}$ ft. L.I. 17 $\frac{1}{2}$ ft.	Fair depth.	Quadruplicate, 15.
<i>Cudobœus ganus</i>	Elongate.	+	1 $\frac{1}{2}$ ft.	Total length of intestines 118 ft.	Sparse, flattened.
<i>Addax naso-maculatus</i>	Very elongate.	Very short.	Oviform.	Rudimentary.	1 ft. 5 in. ♂, aged.	S.I. 53 $\frac{1}{2}$ ft. L.I. 29 $\frac{1}{2}$ ft.	Mostly elongated, cylindrical, some foliaceous.	Shallow.	Quadruplicate, 15.
<i>Portas picta</i>	Present.	Short.	Absent.	+	1 $\frac{1}{2}$ ft. ♀, adult.	S.I. 82 $\frac{1}{2}$ ft. L.I. 42 ft.	Large and foliated.	Well developed.	Quinquiplicate, 10.



Molecular and Morphological Phylogenies of Ruminantia and the Alternative Position of the Moschidae

ALEXANDRE HASSANIN^{1,2,3} AND EMMANUEL J. P. DOUZERY⁴

TABLE 2. Morphological character^a matrix (a = 0 or 1; b = 1 or 2; ? = unknown; - = not applicable).

	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4								
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6					
TRAGULIDAE	0	0	0	1	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0							
ANTILOCAPRIDAE	0	1	?	1	1	2	0	0	1	1	0	0	1	1	1	2	1	0	0	a	0	1	1	0	1	1	1	0	?	0	0	1	0	1	1						
GIRAFFIDAE	0	1	0	a	1	2	1	0	1	1	0	1	1	2	1	1	1	0	0	1	a	0	0	1	1	0	0	0	0	2	0	a	1	1	0	1	1				
CERVIDAE	0	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	a	0	1	1	1	1	1	1	1	0	0	1	1	a	1	1	0	1	1				
MOSCHIDAE	1	1	?	1	1	2	0	1	1	1	a	1	0	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	0	---	---	1	0	1	1	1	0	1			
BOVIDAE	0	1	1	1	1	2	0	a	1	1	0	a	0	1	1	b	1	0	aaa	0	1	a	1	1	1	0	0	1	0	0	1	1	0	a	1	1	0	1	1	0	1

^aSoft anatomy: 1 = abdominal musk gland; 2 = ruminating stomach with four chambers (including a well-developed omasum); 3 = cardiac orifice of rumen more ventrally situated; 4 = gall bladder; 5 = ileocecal gland; 6 = placenta diffuse (0) or cotyledonary with few (1) or many (2) cotyledons; 7 = extensible tongue; 8 = females with four (0) or two (1) mammae. Postcranial: 9 = fibular facet on calcaneum with proximal concavity large, distal concavity small; 10 = astragalus



The Placental Mammal Ancestor and the Post-K-Pg Radiation of Placentals

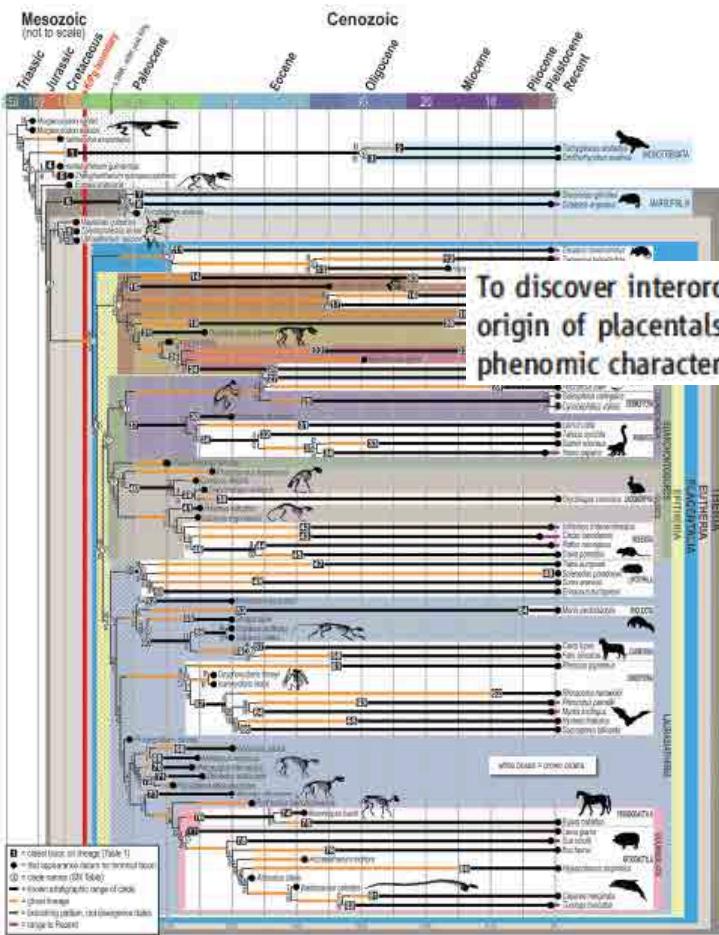
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VOL 339

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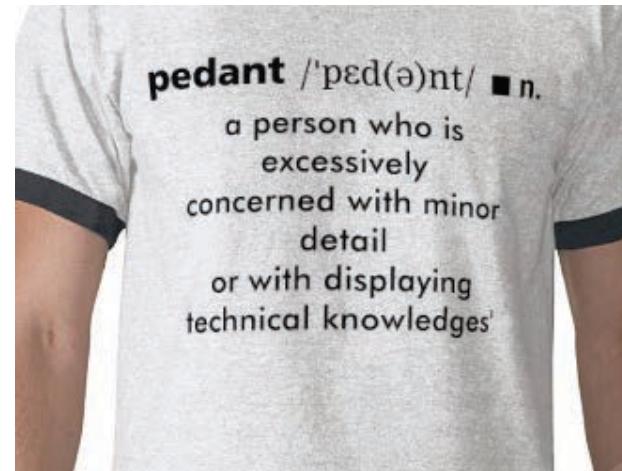
Maureen A. O'Leary,^{1,3¶} Jonathan I. Bloch,² John J. Flynn,³ Timothy J. Gaudin,⁴ Andres Giallombardo,³ Norberto P. Giannini,^{5*} Suzann L. Goldberg,³ Brian P. Kraatz,^{3,6} Zhe-Xi Luo,^{7†} Jin Meng,³ Xijun Ni,^{3‡} Michael J. Novacek,³ Fernando A. Perini,^{3||} Zachary S. Randall,² Guillermo W. Rougier,⁸ Eric J. Sargis,⁹ Mary T. Silcox,¹⁰ Nancy B. Simmons,⁵ Michelle Spaulding,^{3,11} Paúl M. Velazco,⁵ Marcelo Weksler,^{3§} John R. Wible,¹¹ Andrea L. Cirranello^{1,3}





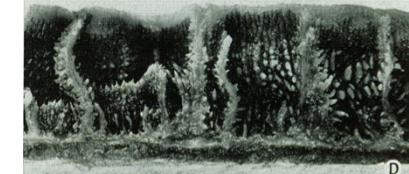
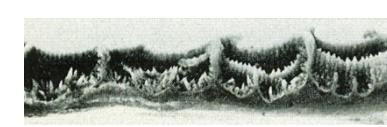
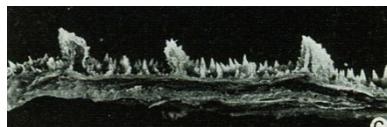
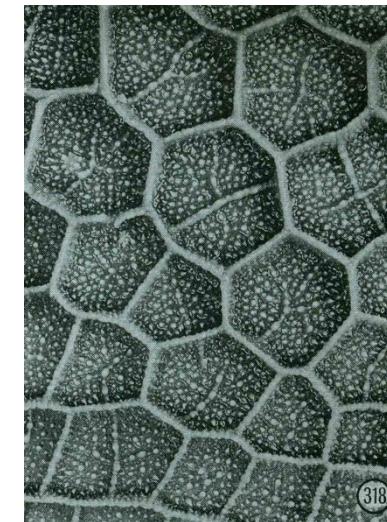
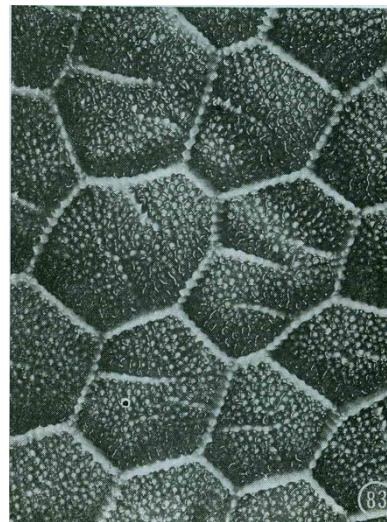
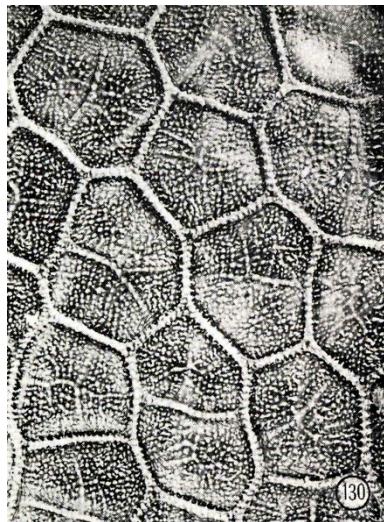
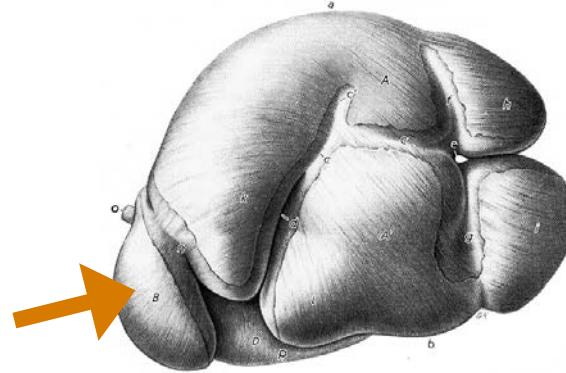
Using (soft tissue) morphology for phylogeny reconstructions

Functional anatomy (convergence) vs.
descriptive ('pedantic'), cataloguing anatomy?





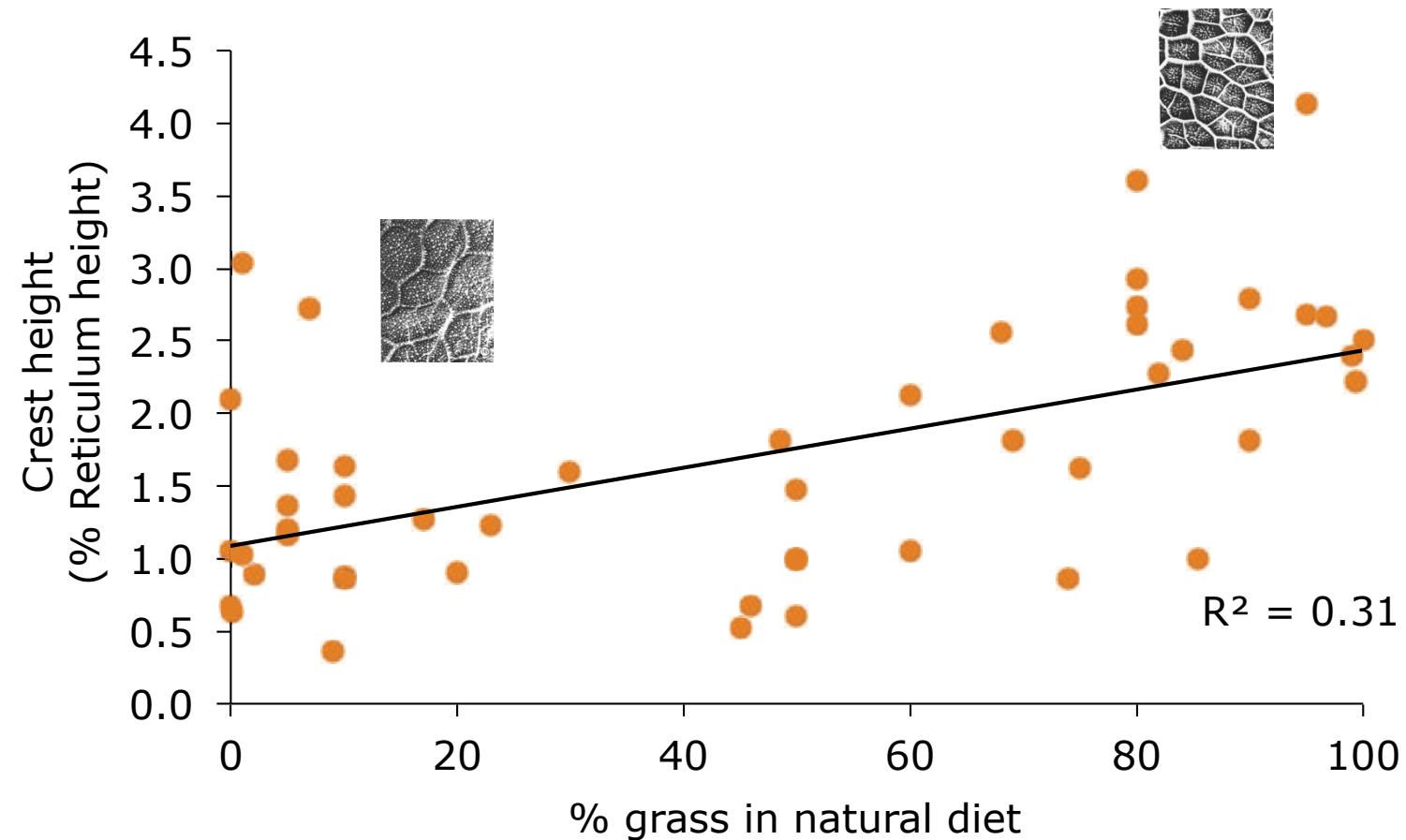
Reticular crests



from Hofmann (1969 & 1973)



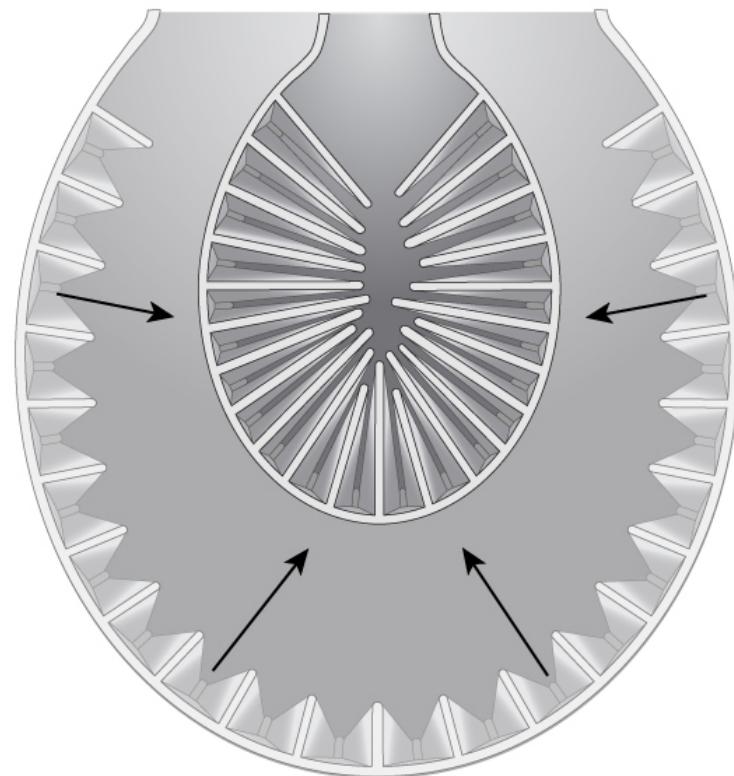
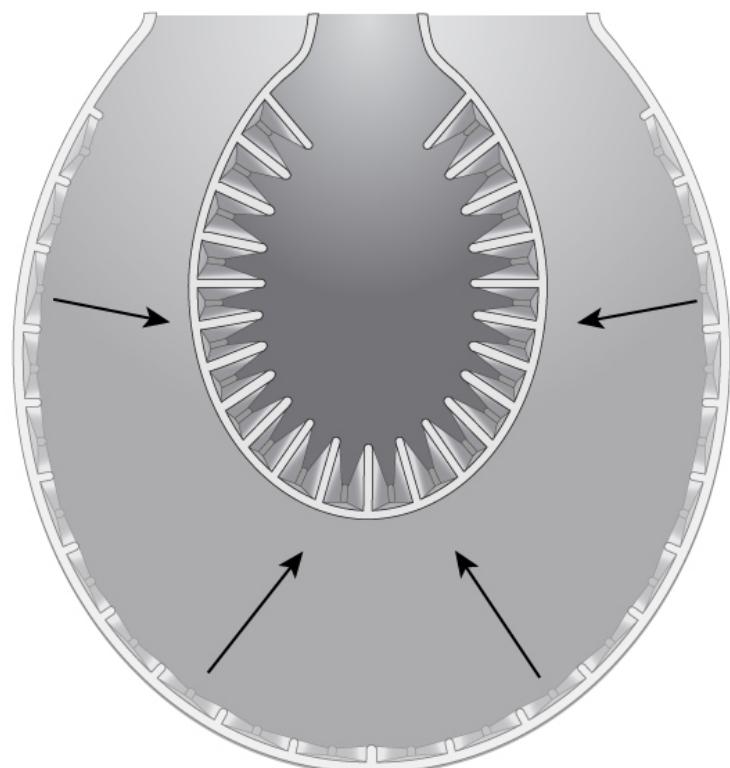
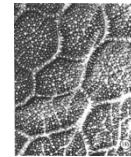
Reticular crests



from Clauss, Hofmann et al. (2010)



Reticular crests



from Clauss, Hofmann et al. (2010)



International Conference on
Ruminant Phylogenetics Munich 2015

Using (soft tissue) morphology for phylogeny reconstructions

How many individuals do you have to measure to be certain about a ‘species trait’?





Using (soft tissue) morphology for phylogeny reconstructions

Do you assume a ‘trait’ at clade level even if not all species of that clade have been measured?

TABLE 2. Morphological character^a matrix (a = 0 or 1; b = 1 or 2; ? = unknown; - = not applicable).

	1111111111222222223333333344444444
	123456789012345678901234567890123456789012345678
TRAGULIDAE	0001100000a000000000000000000-----1000100000a
ANTILOCAPRIDAE	01?112001110011121000a01100112001110?00110110010
GIRAFFIDAE	010a1210110010112111001a0011100000020a110111111
CERVIDAE	0110010011110111110a0101111111100011aa110111011
MOSCHIDAE	11?1120111a1011111001a1110110-----10110111011
BOVIDAE	0111120a110a0111b10aaa01aa111100100110a110111011

^aSoft anatomy: 1 = abdominal musk gland; 2 = ruminating stomach with four chambers (including a well-developed omasum); 3 = cardiac orifice of rumen more ventrally situated; 4 = gall bladder; 5 = ileocecal gland; 6 = placenta diffuse (0) or cotyledonary with few (1) or many (2) cotyledons; 7 = extensible tongue; 8 = females with four (0) or two (1) mammae. Postcranial: 9 = fibular facet on calcaneum with proximal concavity large, distal concavity small; 10 = astragalus



Using (soft tissue) morphology for phylogeny reconstructions

How do you treat unique traits that only occur in a single species?

(and do you follow the same principle for one-species clades and multi-species clades?)





Using (soft tissue) morphology for phylogeny reconstructions

How do you treat quantitative data?

(how do you ensure your process of threshold definition is not influenced by concepts of phylogeny?)



The Placental Mammal Ancestor and the Post-K-Pg Radiation of Placentals

8 FEBRUARY 2013 VOL 339 SCIENCE www.sciencemag.org

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John R. Wible,¹¹ Andrea L. Cirranello^{1,3}

Taxon \ Character	4529	4530	*Behavior - C
64 Rattus norvegicus	absent*	-	
65 Orycteropus afer	present*	1-100 CH4 (methane) nmol/g/h MEAN*	faunivory
66 Equus caballus	present*	101-200	herb
67 Sus scrofa	present*	1-100 CH4 (methane) nmol/g/h MEAN*	
68 Tursiops truncatus	absent*	-	faunivory
69 Hippopotamus amphibius	present*	?	herb
70 *Lama glama	?	?	herb
71 Bos taurus	present*	201-300*	herb

Hackstein and Alen, 1996

[t.65 c.4530 s.0] Metabolism - Methanogenesis quantity: (0)* 1-100 CH4 (methane) nmol/g/h MEAN; (1) 101-200; (2) 201-300; (3) 301-400, (4) 401-500;



Using (soft tissue) morphology for phylogeny reconstructions

How do you make sure you do not code for the same (complex) trait over and over again by coding its many different morphological/physiological details?



Using (soft tissue) morphology for phylogeny reconstructions

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John R. Wible,¹³ Andrea L. Cirranello^{3,†}

We included characters that met the definition of logical independence (98).

Using (soft tissue) morphology for phylogeny reconstructions

How do you make sure you do not code for the same (complex) trait over and over again by coding its many different morphological/physiological details?

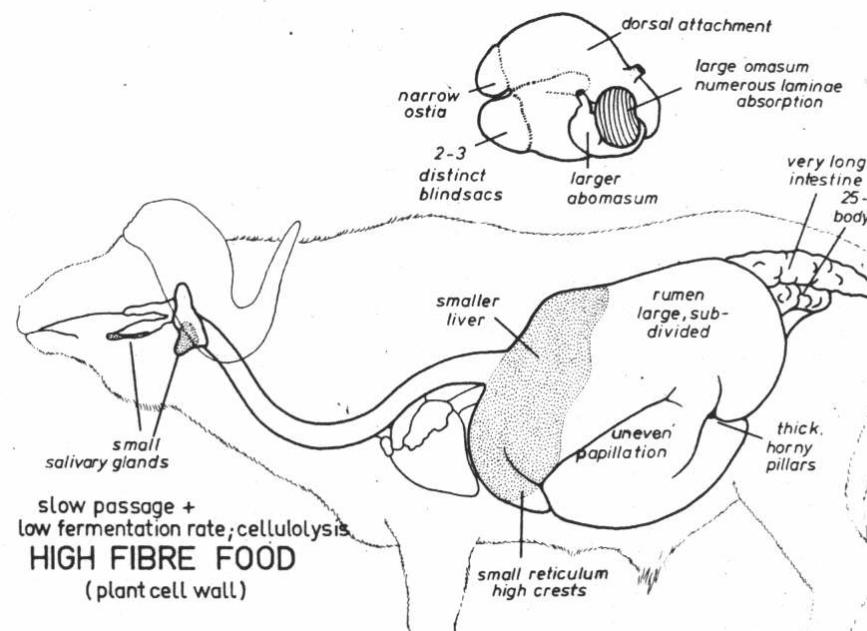


Fig. 1: The African buffalo, a non-selective roughage grazer.

from Hofmann (1989)

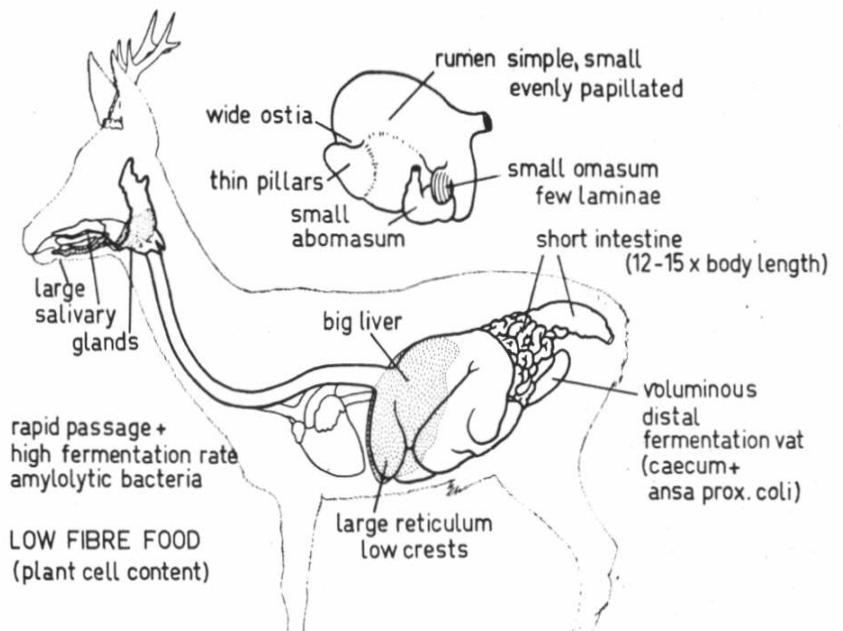


Fig. 2: The roe deer, a concentrate selector.



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I [] ? [] [] []	Taxon \ Character	4529	4530	*Behavior - D
		*Metabolism – Methanogenesis presence	*Metabolism – Methanogenesis quantity	
	64 <i>Rattus norvegicus</i>	absent*	–	
	65 <i>Orycteropus afer</i>	present*	1–100 CH ₄ (methane) nmol/g/h MEAN*	faunivory
	66 <i>Equus caballus</i>	present*	101–200	herb
	67 <i>Sus scrofa</i>	present*	1–100 CH ₄ (methane) nmol/g/h MEAN*	
	68 <i>Tursiops truncatus</i>	absent*	–	faunivory
	69 <i>Hippopotamus amphibius</i>	present*	?	herb
	70 * <i>Lama glama</i>	?	?	herb
	71 <i>Bos taurus</i>	present*	201–300*	herb

Hackstein and Alen, 1996

[t.65 c.4530 s.0] Metabolism – Methanogenesis quantity: (0)* 1–100 CH₄ (methane) nmol/g/h MEAN; (1) 101–200; (2) 201–300; (3) 301–400; (4) 401–500;



The Placental Mammal Ancestor and the Post-K-Pg Radiation of Placentals

8 FEBRUARY 2013 VOL 339 SCIENCE www.sciencemag.org

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John R. Wible,¹¹ Andrea L. Cirranello^{1,3}

I Taxon \ Character	Taxon \ Character	4534	4530	
			*Behavior - Chews the cud	*Metabolism - Methanogenesis quantity
	64 Rattus	64 Rattus norvegicus	absent	-
	65 Orycte	65 Orycteropus afer	-*	1-100 CH4 (methane) nmol/g/h MEAN*
	66 Equu	66 Equus caballus	absent*	101-200
	67 Sus scro	67 Sus scrofa	absent*	1-100 CH4 (methane) nmol/g/h MEAN*
	68 Tursiop	68 Tursiops truncatus	-*	-
	69 Hippop	69 Hippopotamus amphibius	absent	?
	*Lama	*Lama glama	present	?
	71 Bos tau	71 Bos taurus	present	201-300*

Hackstein and Alen, 1996

[t.65 c.4530 s.0] Metabolism - Methanogenesis quantity: (0)* 1-100 CH4 (methane) nmol/g/h MEAN; (1) 101-200; (2) 201-300; (3) 301-400; (4) 401-500;



Using (soft tissue) morphology for phylogeny reconstructions

How do you make sure you do not code for body size over and over again?



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Taxon \ Character	4287 *Development - Gestation time
64 <i>Rattus norvegicus</i>	1 month or less
65 <i>Orycteropus afer</i>	7 to 8 months*
66 <i>Equus caballus</i>	10 to 12 months*
67 <i>Sus scrofa</i>	3 to 4 months*
68 <i>Tursiops truncatus</i>	10 to 12 months/12 to 14 months*
69 <i>Hippopotamus amphibius</i>	7 to 8 months*
70 * <i>Lama glama</i>	10 to 12 months*
71 <i>Bos taurus</i>	8 to 9 months*



Using (soft tissue) morphology for phylogeny reconstructions

Is the character you are coding appropriate for the taxonomic level you are aiming at?

(and on what criteria do you base *that* decision?)



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Project 352: Bärmann, E.V.

Towards a comprehensive phylogeny of
Bovidae, Chapter 2: A total evidence
analysis of bovid phylogeny - Dissertation
by Eva Bärmann, University of Cambridge
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Taxon \ Character		15	16	17
1	Addax nasomaculatus	absent	absent	absent*
2	Aepyceros melampus	present	absent	present
3	Alcelaphus buselaphus	absent	absent	absent
4	Ammendorcas clarkei	present	absent	present
5	Antilope cervicapra	present	absent*	present*
6	Antidorcas marsupialis	present	absent	present



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Taxon \ Character	15	16	17
	white stripe over eye	white vertical stripes	white rump patch
1 <i>Addax nasomaculatus</i>	absent	absent	absent*
2 <i>Aepyceros melampus</i>	present	absent	present

Taxon \ Character	23	24	25	26	27
	number of offspring (per breeding attempt)	behaviour of young	stotting	standing on hind feet to reach vegetation	adapted to arid environment
1 <i>Addax nasomaculatus</i>	usually one calf	laying out for at least 2 weeks	absent	absent	yes, no permanent water access necessary
2 <i>Aepyceros melampus</i>	usually one calf	start following mother within a few days after birth	absent	absent*	no, need water on a regular basis*
3 <i>Alcelaphus buselaphus</i>	usually one calf	laying out for at least 2 weeks	present	absent	no, need water on a regular basis*
4 <i>Ammodorcas clarkei</i>	usually one calf	laying out for at least 2 weeks	absent	regularly feeding on hind feet	yes, no permanent water access necessary
5 <i>Antidorcas marsupialis</i>	usually one calf	laying out for at least 2 weeks	present	occasionally	yes, no permanent water access necessary
6 <i>Antilope cervicapra</i>	usually one calf*	laying out for at least 2 weeks	present	absent*	?
7 <i>Boselaphus tragocamelus</i>	one or two calves	laying out for at least 2 weeks	absent	occasionally	yes, no permanent water access necessary
8 <i>Capra falconeri</i>	one or two calves	start following mother within a few days after birth	absent	occasionally	no, need water on a regular basis
9 <i>*Cephalophus rufilatus</i>	usually one calf	laying out for at least 2 weeks	absent	absent	no, need water on a regular basis



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Taxon \ Character	4531	4532	4533
Behavior - Diet	*Behavior - Faunivory type	*Behavior - Herbivory type	
64 <i>Rattus norvegicus</i>	omnivory	(general insectivory)/aquatic macroinvertebrates/fish (piscivory)/vertebrates	-*
65 <i>Orycteropus afer</i>	faunivory (includes insectivory, carnivory, and sanguivory)*	ants and/or termites (myrmecophagy)*	-
66 <i>Equus caballus</i>	herbivory (includes frugivory, nectarivory, folivory)	-	folivory
67 <i>Sus scrofa</i>	omnivory*	diverse arthropods (general insectivory)/vertebrate prey (carnivory)*	-
68 <i>Tursiops truncatus</i>	faunivory (includes insectivory, carnivory, and sanguivory)*	aquatic macroinvertebrates/fish (piscivory)*	-
69 <i>Hippopotamus amphibius</i>	herbivory (includes frugivory, nectarivory, folivory)	-	folivory
70 * <i>Lama glama</i>	herbivory (includes frugivory, nectarivory, folivory)	-	folivory
71 <i>Bos taurus</i>	herbivory (includes frugivory, nectarivory, folivory)	-	folivory



Using (soft tissue) morphology for phylogeny reconstructions

... and maybe the most hopeful question:

Do datasets exist one can easily include in a phylogenetic analysis?

(and if they do, what are your quality criteria for using them?)



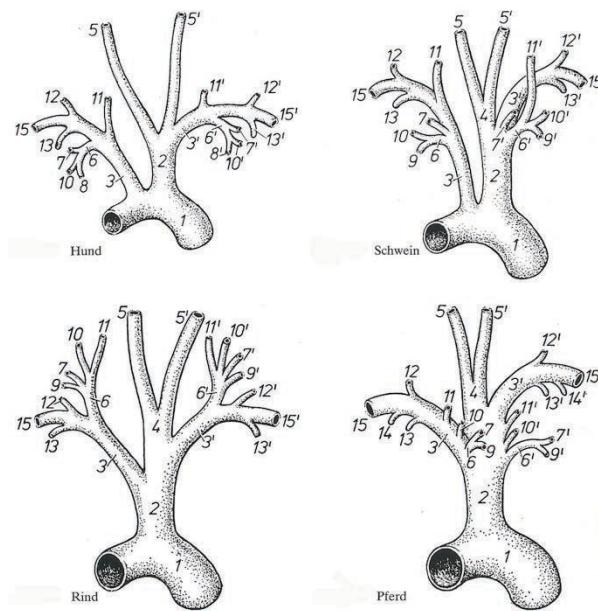
Typical soft tissue morphology for phylogenetic studies

Shape (as opposed to volume/mass, area or length) that is unrelated to a specific function

Typical soft tissue morphology for phylogenetic studies

Shape (as opposed to volume/mass, area or length) that is unrelated to a specific function

Branching patterns of vessels/ducts



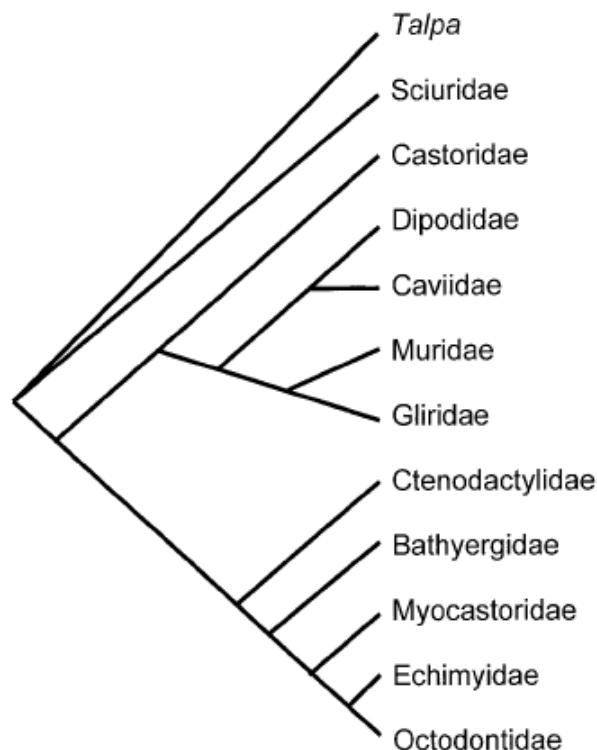
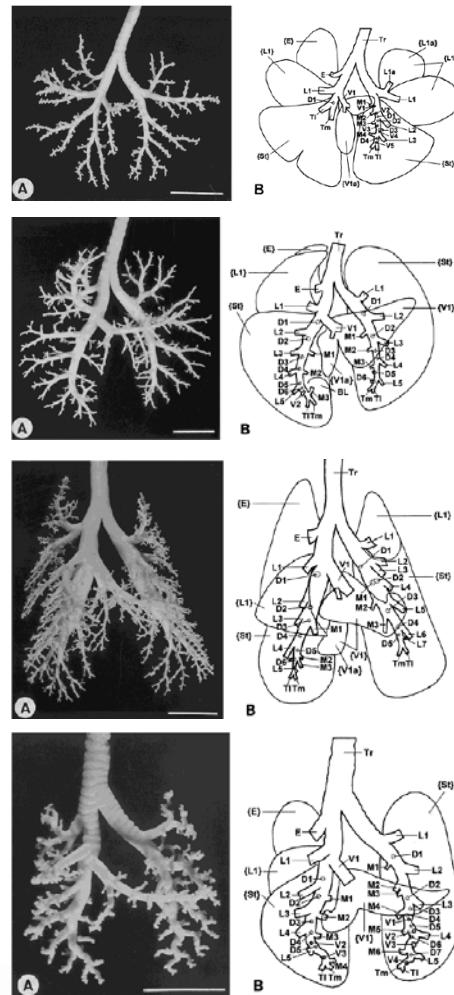
from Nickel et al. (2004)



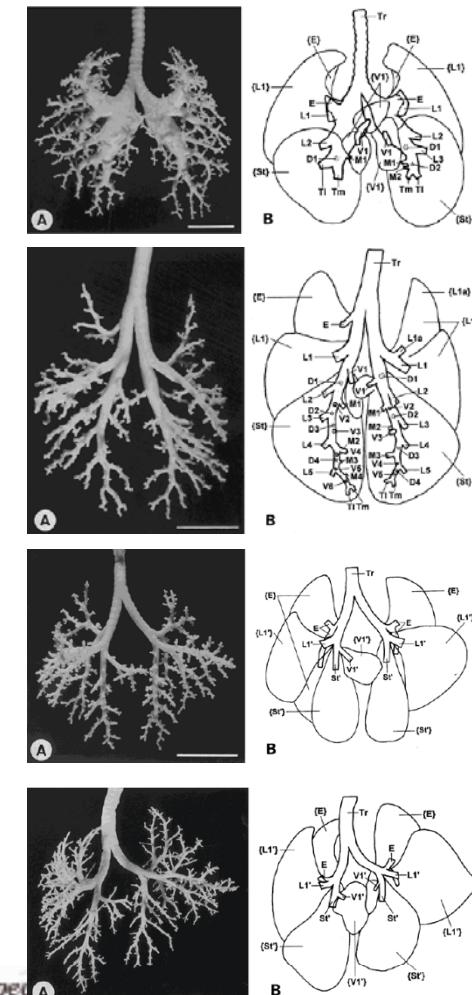
Lung Morphology in Rodents (Mammalia, Rodentia) and Its Implications for Systematics

Bernd R. Wallau,* Anke Schmitz, and Steven F. Perry

JOURNAL OF MORPHOLOGY 246:228–248 (2000)



Lung character values of 40 rodent and five nonrodent species

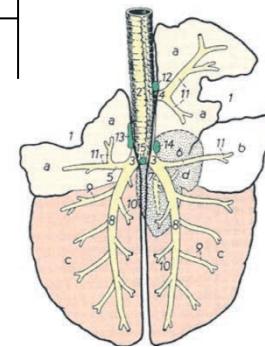
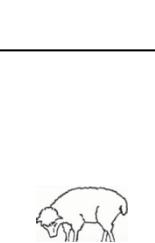
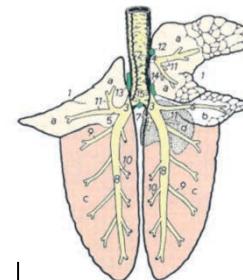
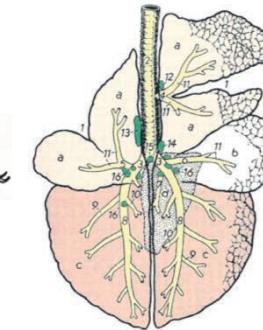
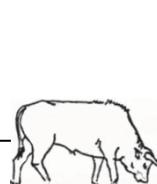
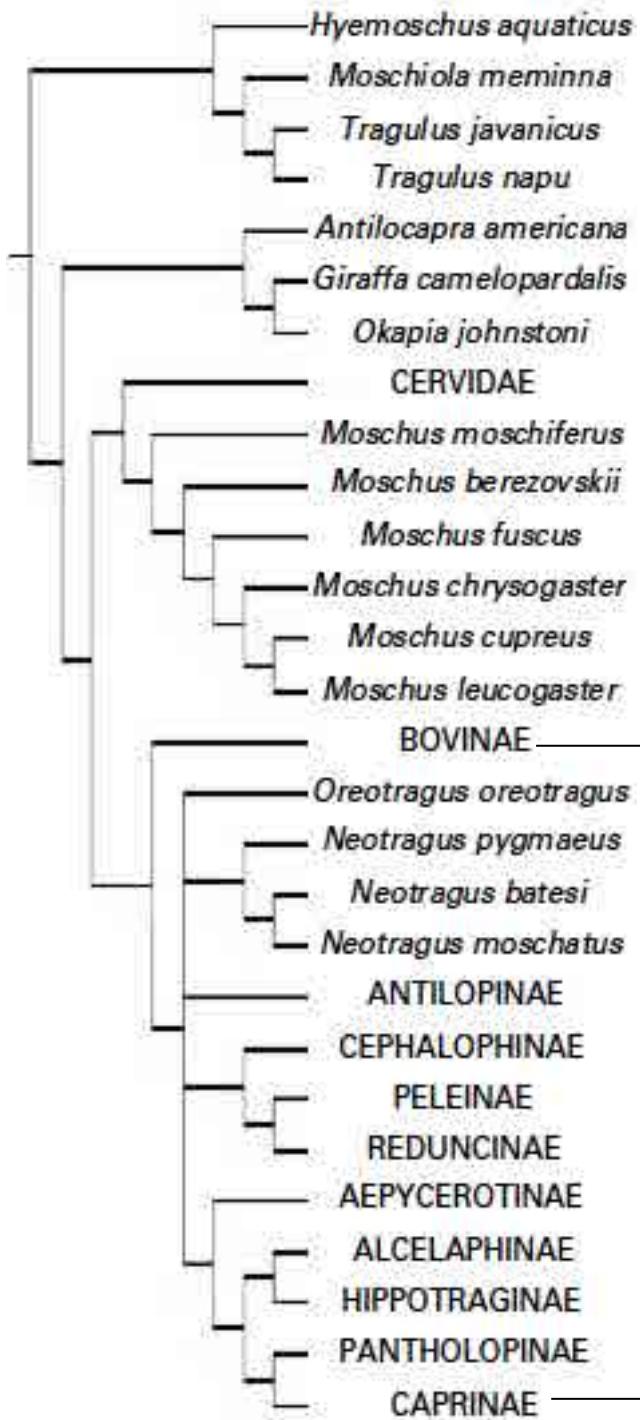


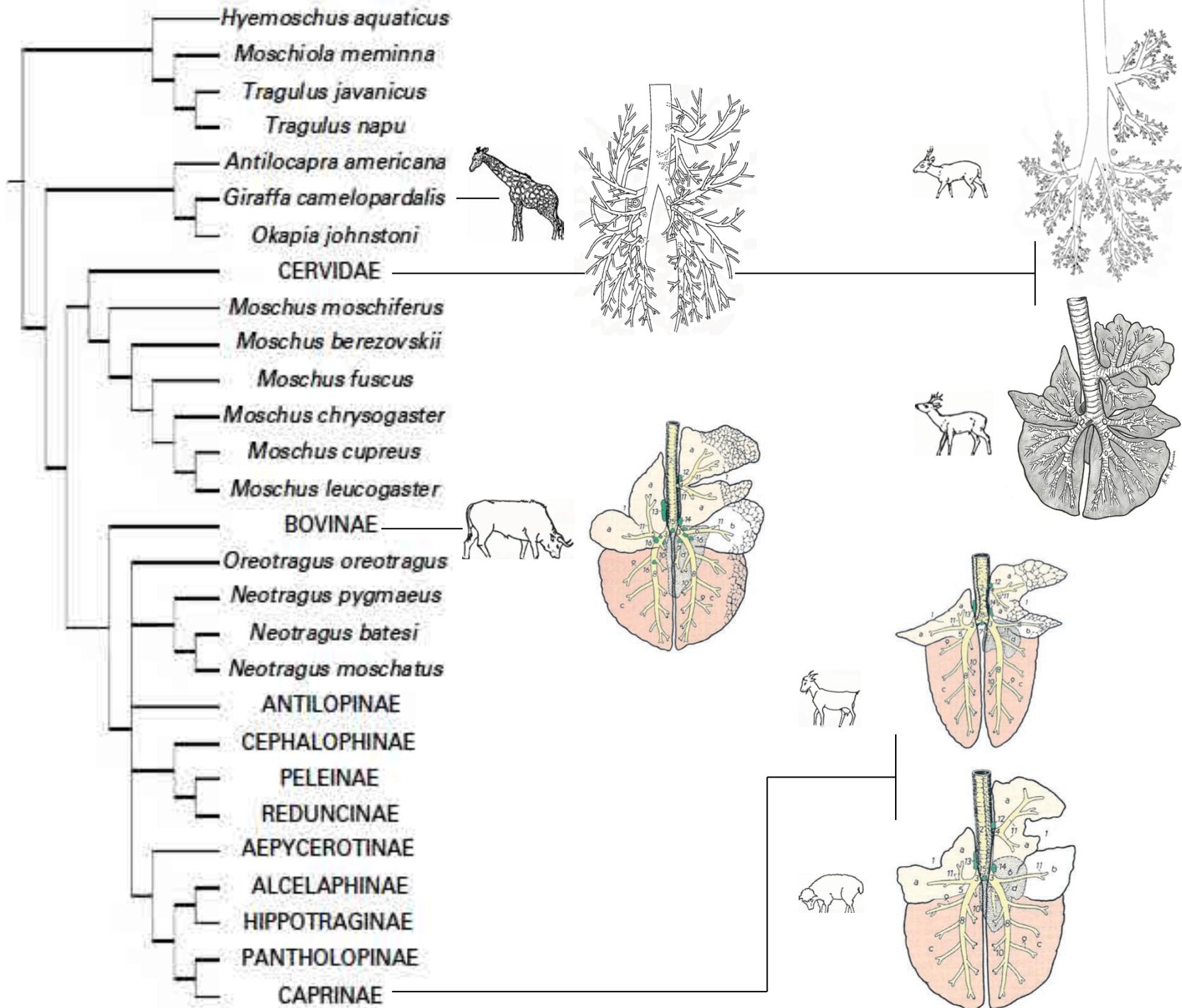
Rodent species	1 N	2 rEL	3 rLL	3a rVL	4 rVd	5 rBL	IEL	6 ILL	7 IVL	8 RC	9 rEB	10 IEB	11 rNL	12 rND	13 rNM	14 rNV	15 rNR									
<i>Acomys rosatus levisi</i>	1	1	1	1	0	1	0	0	0	0	1	1	0	1	5	5	4	4	3	3	1	1	1	13	13	13
<i>Alticola barakshin</i>	1	1	1	1	1	1	0	0	0	0	1	1	0	1	5	5	5	5	2	2	2	2	2	14	14	14



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Lung







Sources (lungs)

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Nickel R, Schummer A, Seiferle E (2004) Lehrbuch der Anatomie der Haustiere. Band II: Eingeweide. Parey, Stuttgart (Domestic ruminants)



Typical soft tissue morphology for phylogenetic studies

Shape can be a function of body mass

Typical soft tissue morphology for phylogenetic studies

Shape can be a function of body mass

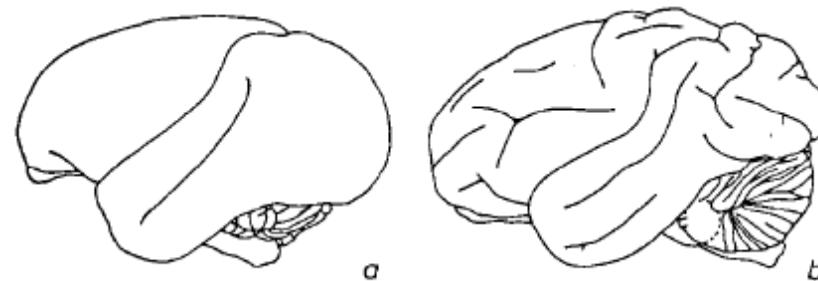


Abb. 4. Lateralansichten der Gehirne von Neuweltaffen (Familie Cebidae). a *Saimiri sciureus* (KM 540 g), b *Ateles* spec. (KM 6000 g). Der unterschiedliche Furchungsgrad der Vorderhirne ist wesentlich durch die verschiedene Körpermasse der beiden Arten bedingt
(aus BRAUER & SCHOBER, 1970).

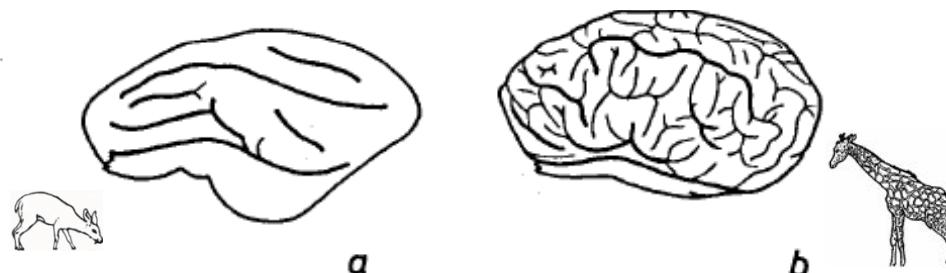


Abb. 21. Lateralansichten der Vorderhirne von a) Moschustier und b) Giraffe (aus KLATT, 1954). Das ursprüngliche, längsorientierte Furchenmuster (a) wird mit zunehmender Körpermasse und Cerebralisation kompliziert und damit deutlicher (b).

from Hackethal (1981)



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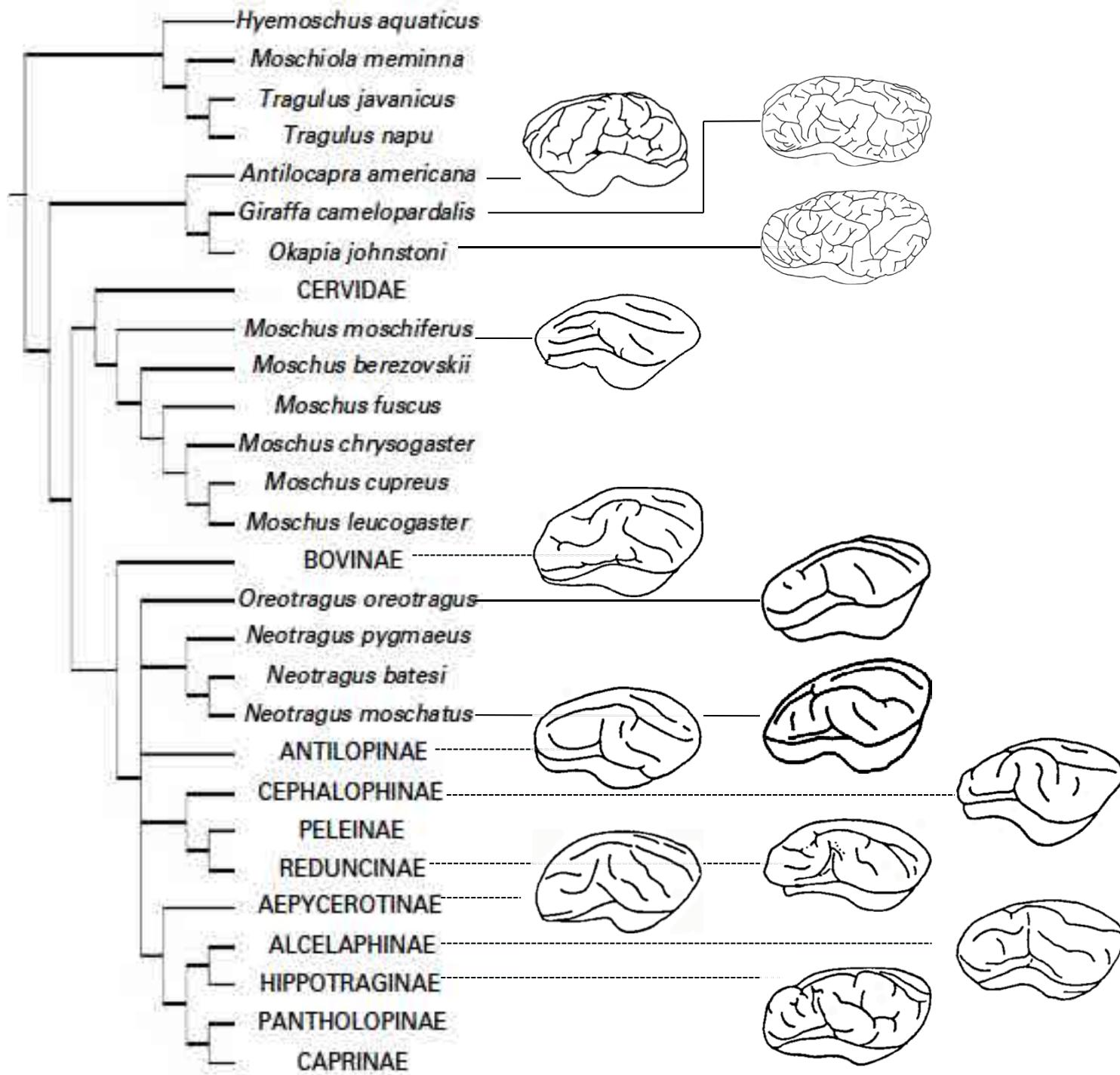
Brain

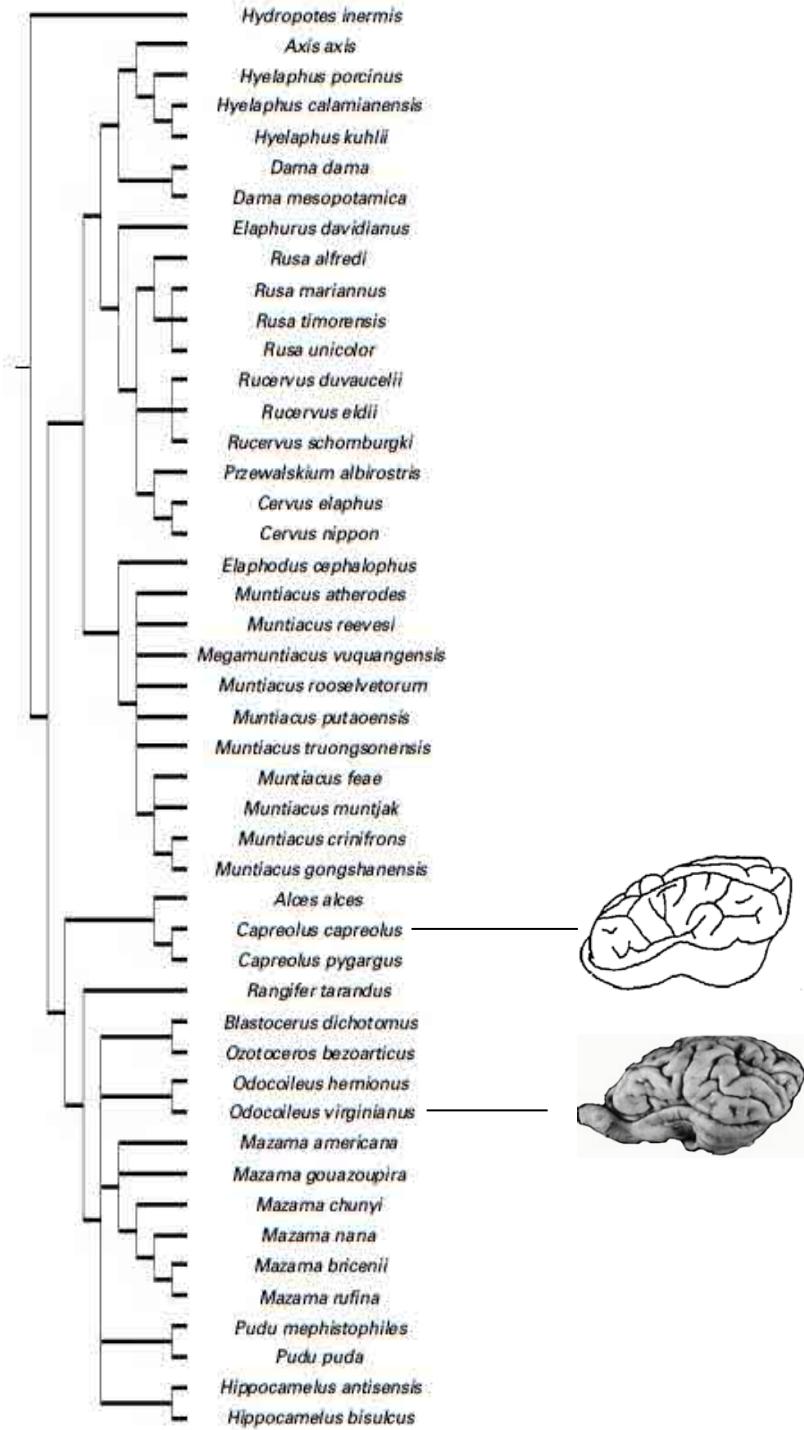
Brain Behav. Evol. 22: 60-69 (1983)

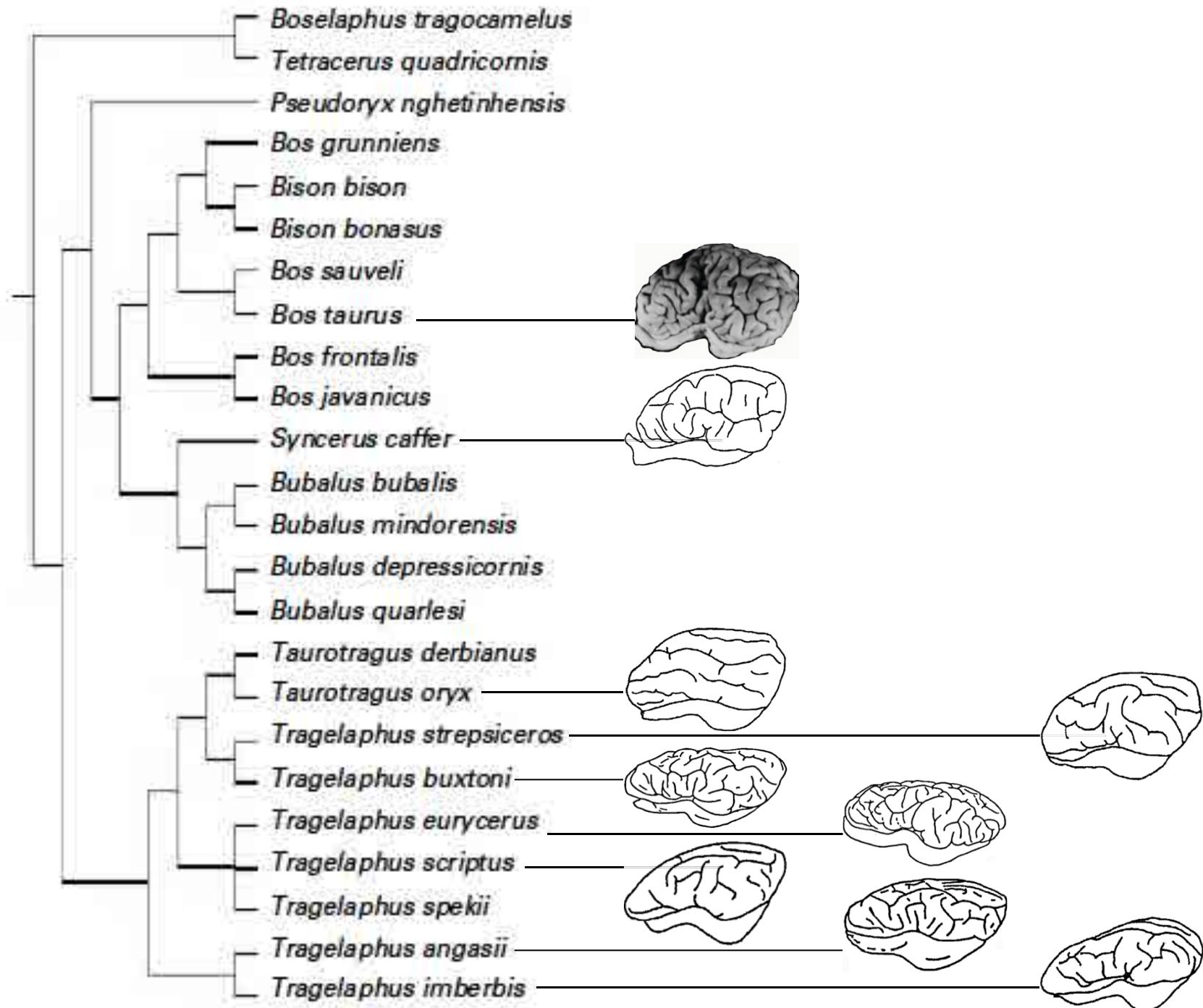
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0006-8977/83/0221-0060 \$ 2.75/0

Phylogeny through Brain Traits: Trees Generated by Neural Characters

John A. W. Kirsch^a, John Irwin Johnson^b

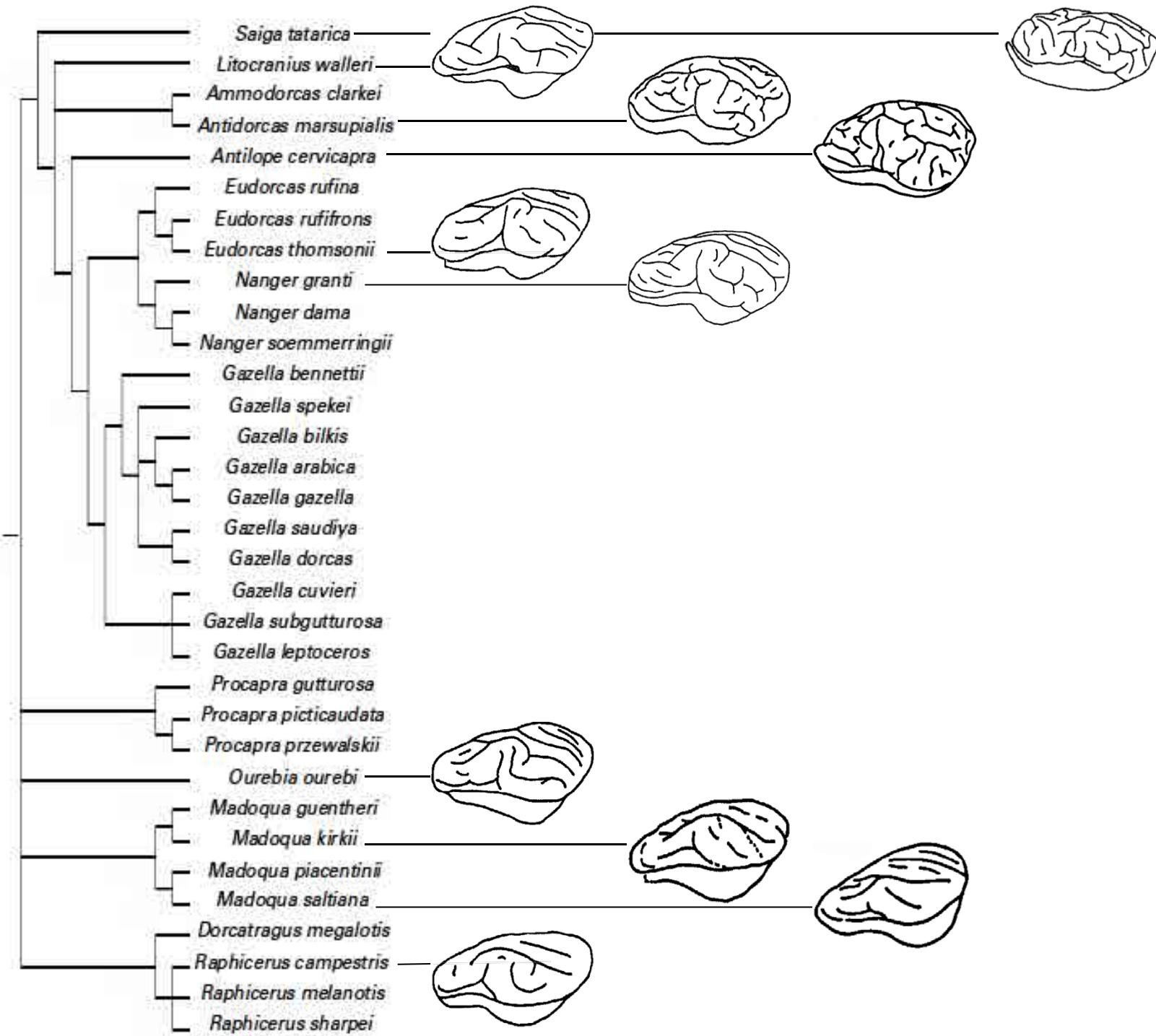


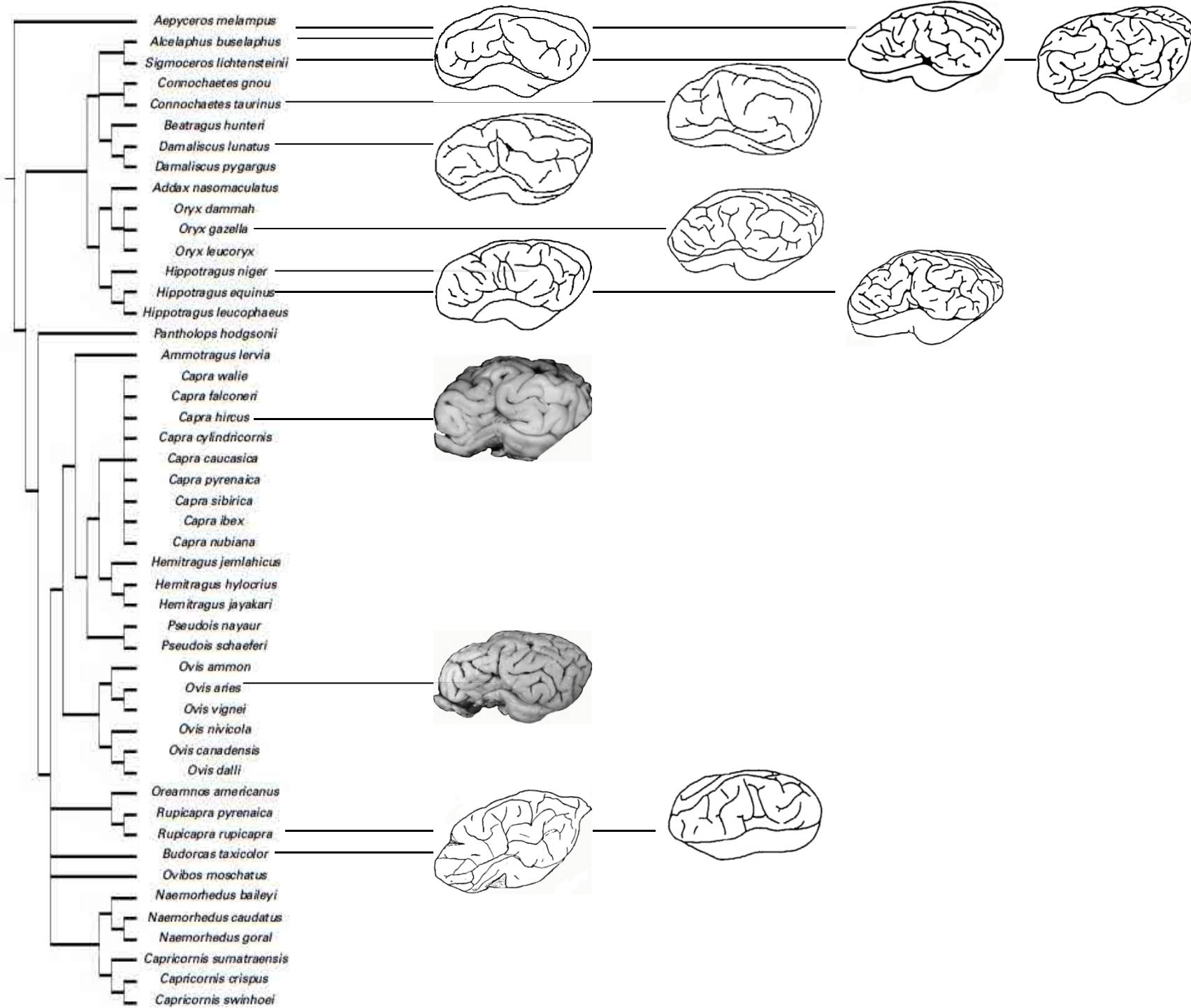


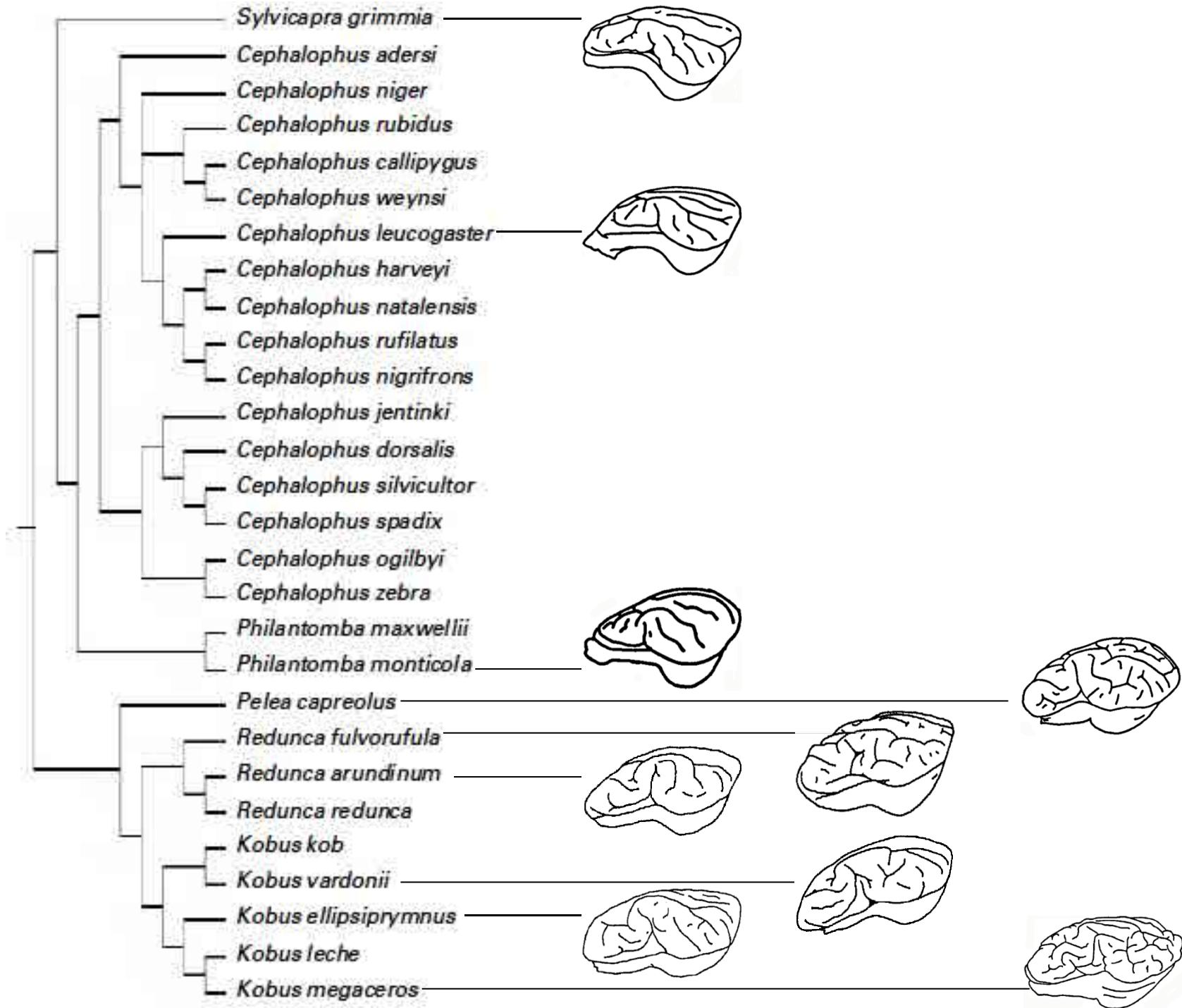




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Sources (brain)

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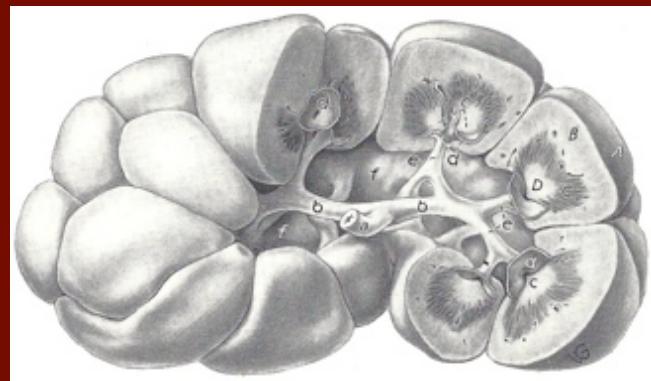
Ronnefeld U (1970) Morphologische und quantitative Neocortexuntersuchungen bei Boviden, ein Beitrag zur Phylogenie dieser Familie. I. Formen mittlerer Grösse (25-75 kg). Morphologisches Jahrbuch 115:165-230

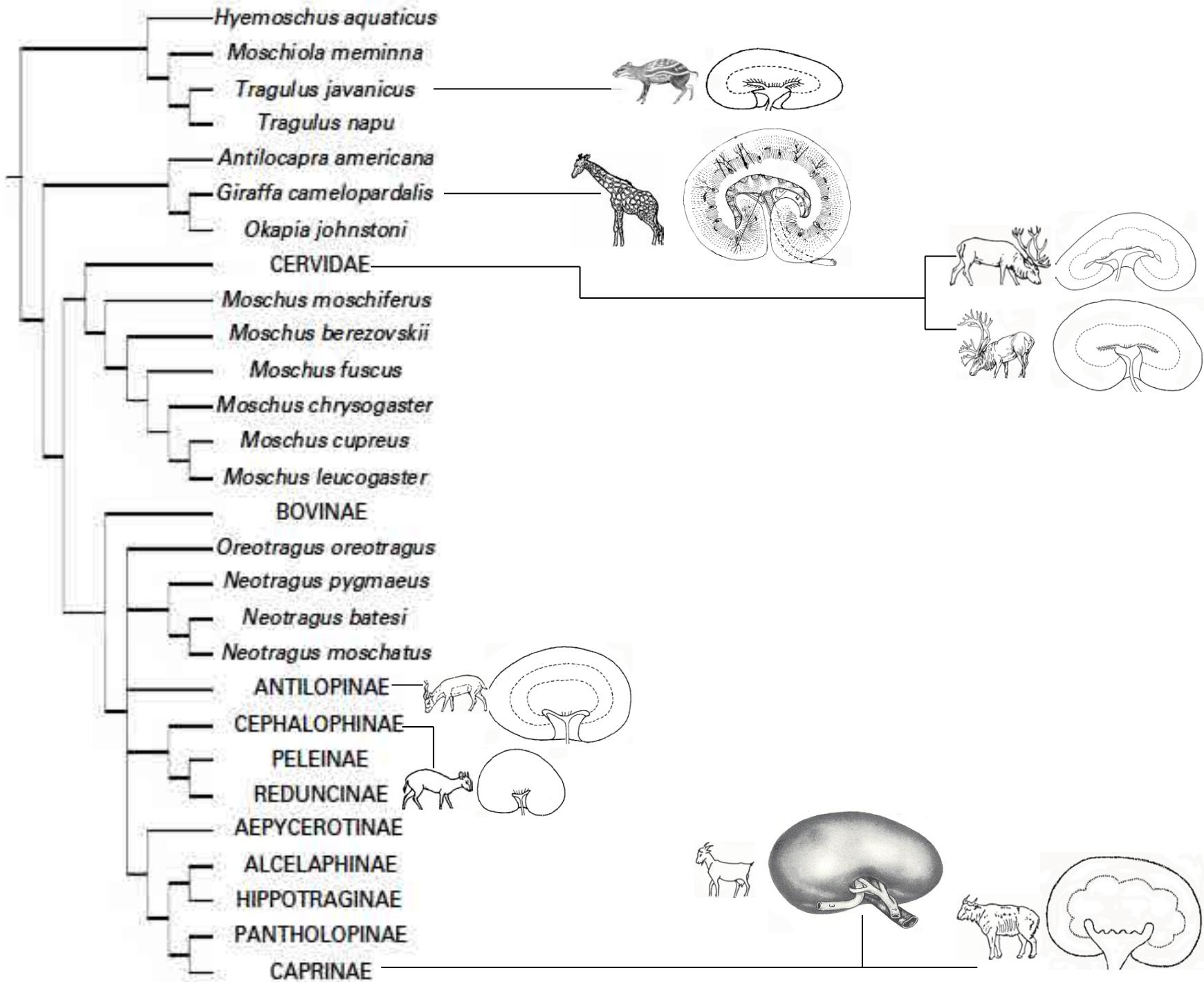
von Tyszka H (1966) Das Grosshirnfurchenbild als Merkmal der Evolution. Untersuchungen an Boviden I. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 63:121-158

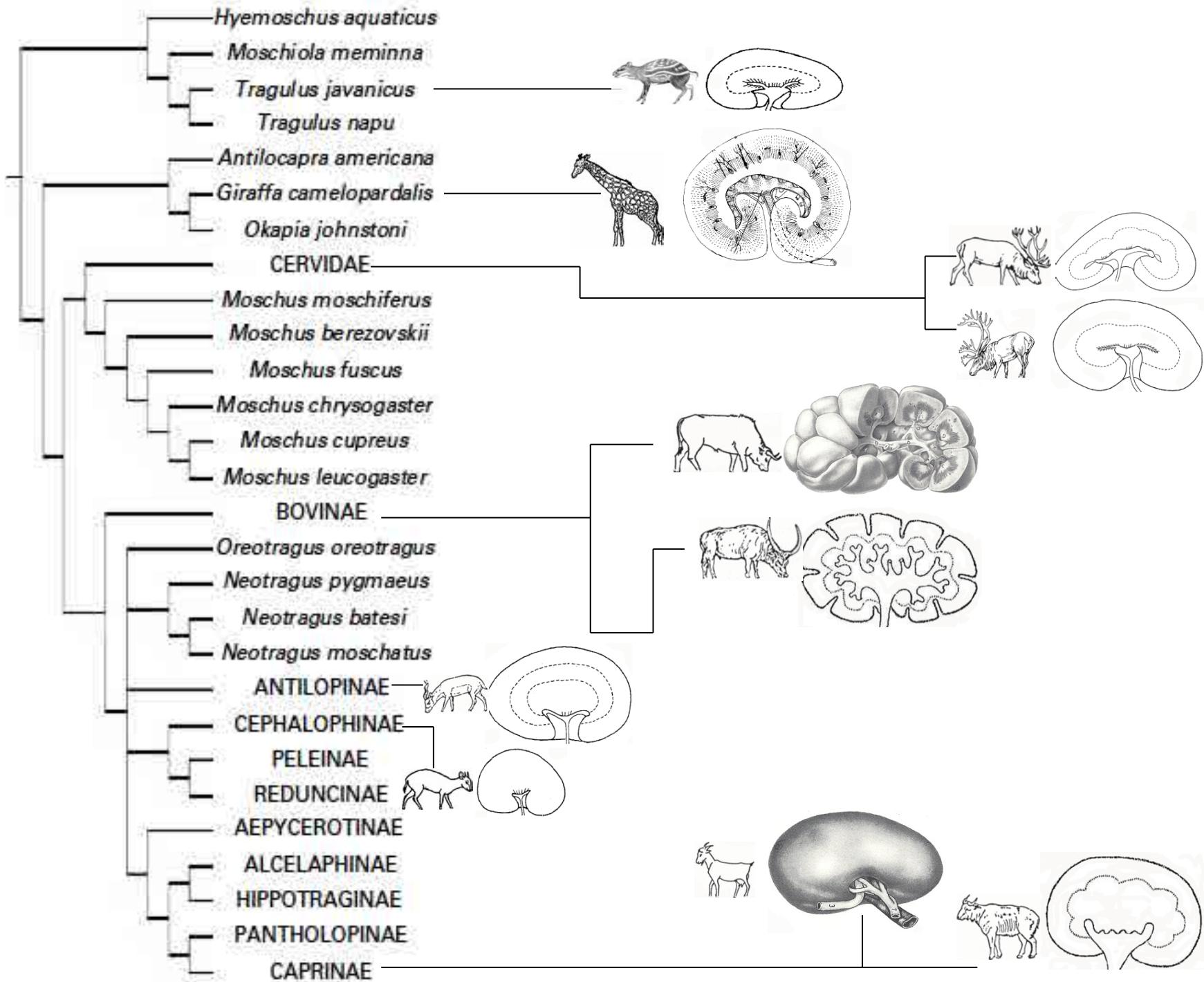


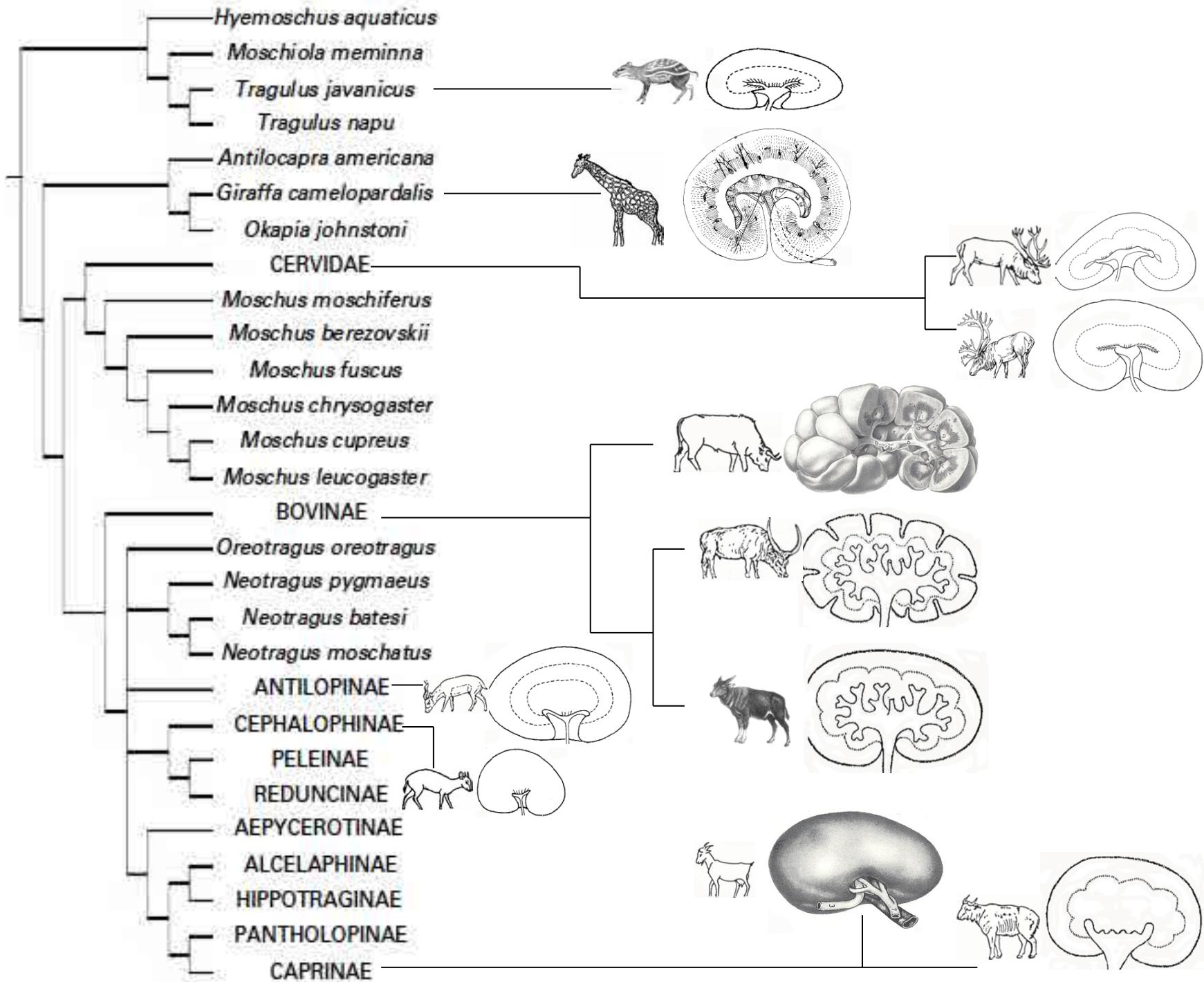
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Kidney











Sources (kidney)

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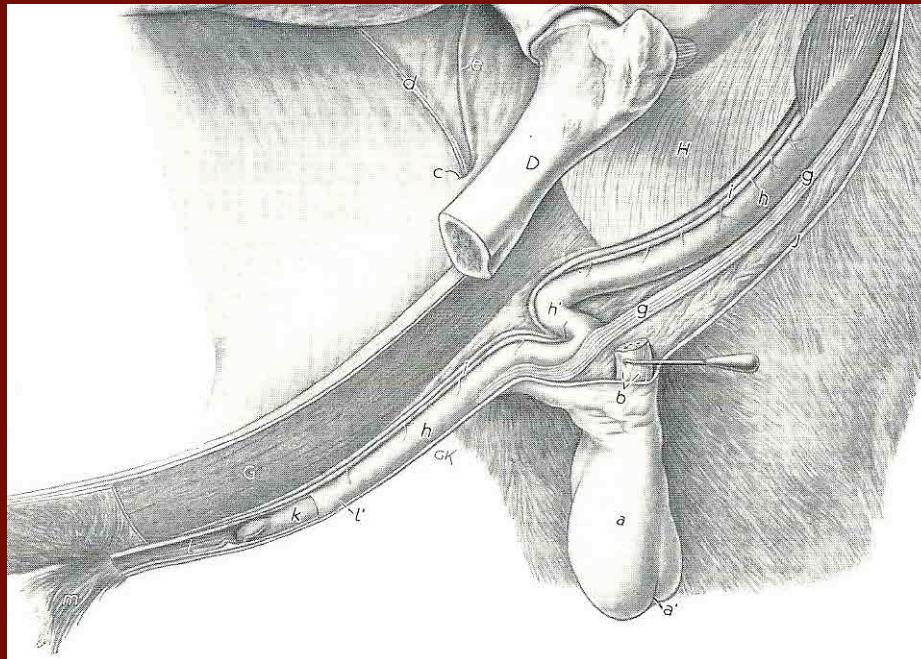
Sperber I (1944) Studies on the mammalian kidney. Zoologiska Bidrag, Uppsala 22:249-431 (*Tragulus javanicus*, *Cervus elaphus*, *Rangifer tarandus*, *Antilope cervicapra*, *Cephalophus* sp., *Bubalus depressicornis*)

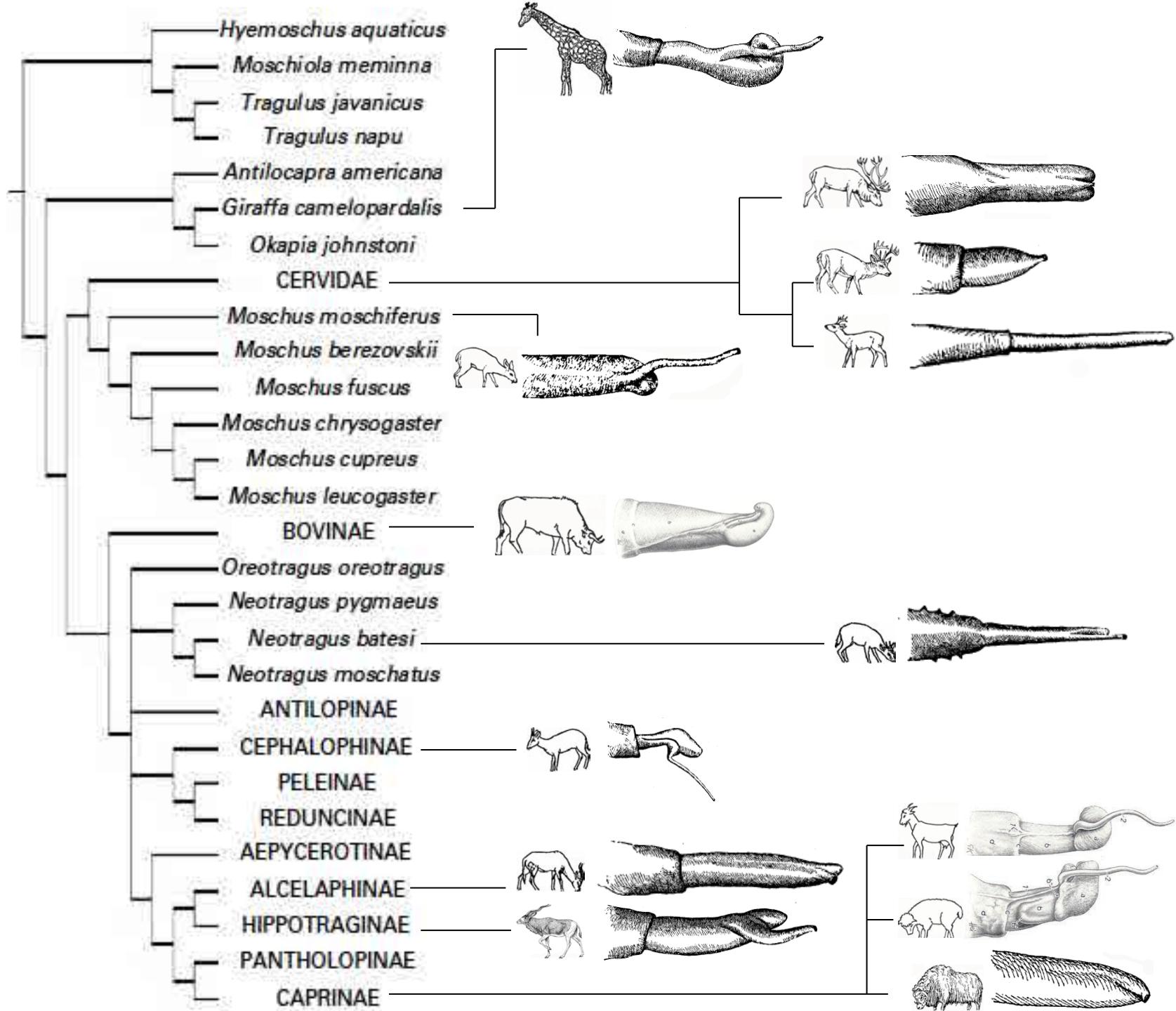
Yi Z, Ping D, Qijun W, Zhanyun W, Jiguang Y (1987) An anatomical classification of kidneys in mammals. Acta Anatomica Sinica 18:353-359 (*Bubalus depressicornis*, *Budorcas taxicolor*)



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Penis







Sources (penis)

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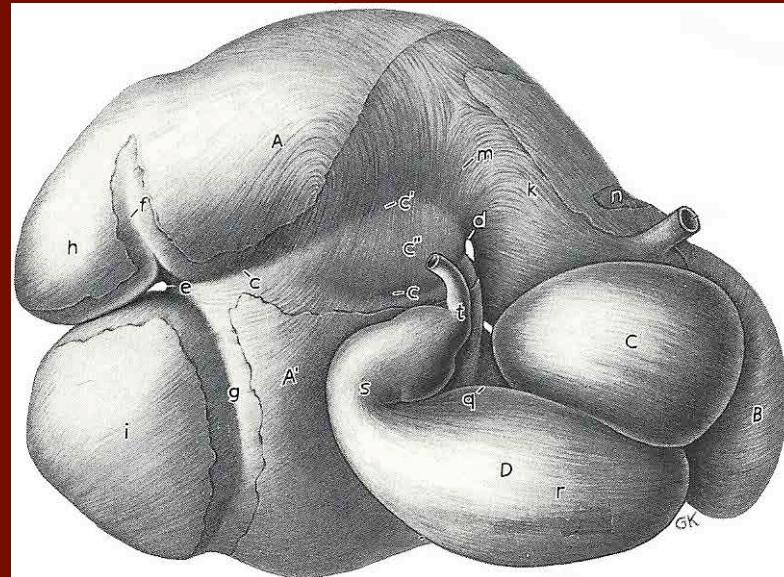
Nickel R, Schummer A, Seiferle E (2004) Lehrbuch der Anatomie der Haustiere. Band II: Eingeweide. Parey, Stuttgart (Domestic ruminants)

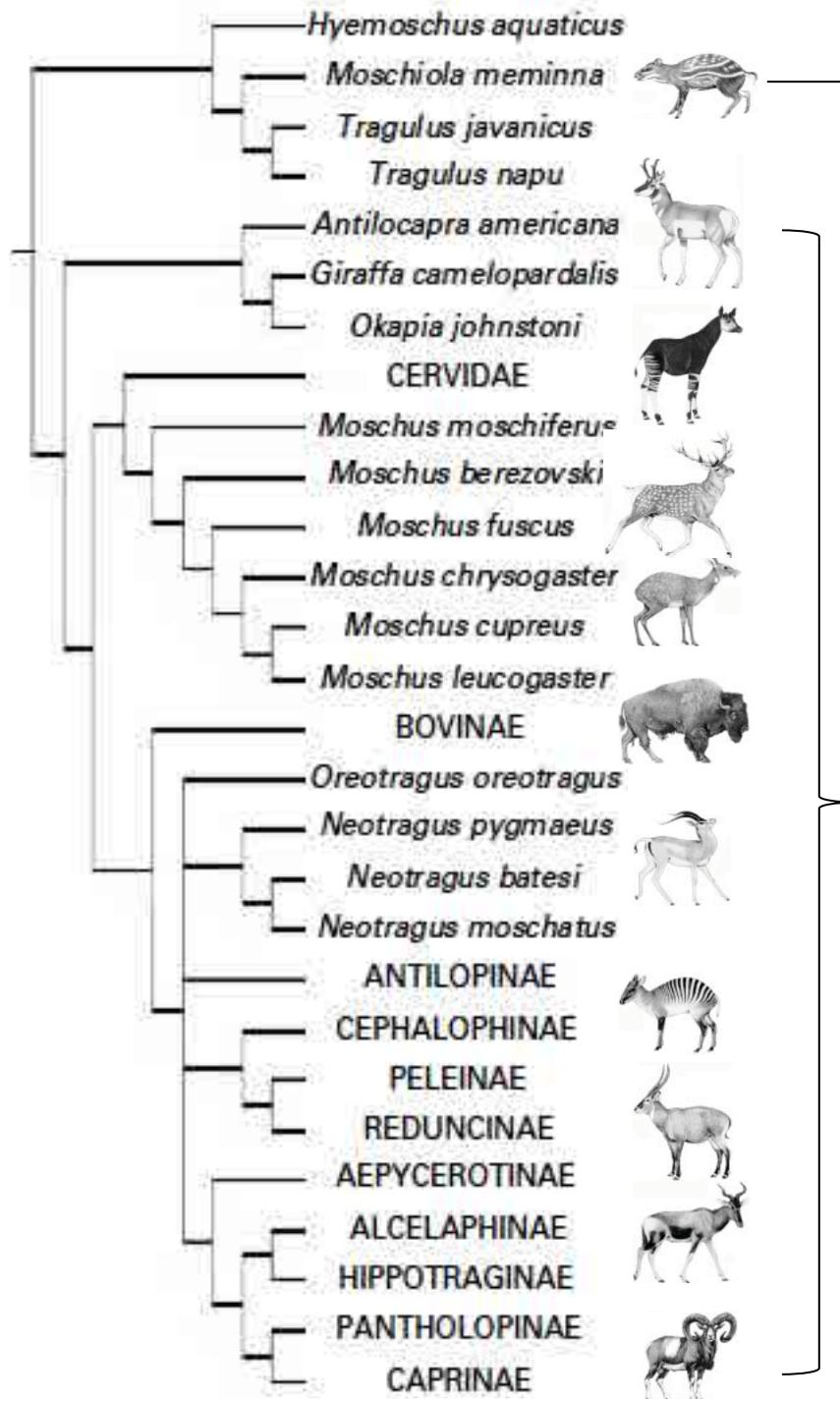
someone mentioned an old Pocock paper on this I overlooked

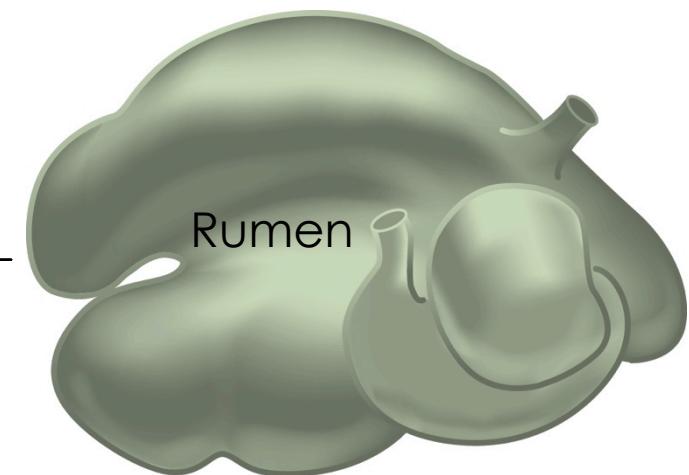
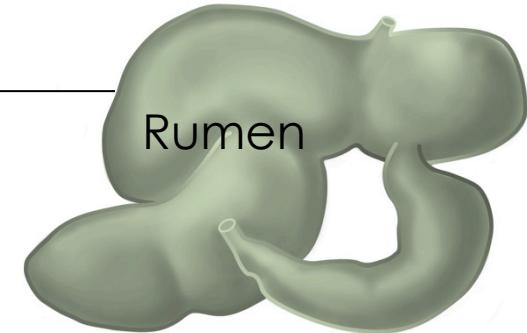
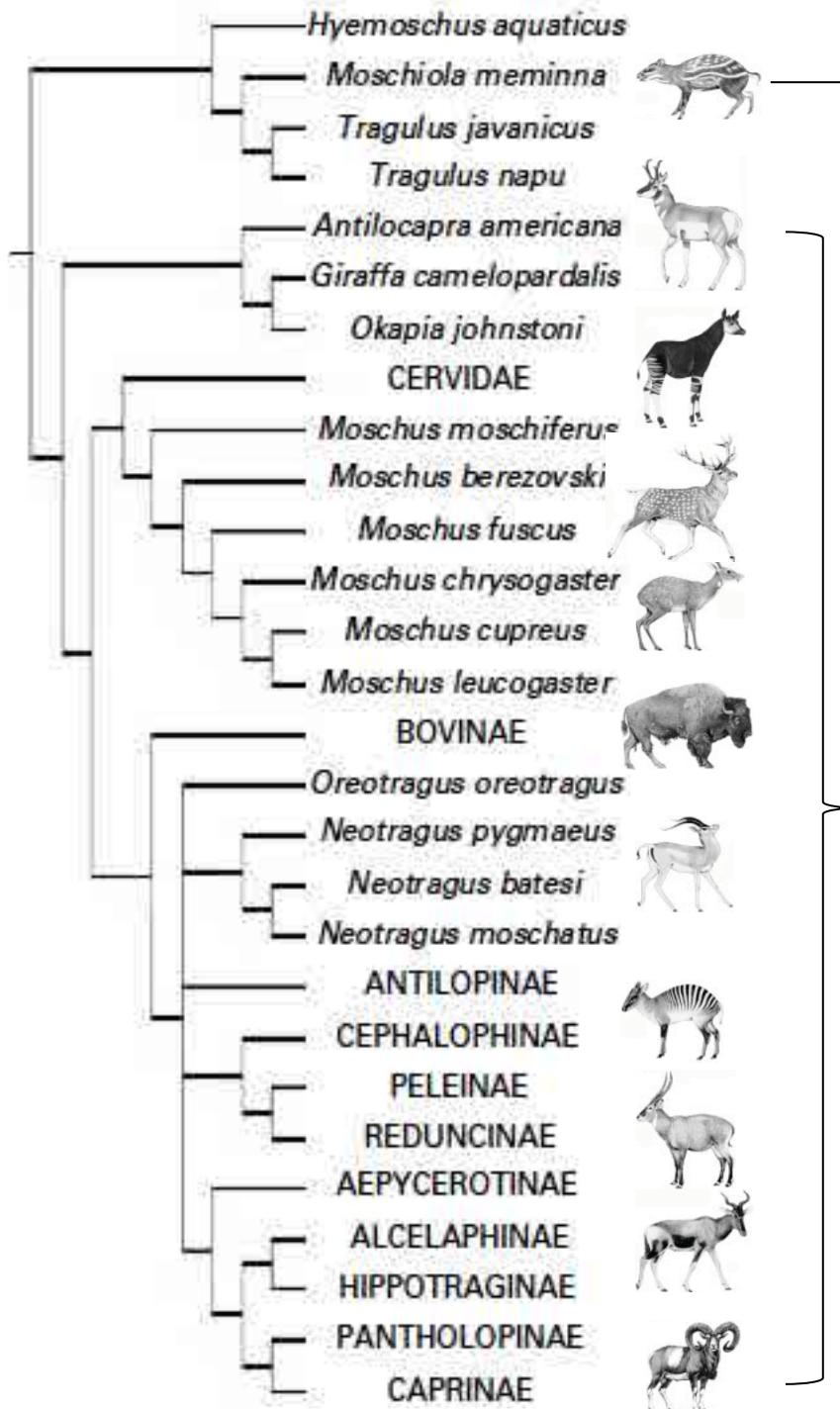


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Forestomach

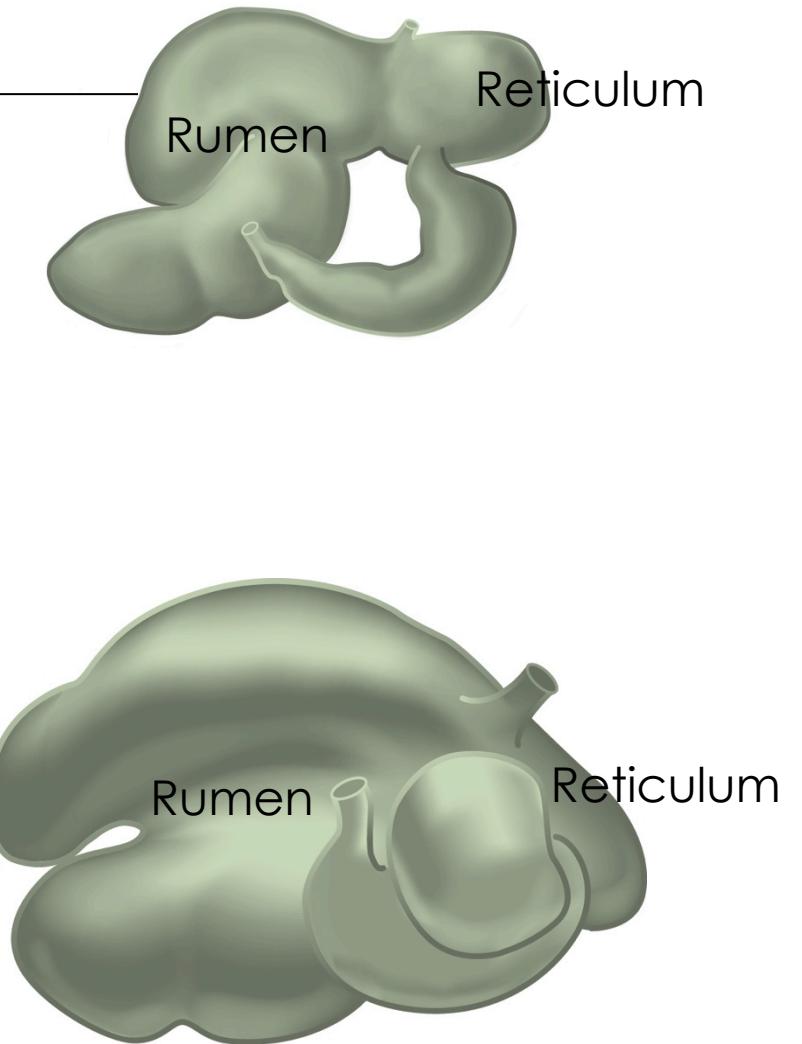
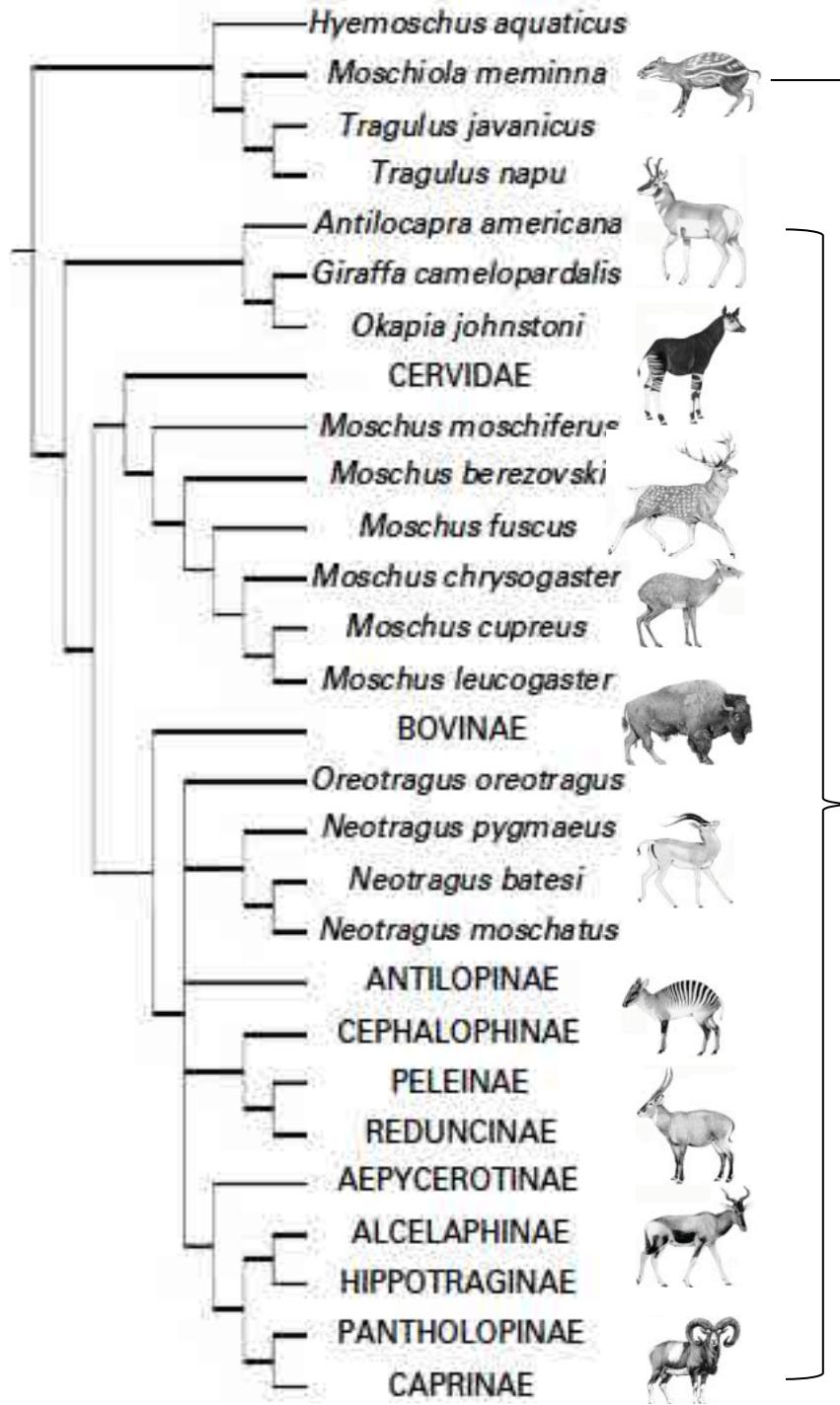


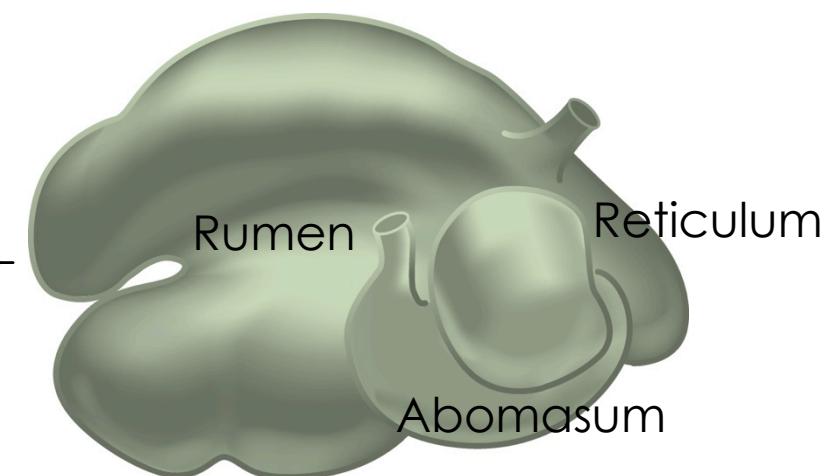
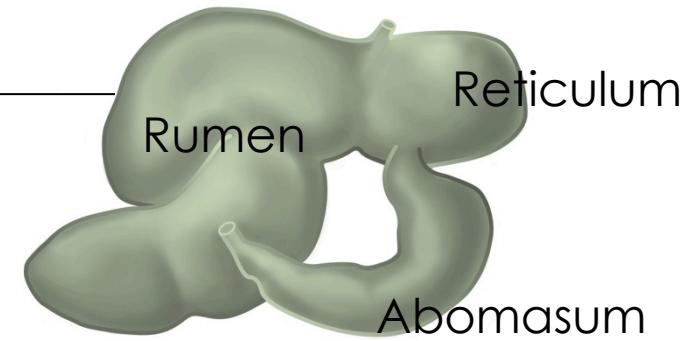
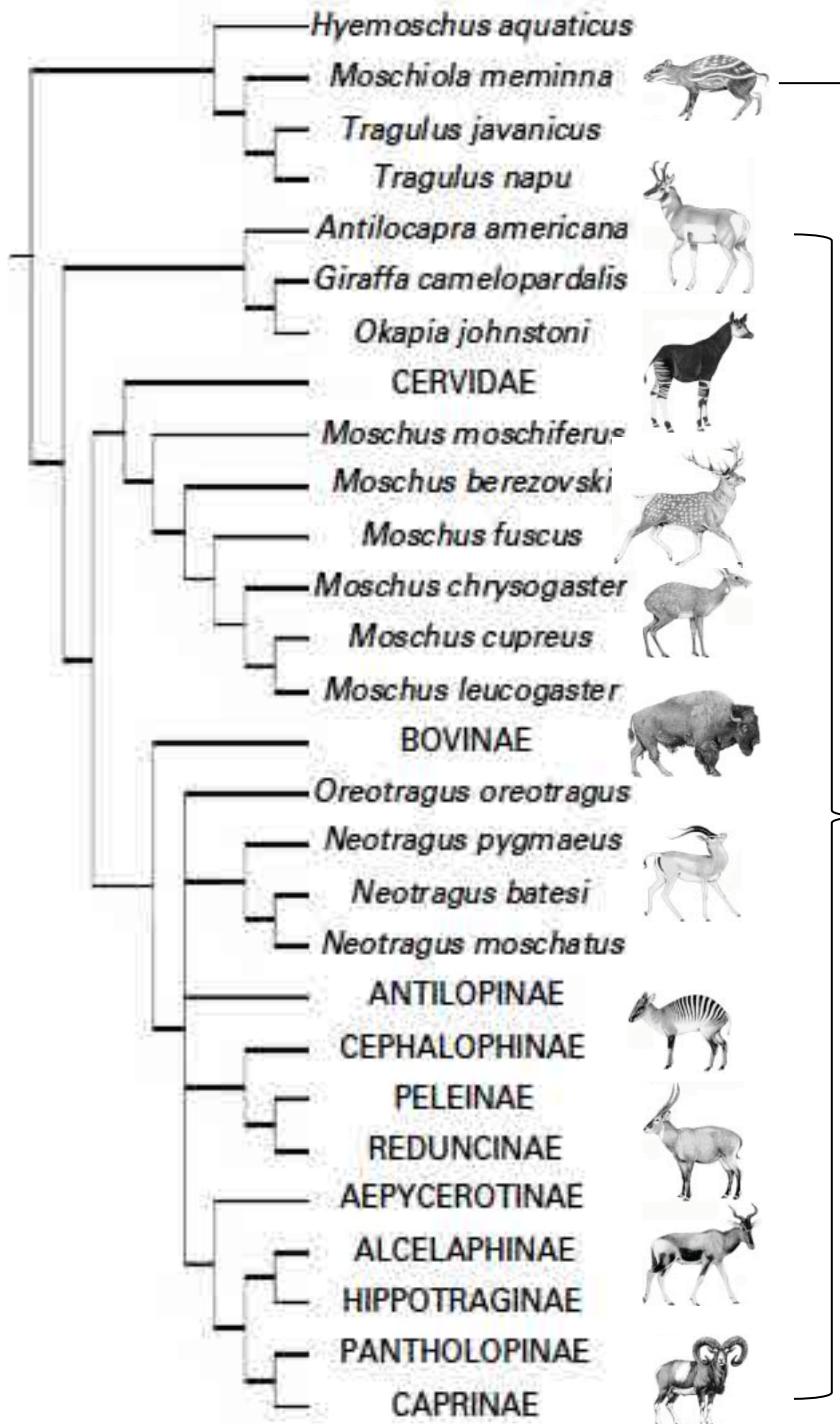


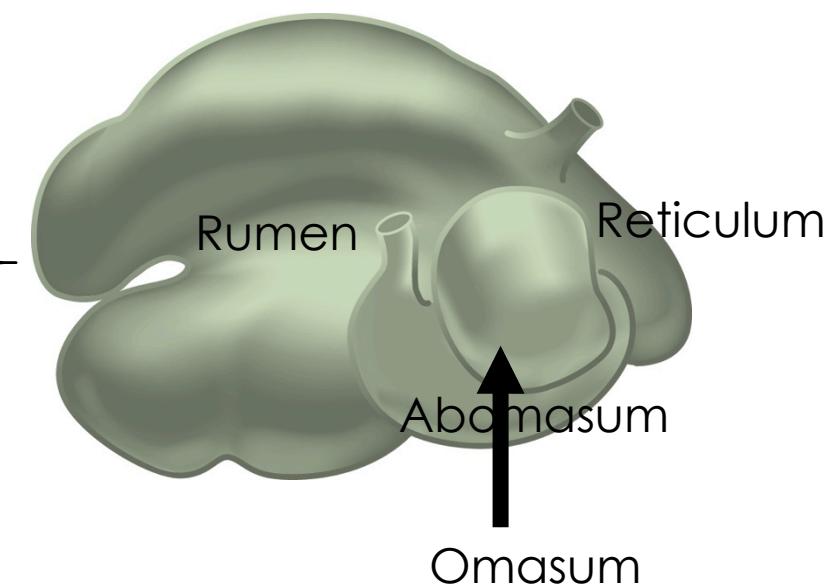
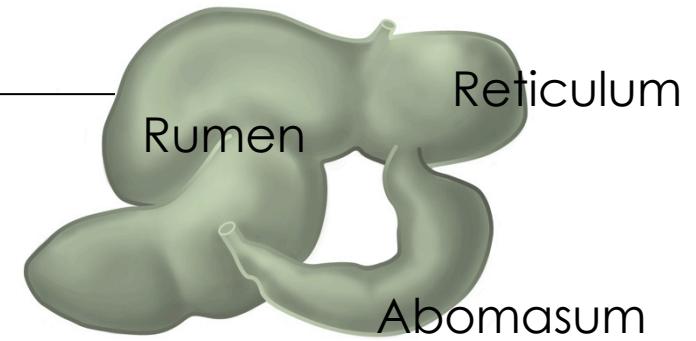
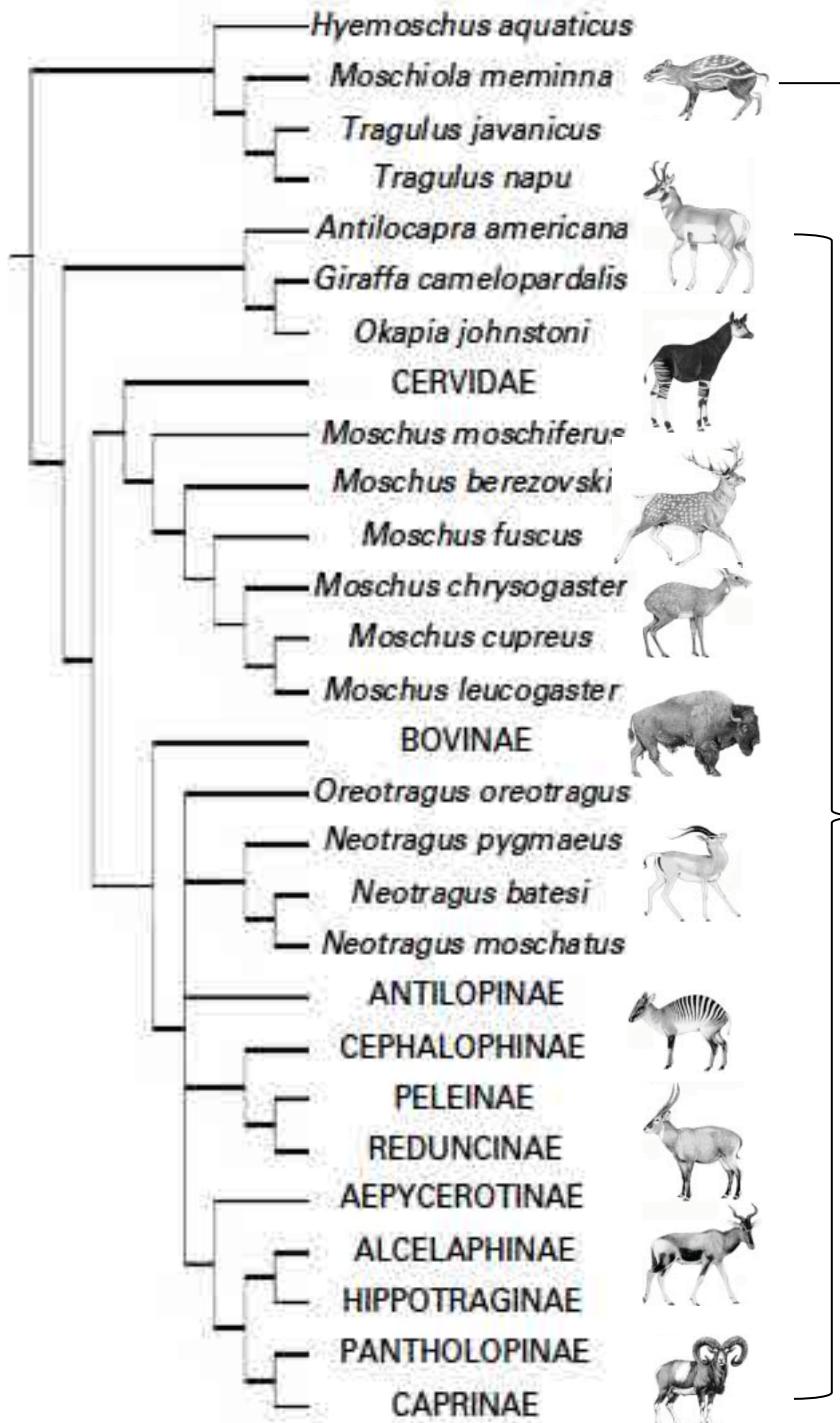


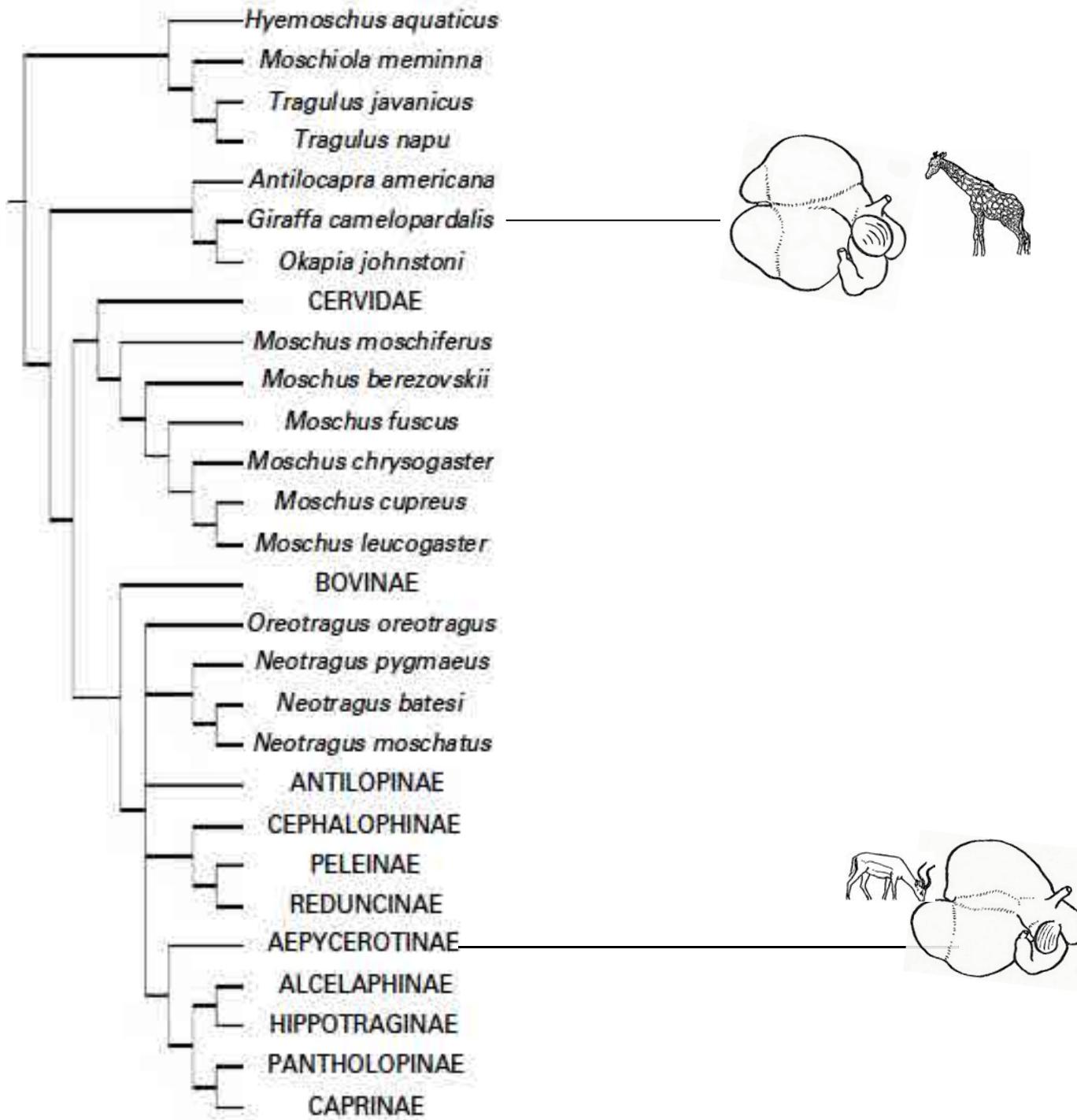


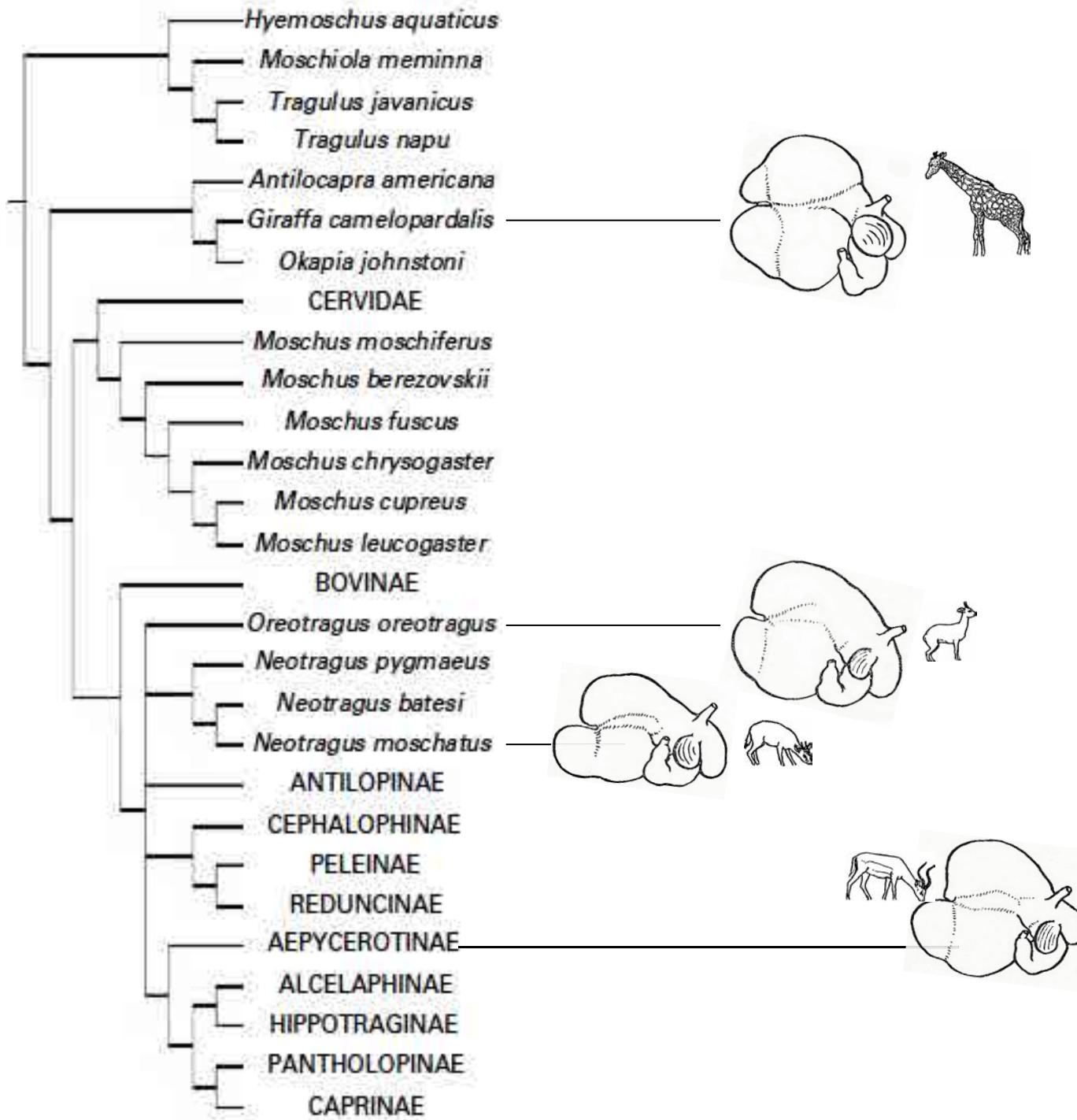
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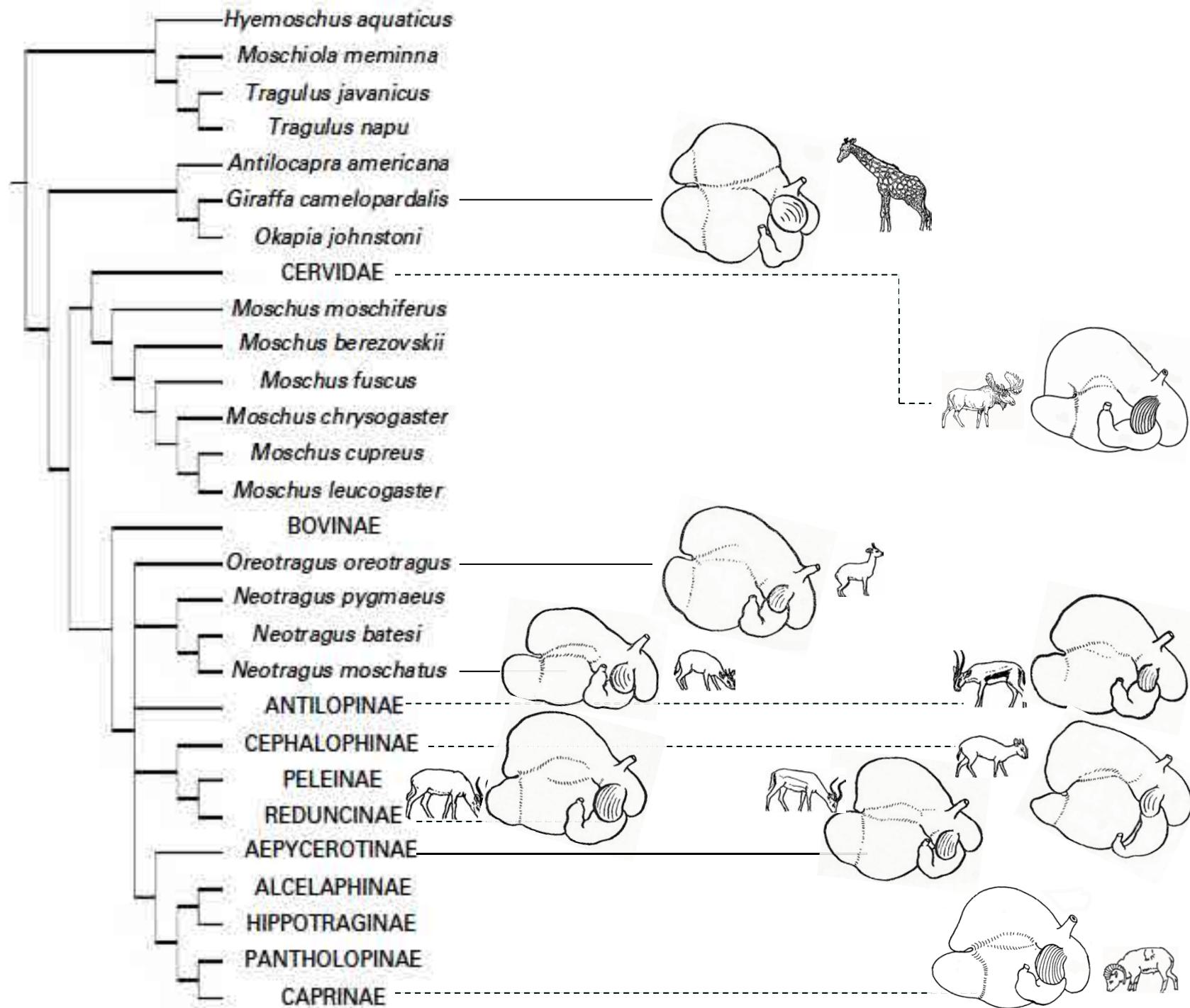


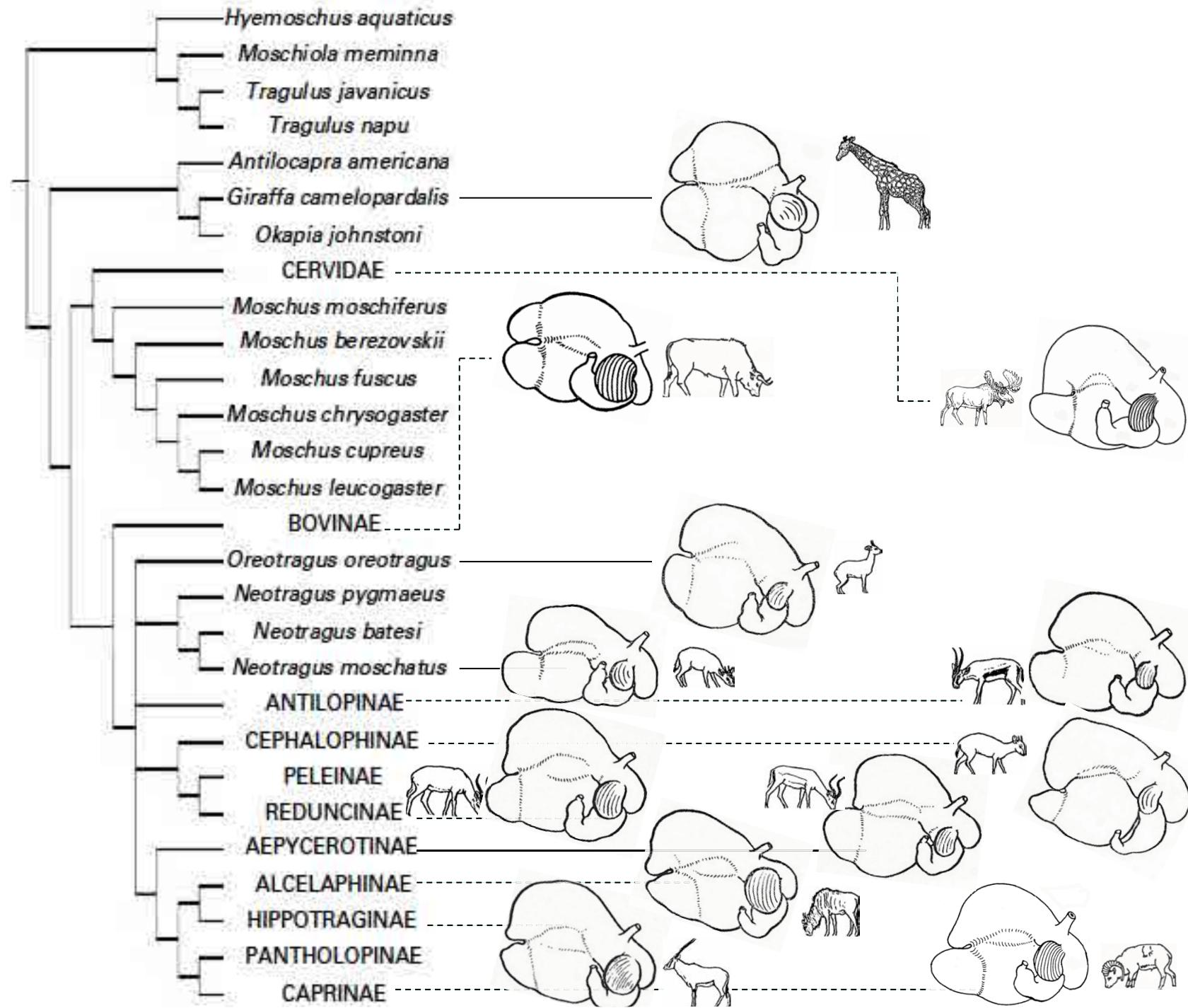


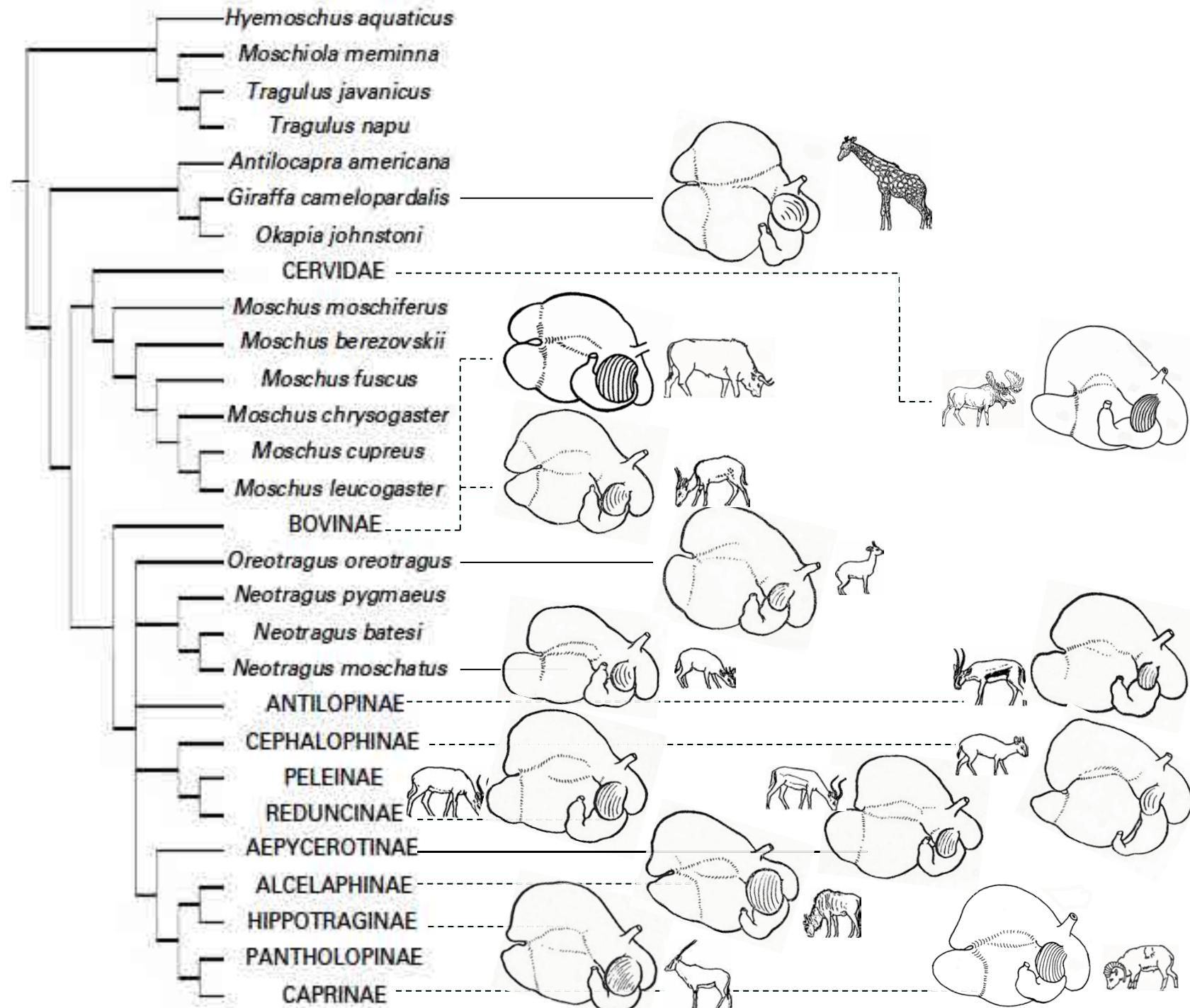


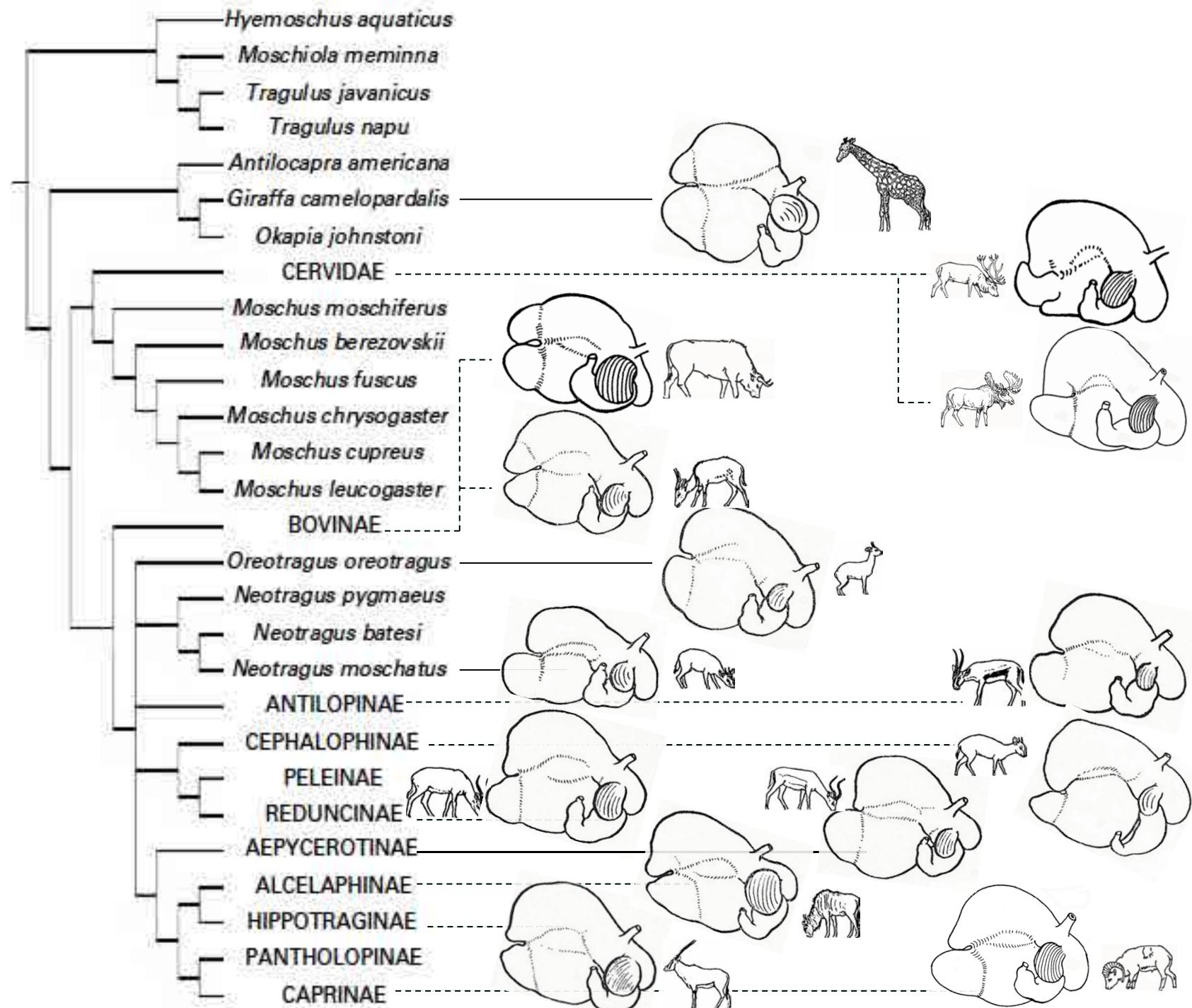


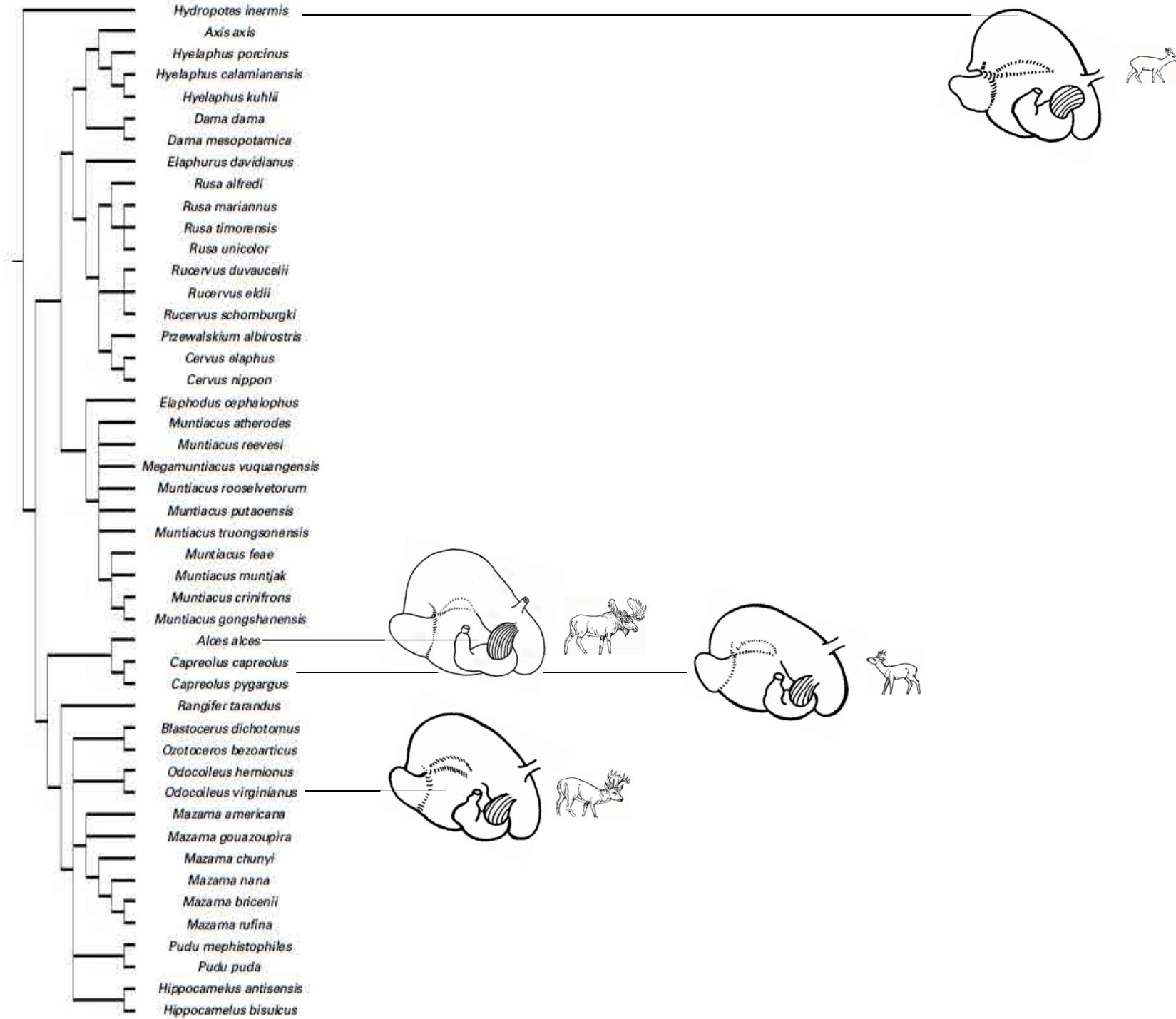


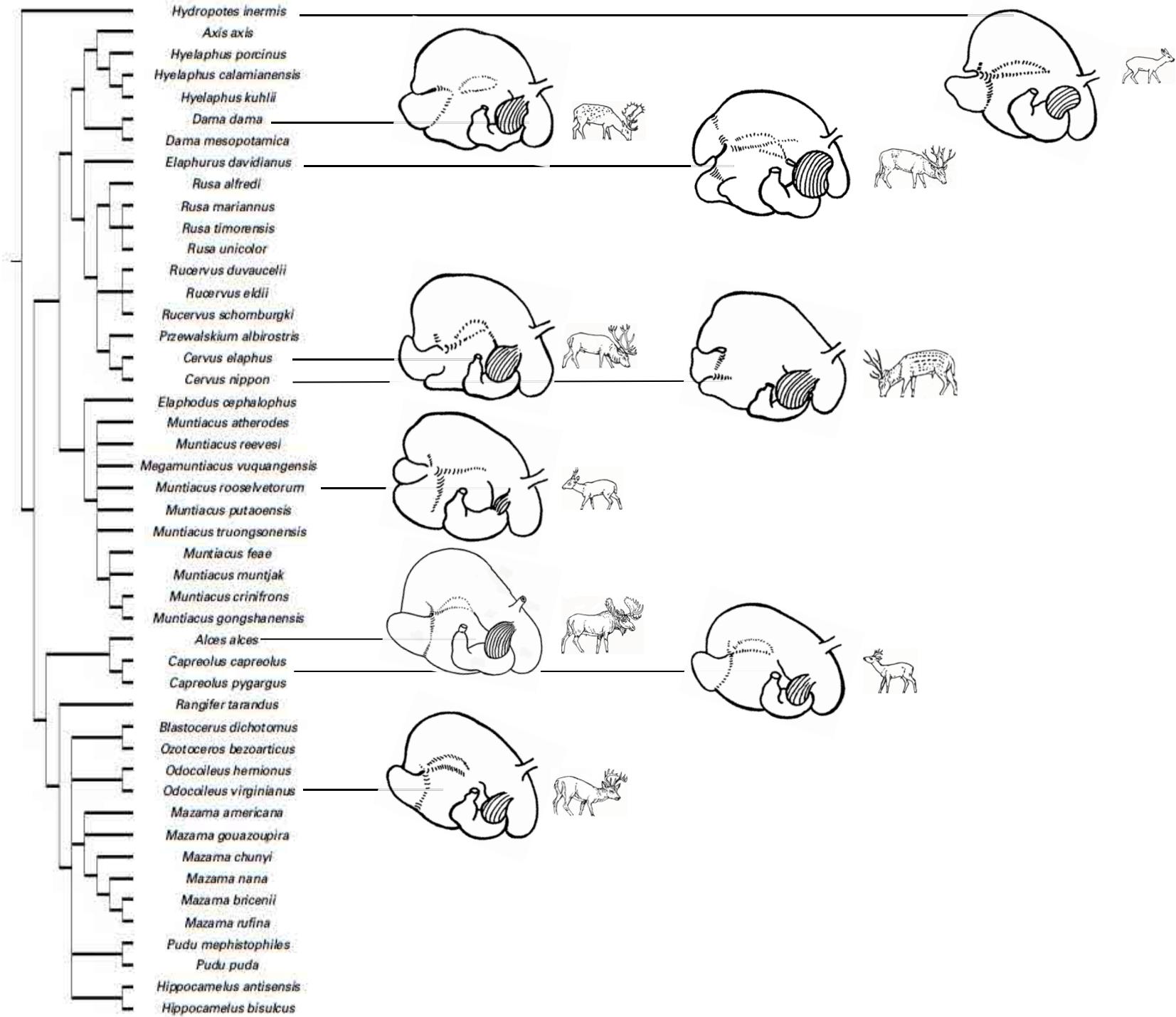


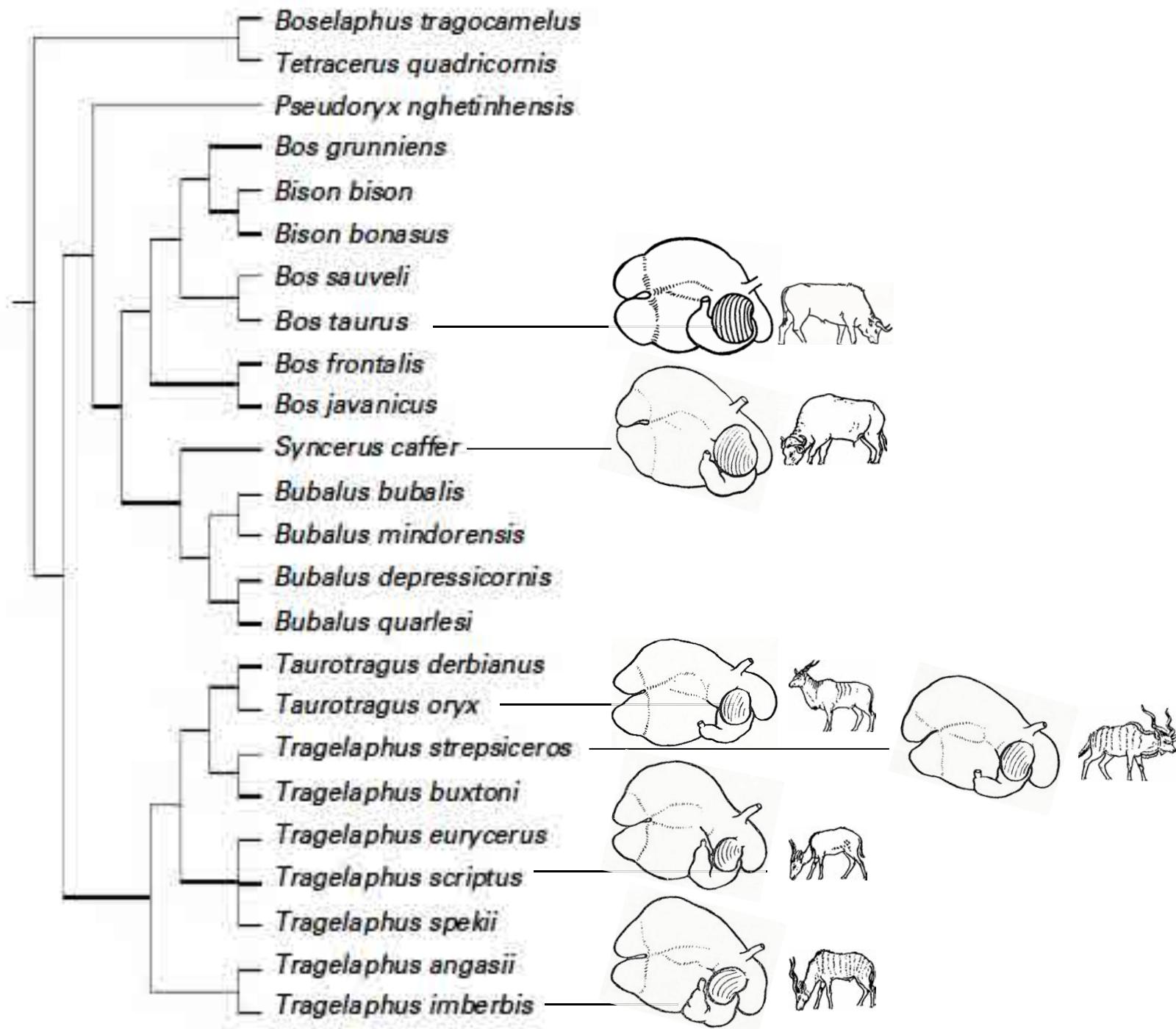


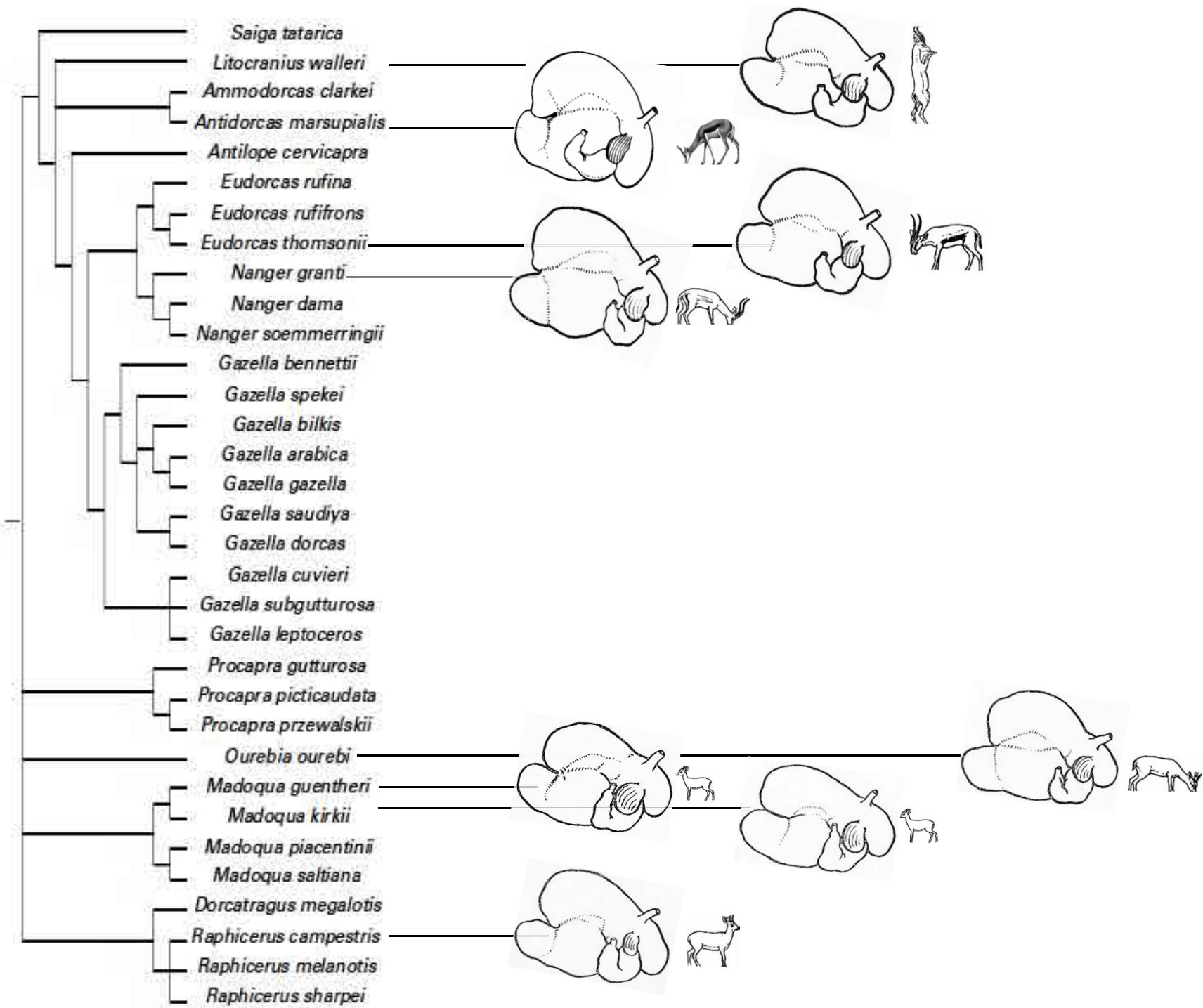


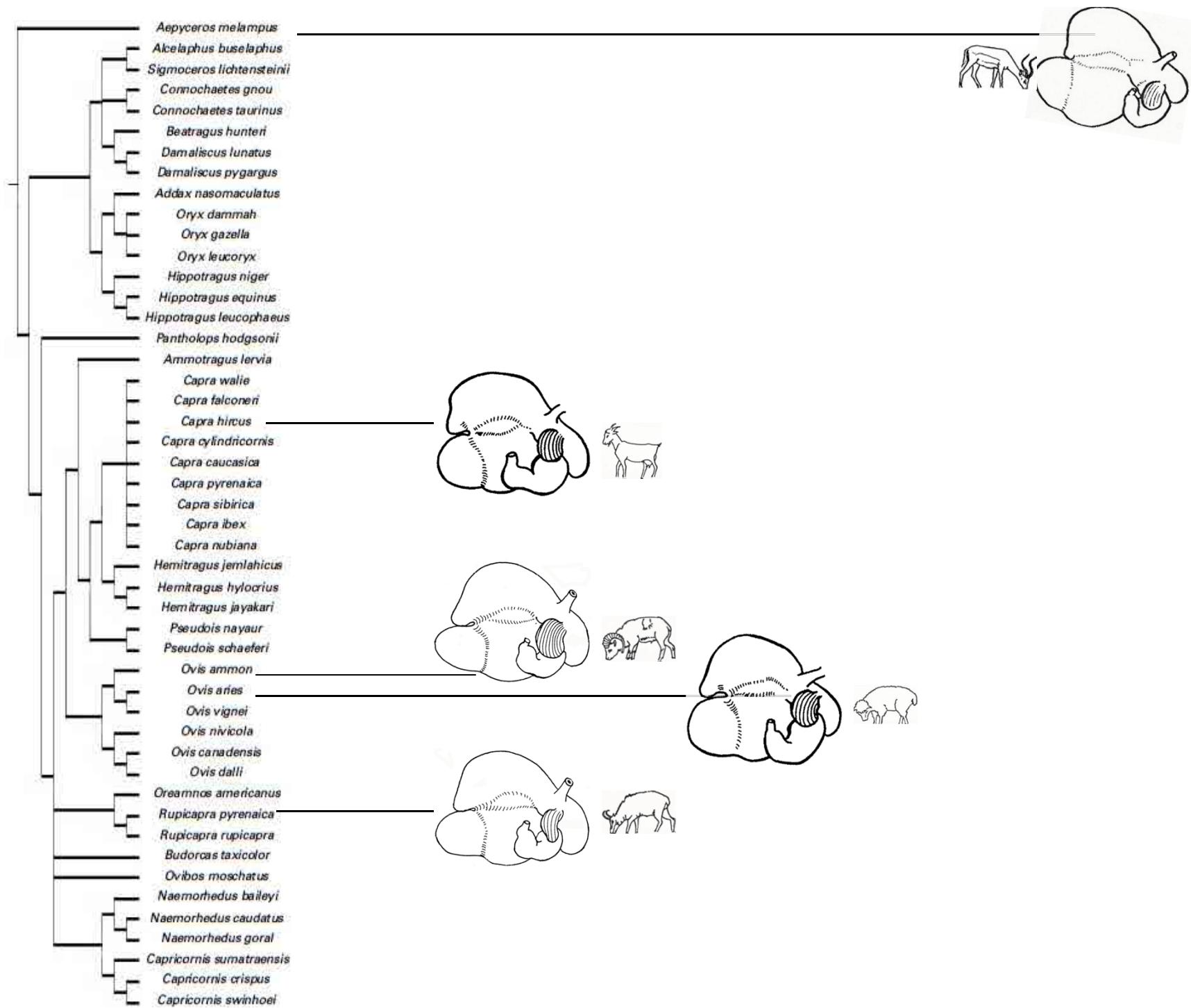


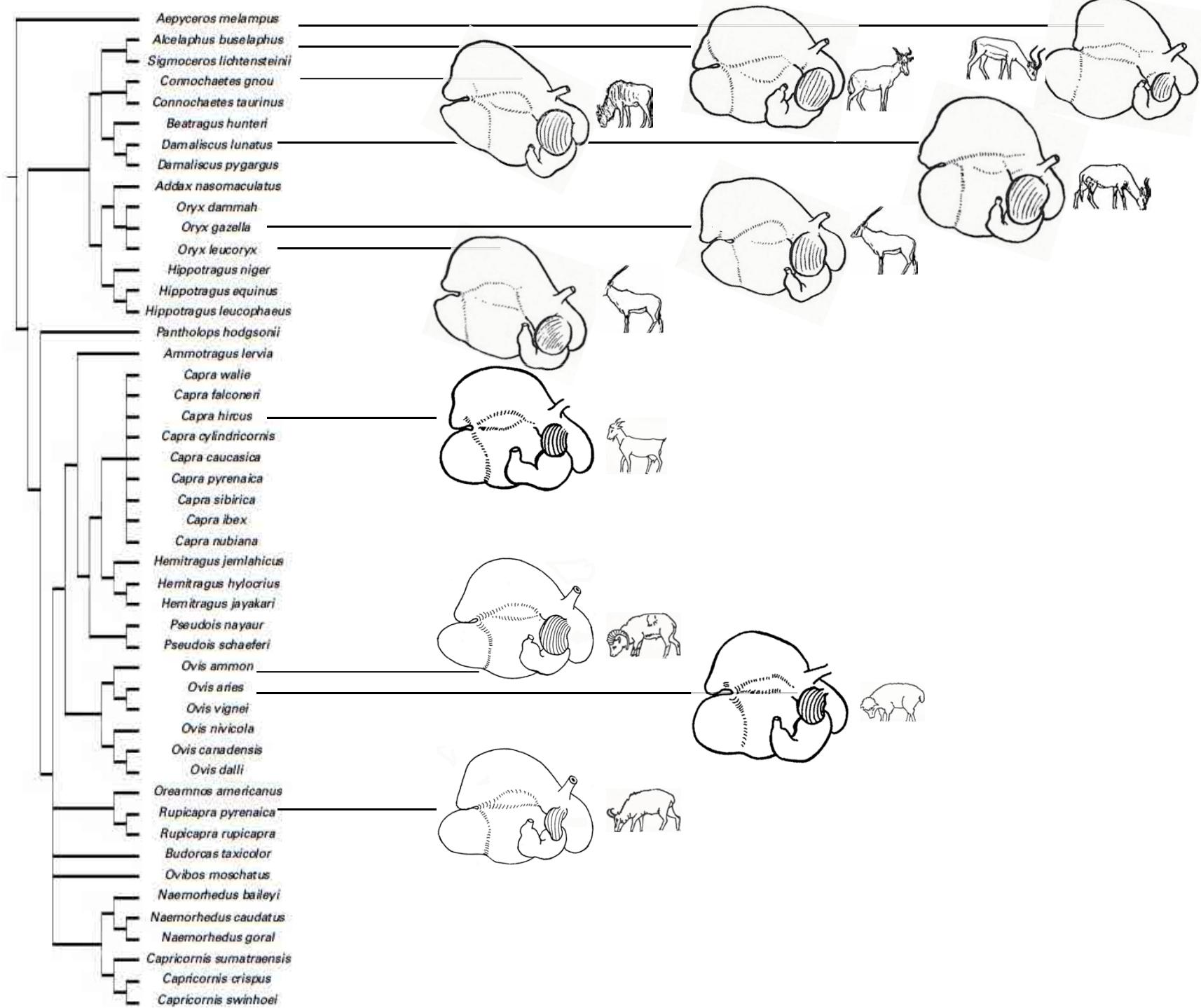


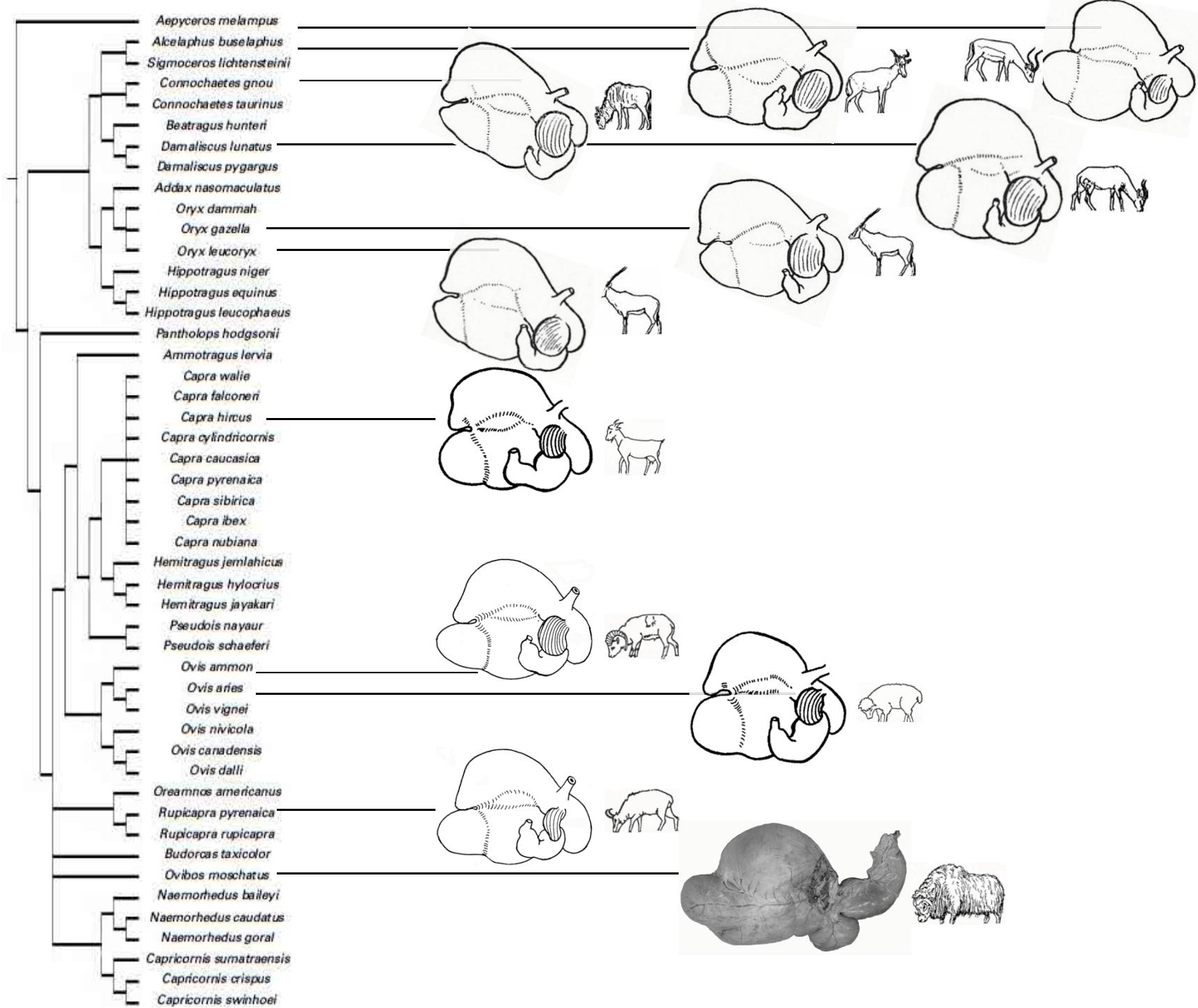


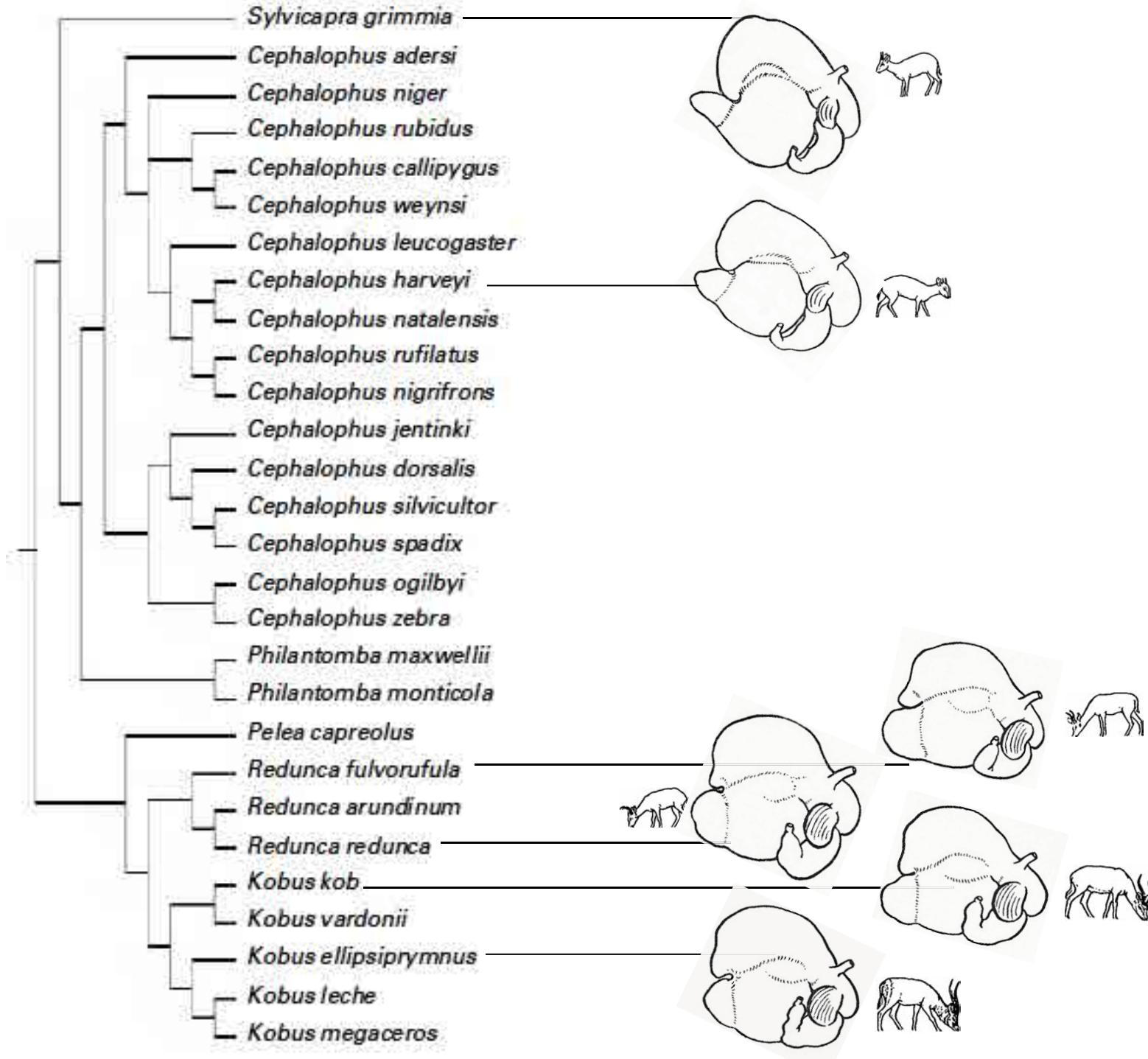














Sources (Forestomach shape)

Hofmann RR (1969) Zur Topographie und Morphologie des Wiederkäuermagens im Hinblick auf seine Funktion (nach vergleichenden Untersuchungen an Material ostafrikanischer Wildarten). Zentralblatt für Veterinärmedizin Supplement 10:1-180

Hofmann RR (1984) Feeding habits of mouflon (*Ovis ammon musimon*) and chamois (*Rupicapra rupicapra*) in relation to the morphophysiological adaptation of their digestive tracts. In: Hoefs M (ed) Proceedings of the Fourth Biennial Symposium of the Northern Wild Sheep and Goat Council. Yukon Wildlife Branch, Whitehorse, Yukon, pp 341-355

Hofmann RR (1985) Digestive physiology of deer - their morphophysiological specialisation and adaptation. Royal Society of New Zealand Bulletin 22:393-407

Hofmann RR, Nygren K (1992) Morphophysiological specializations and adaptations of the moose digestive system. Alces Suppl. 1:91-100

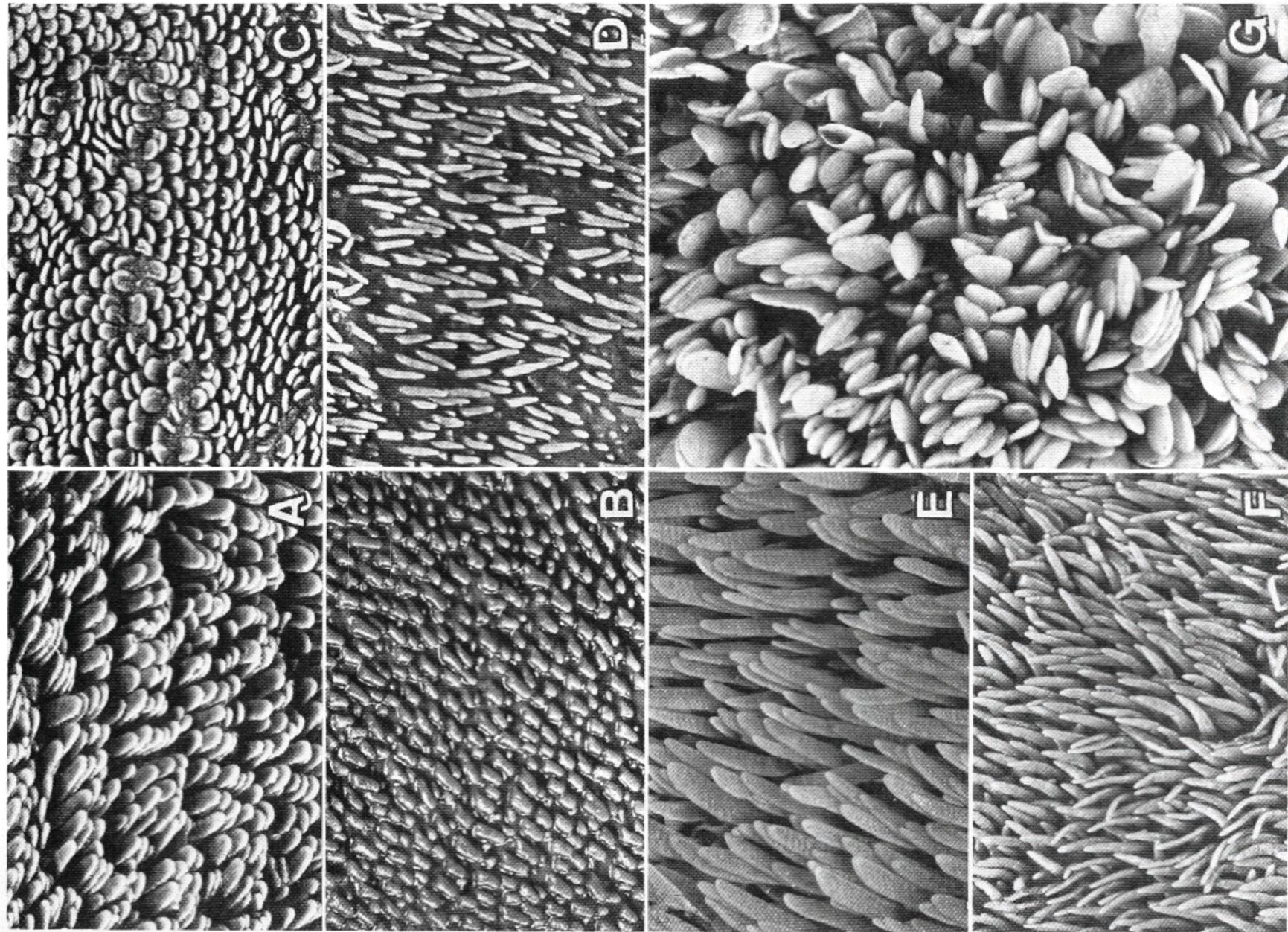
Hofmann RR, Knight MH, Skinner JD (1995) On structural characteristics and morphophysiological adaptation of the springbok (*Antidorcas marsupialis*) digestive system. Transactions of the Royal Society of South Africa 50:125-142



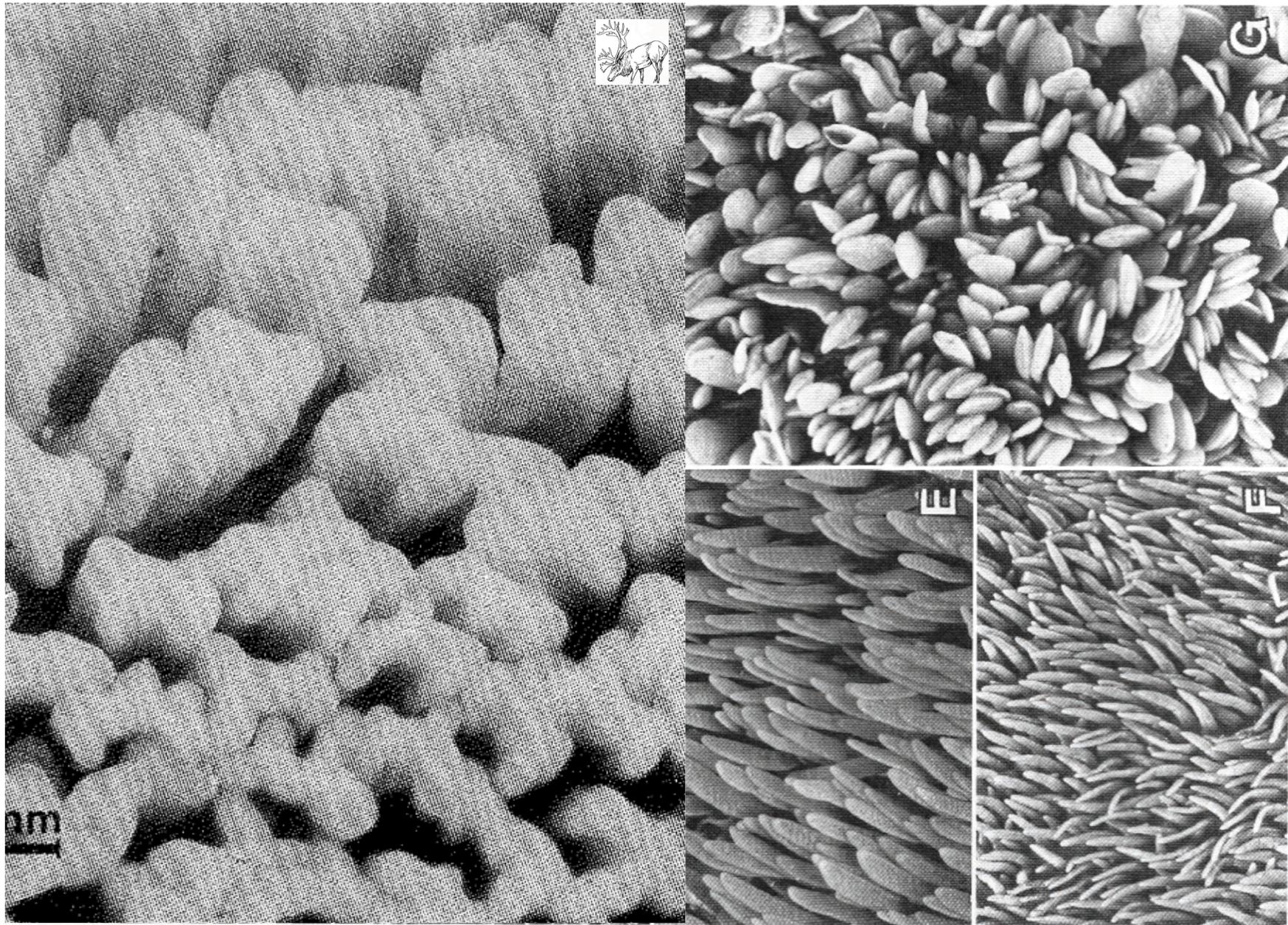
Using (soft tissue) morphology for phylogeny reconstructions

How do you treat unique traits that only occur in a single species?

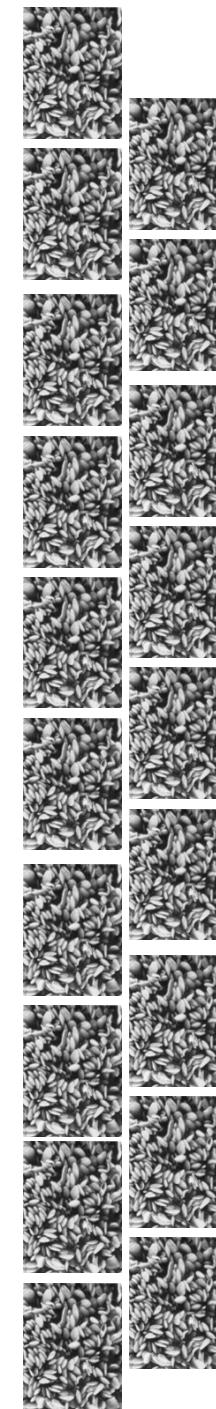
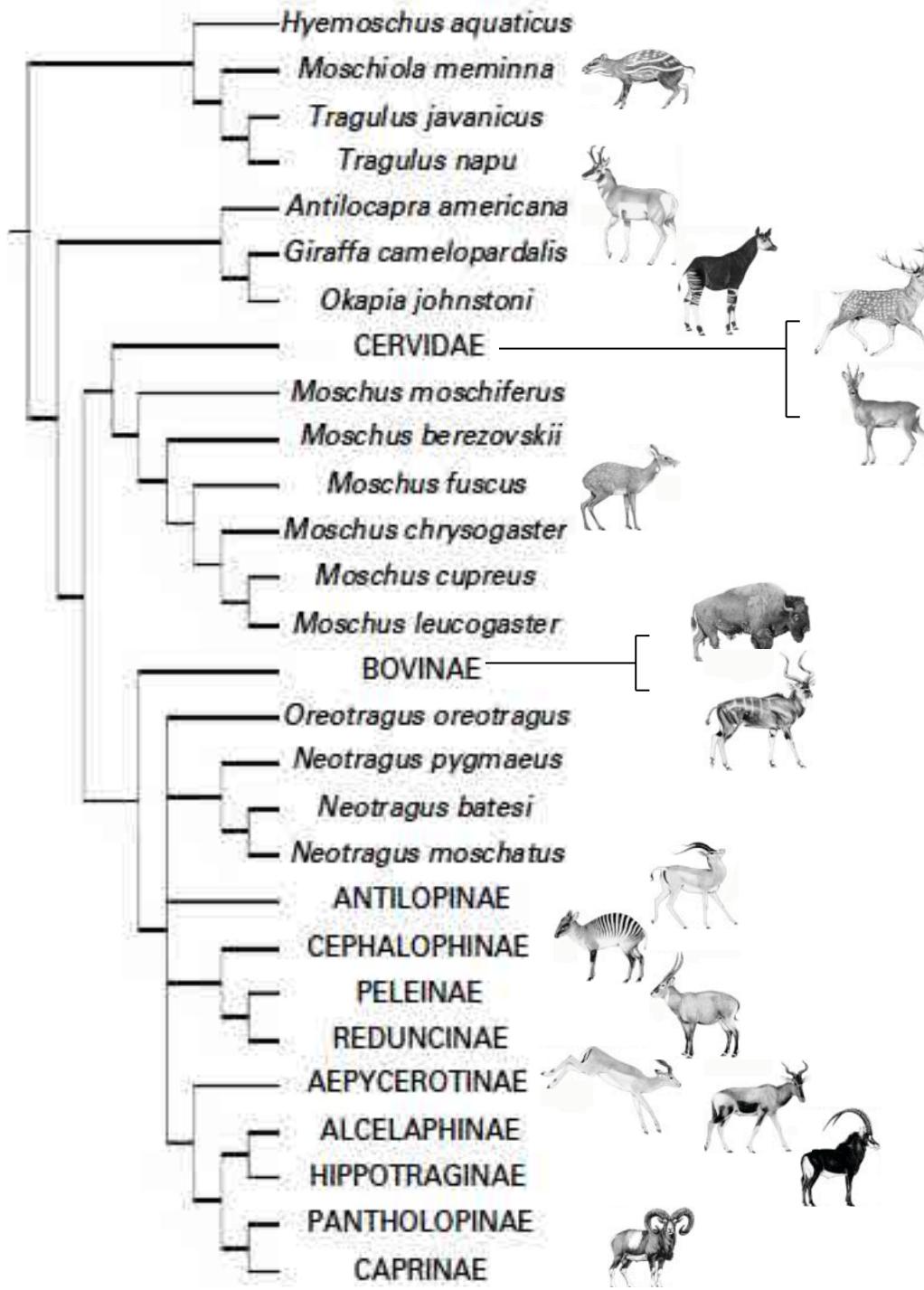
(and do you follow the same principle for one-species clades and multi-species clades?)



(from Hofmann & Schnorr 1982)

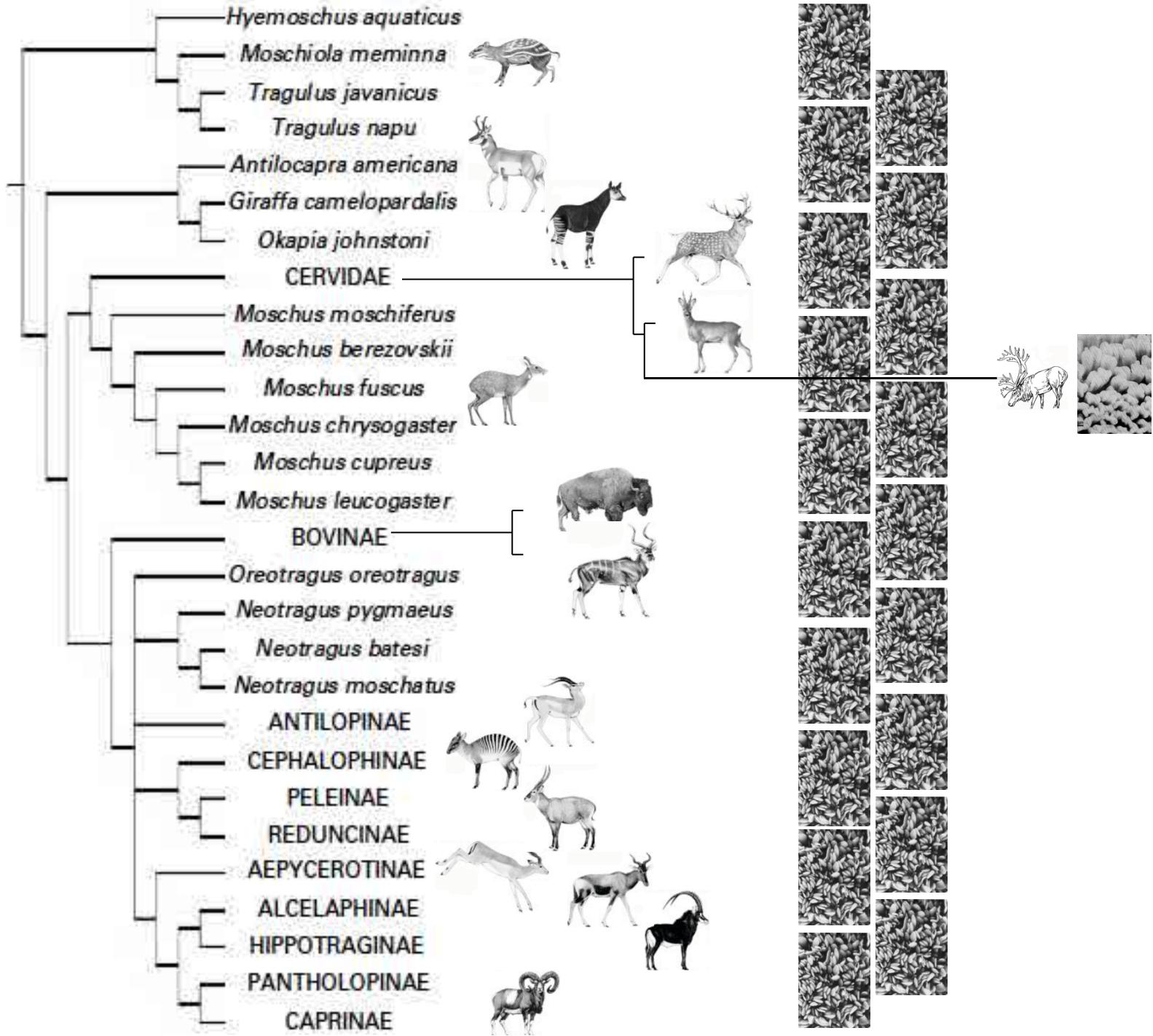


(from Hofmann & Schnorr 1982)





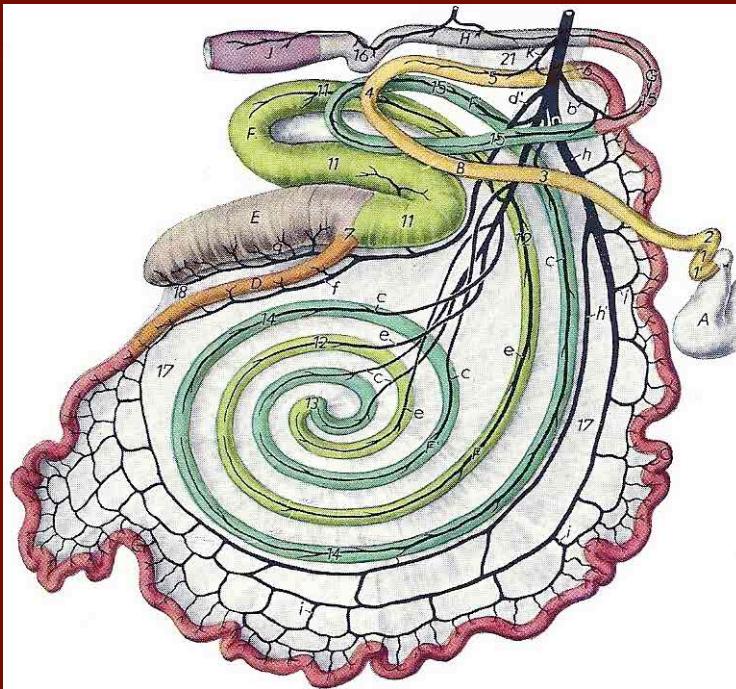
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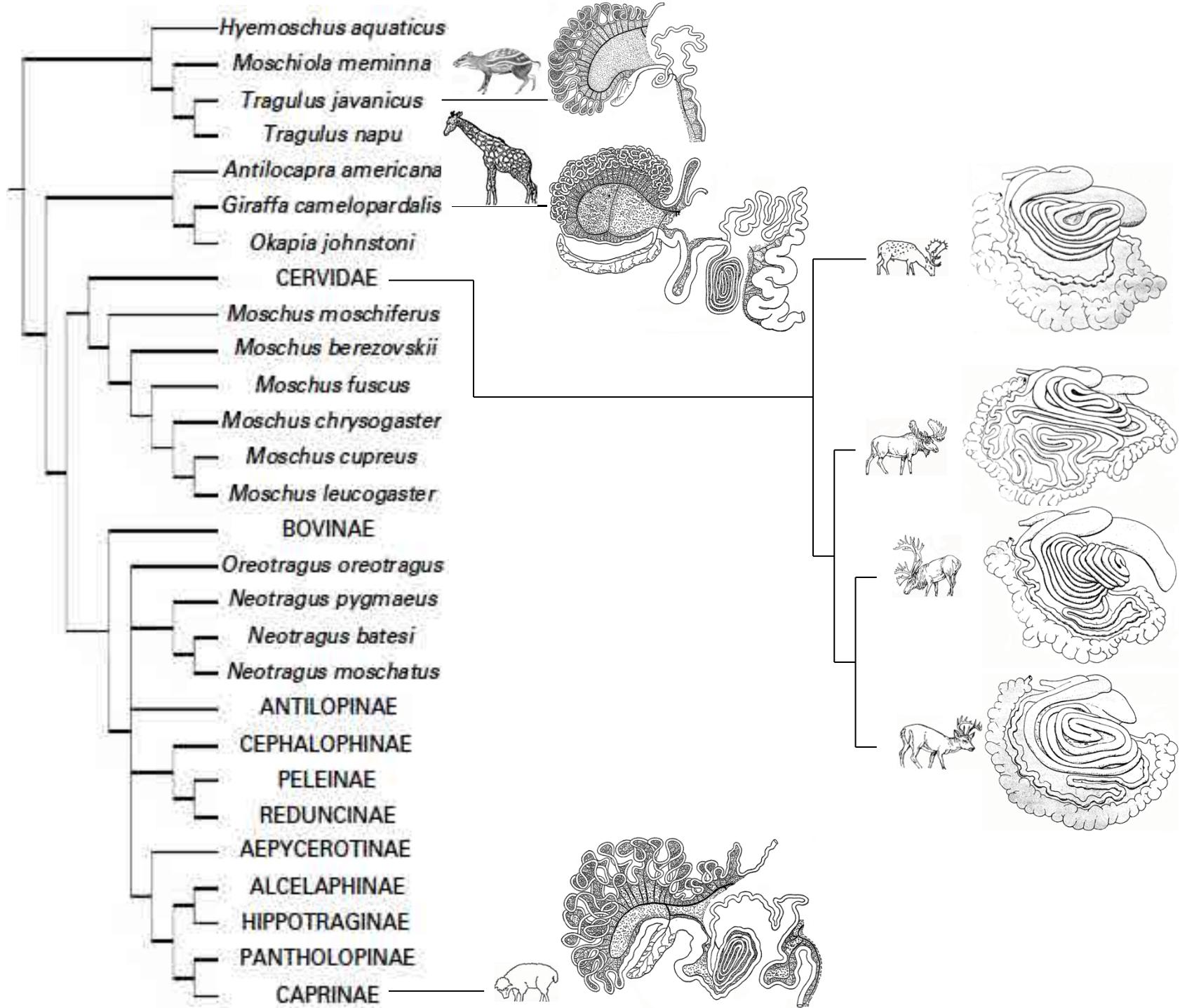




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Intestine







Sources (large intestine)

Mitchell PC (1903-6) On the intestinal tract of mammals. *Transactions of the Zoological Society of London* 17:437-536

Westerling B (1975) A comparative study of the intestinal anatomy of deer. *Anatomischer Anzeiger* 137:178-186



Using (soft tissue) morphology for phylogeny reconstructions

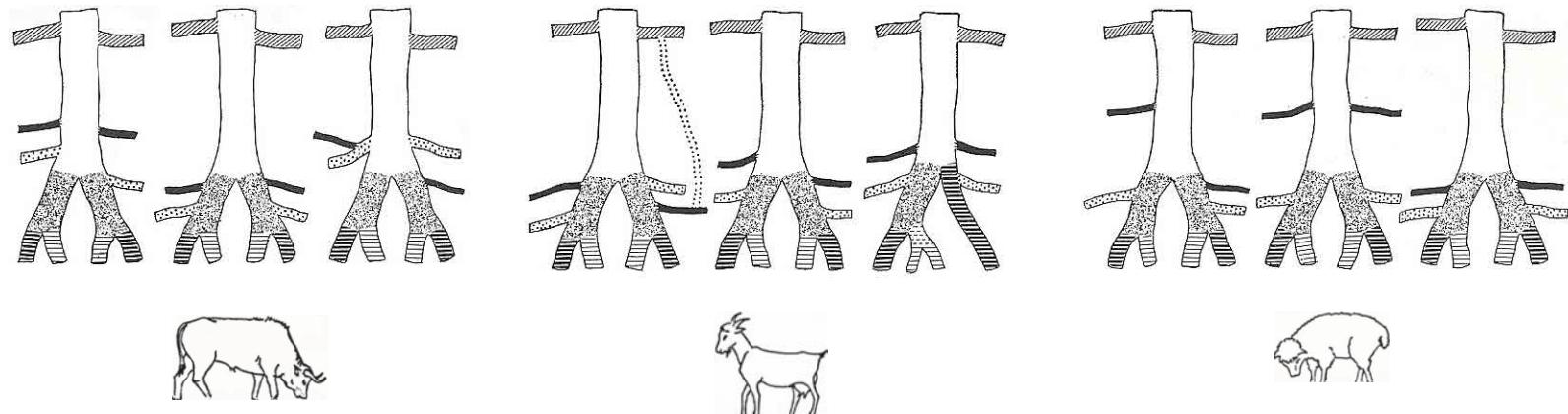
How many individuals do you have to measure to be certain about a ‘species trait’?



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Using (soft tissue) morphology for phylogeny reconstructions

How many individuals do you have to measure to be certain about a ‘species trait’?



(from Nickel et al. 2004)



Using (soft tissue) morphology for phylogeny reconstructions

How many individuals do you have to measure to be certain about a ‘species trait’?

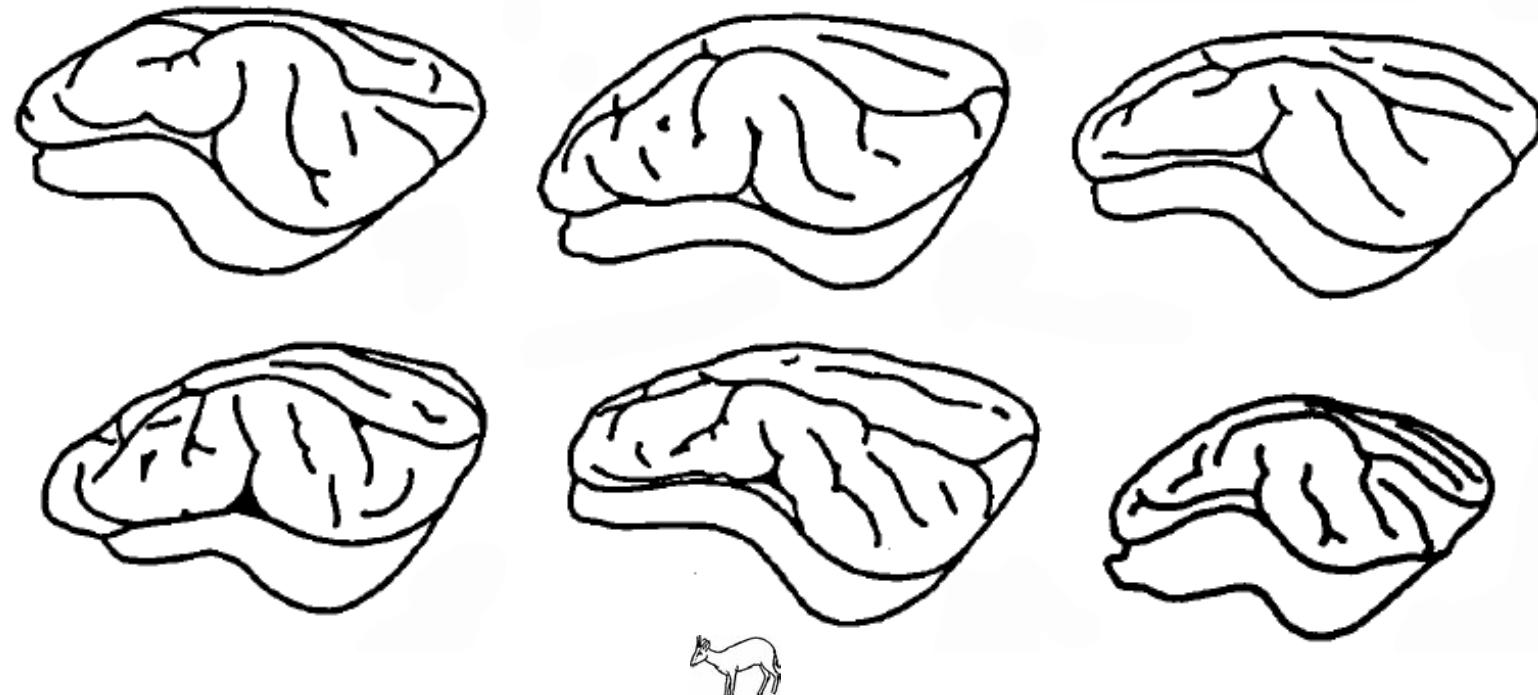


(from Westerling et al. 1975)



Using (soft tissue) morphology for phylogeny reconstructions

How many individuals do you have to measure to be certain about a 'species trait'?



(from Oboussier 1966)



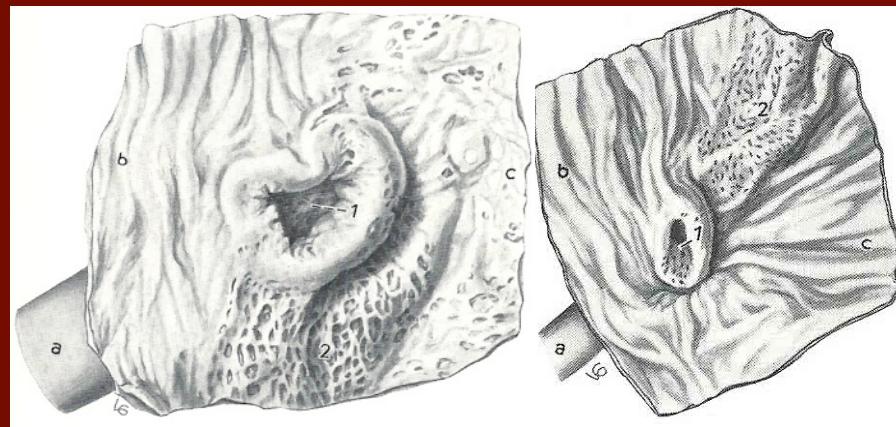
Using (soft tissue) morphology for phylogeny reconstructions

Do you assume a 'trait' at clade level even if not all species of that clade have been measured?



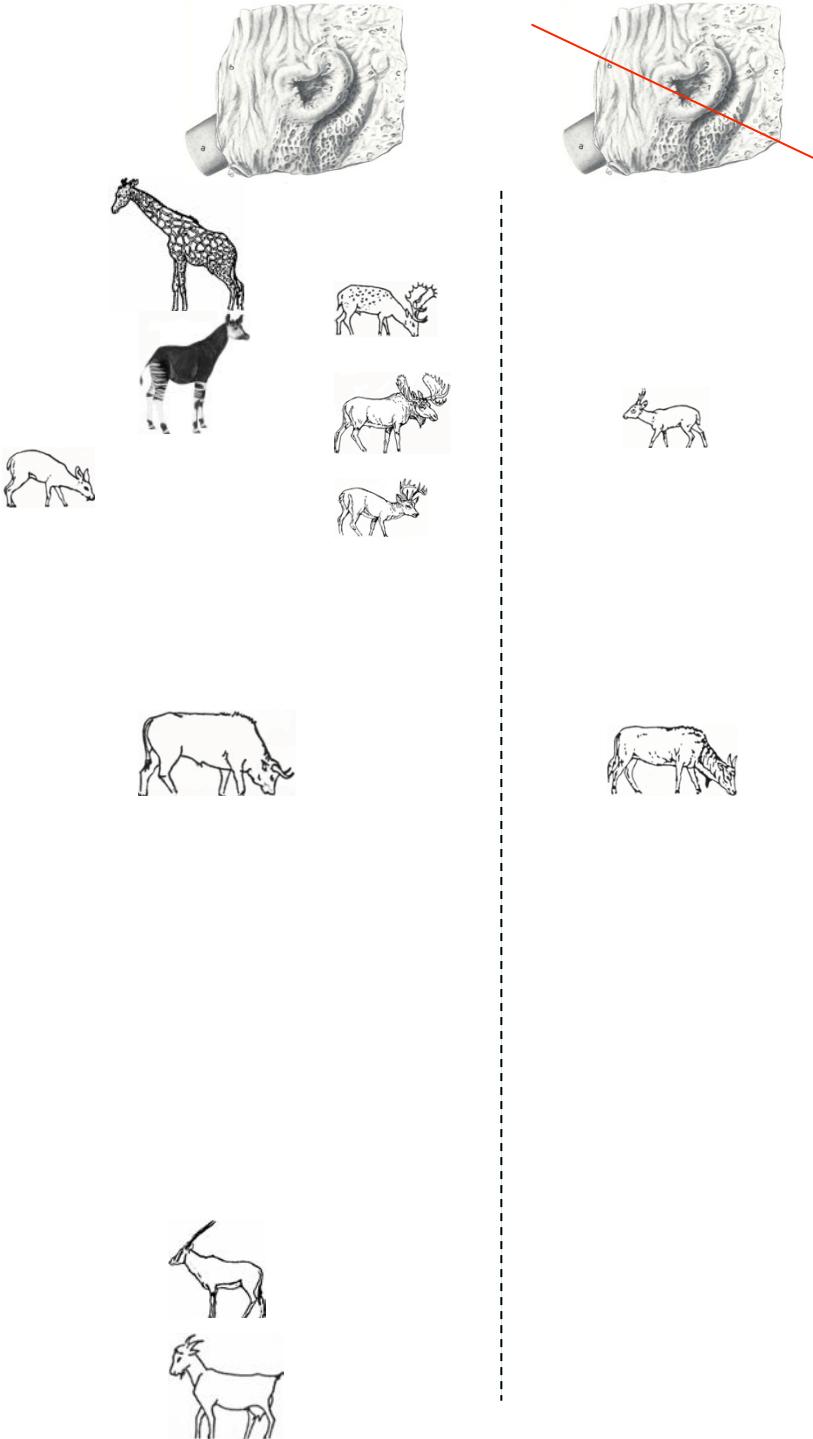
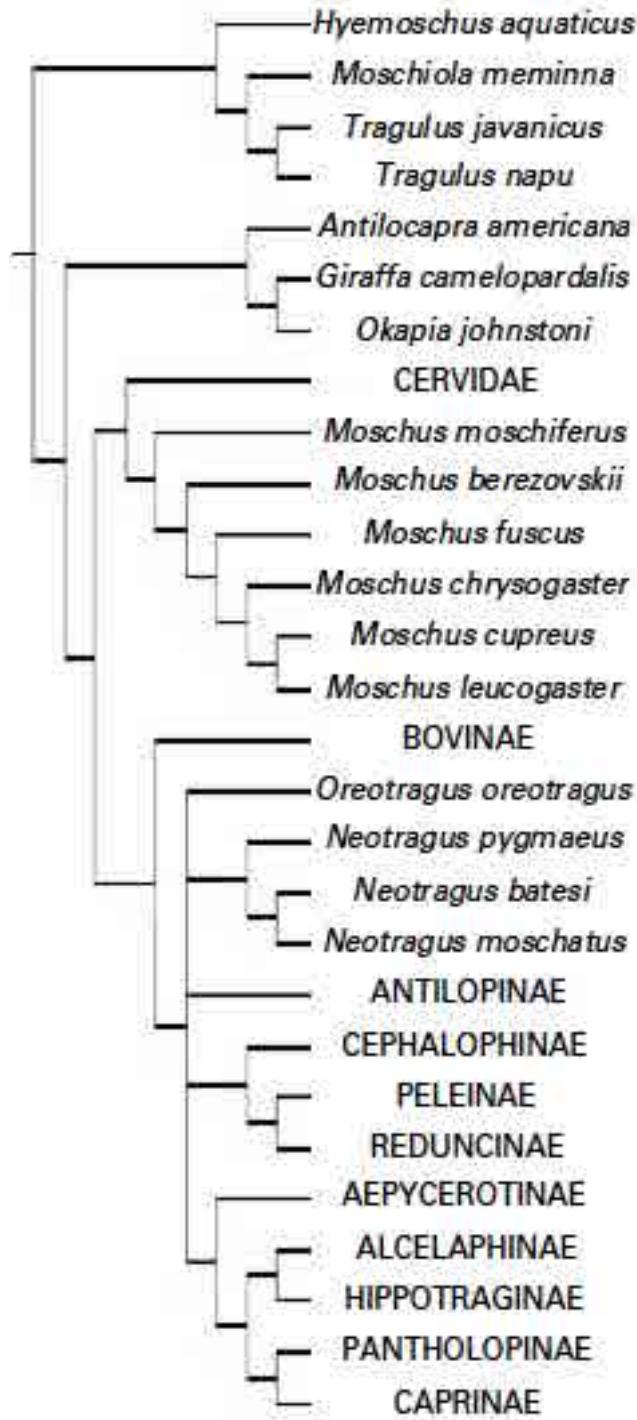
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Illeocaecal gland





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Sources (ileocaecal gland)

Derscheid JM, Neuville H (1924) Recherches anatomiques sur l'okapi I. Le caecum et la grande ileocaecale. *Revues Zoologiques Africaines* 12:499-507 (incl. references for other species)

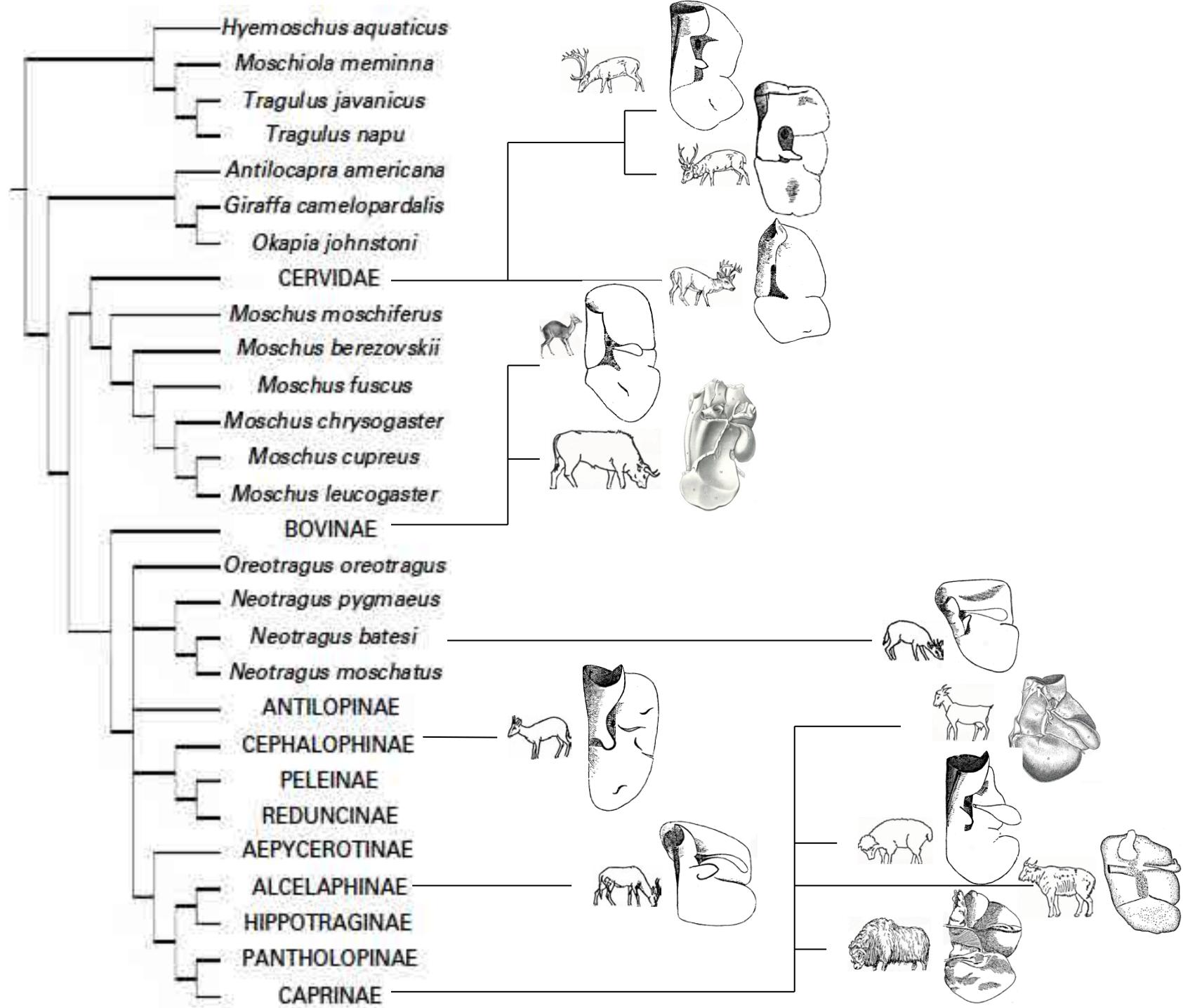
Nickel R, Schummer A, Seiferle E (2004) Lehrbuch der Anatomie der Haustiere. Band II: Eingeweide. Parey, Stuttgart (Domestic ruminants)



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Liver & Gall bladder







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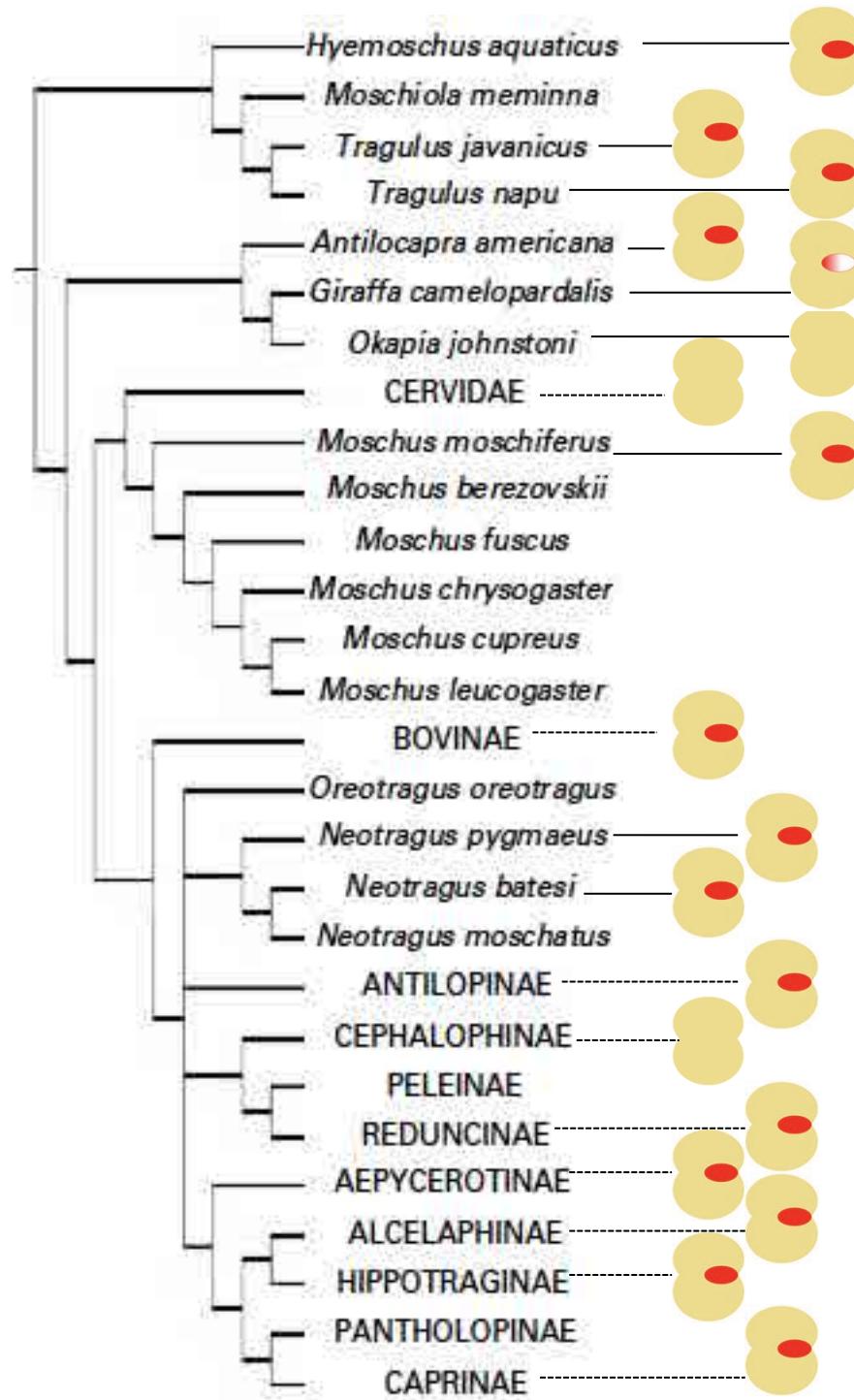
Sources (liver)

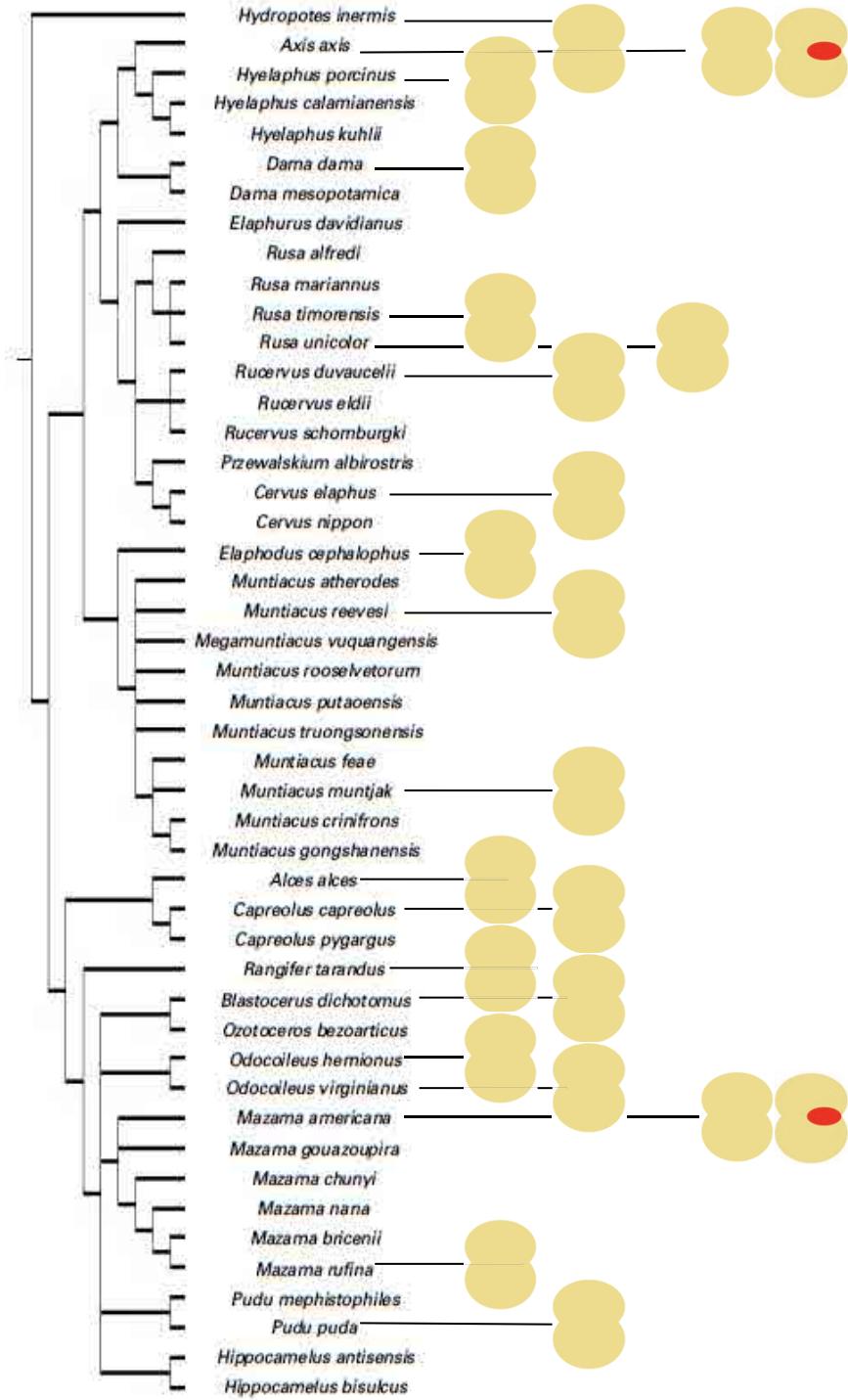
Garrod AH (1877) Notes on the visceral anatomy and osteology of the ruminants, with a suggestion regarding a method of expressing the relations of species by means of formulae. Proceedings of the Zoological Society of London, pp 2-18

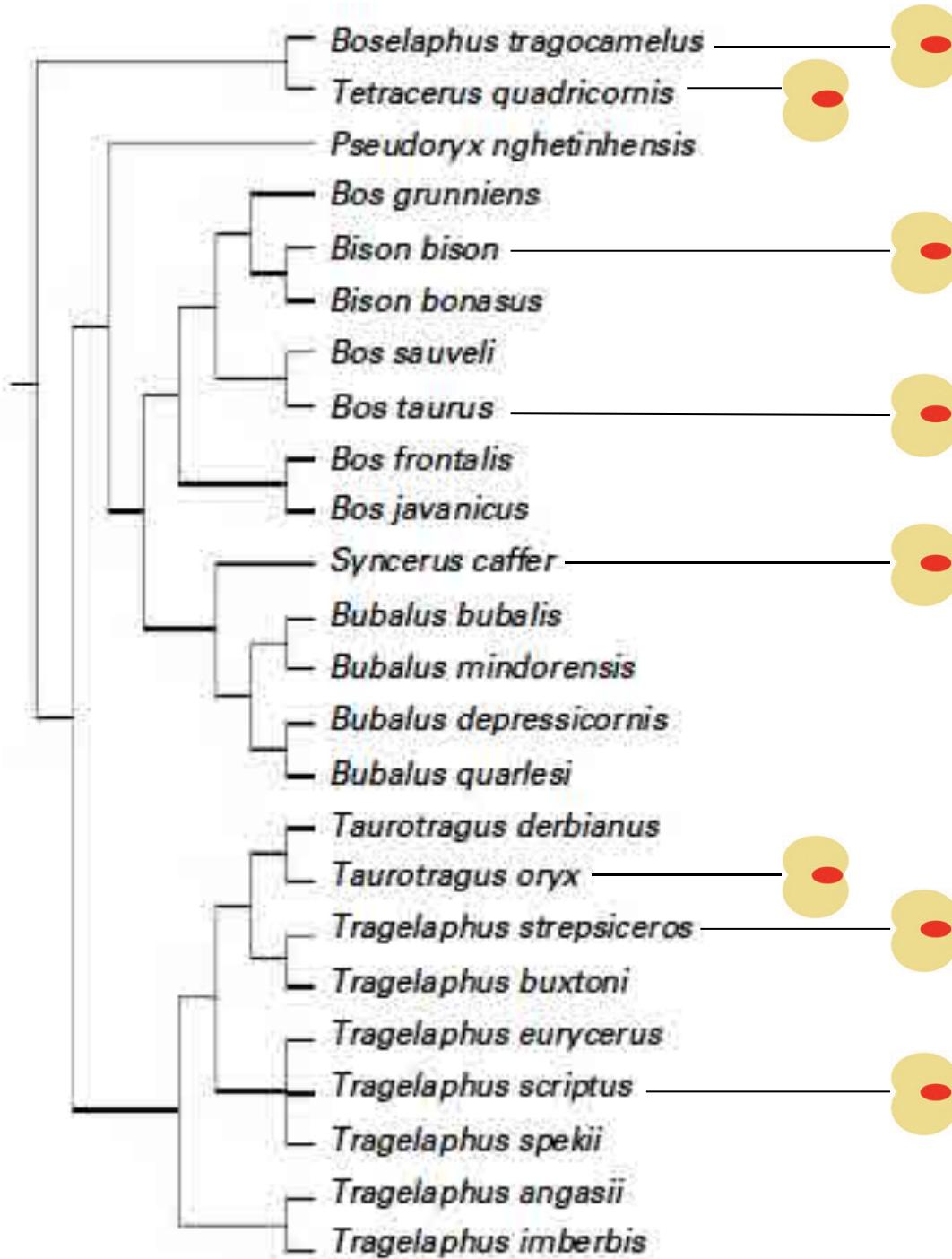
Lander KF (1919) Some points in the anatomy of the takin (*Budorcas taxicolor*). Based on the examination of a specimen in the Gardens of the Zoological Society of London. Proceedings of the Zoological Society of London, pp 203-218

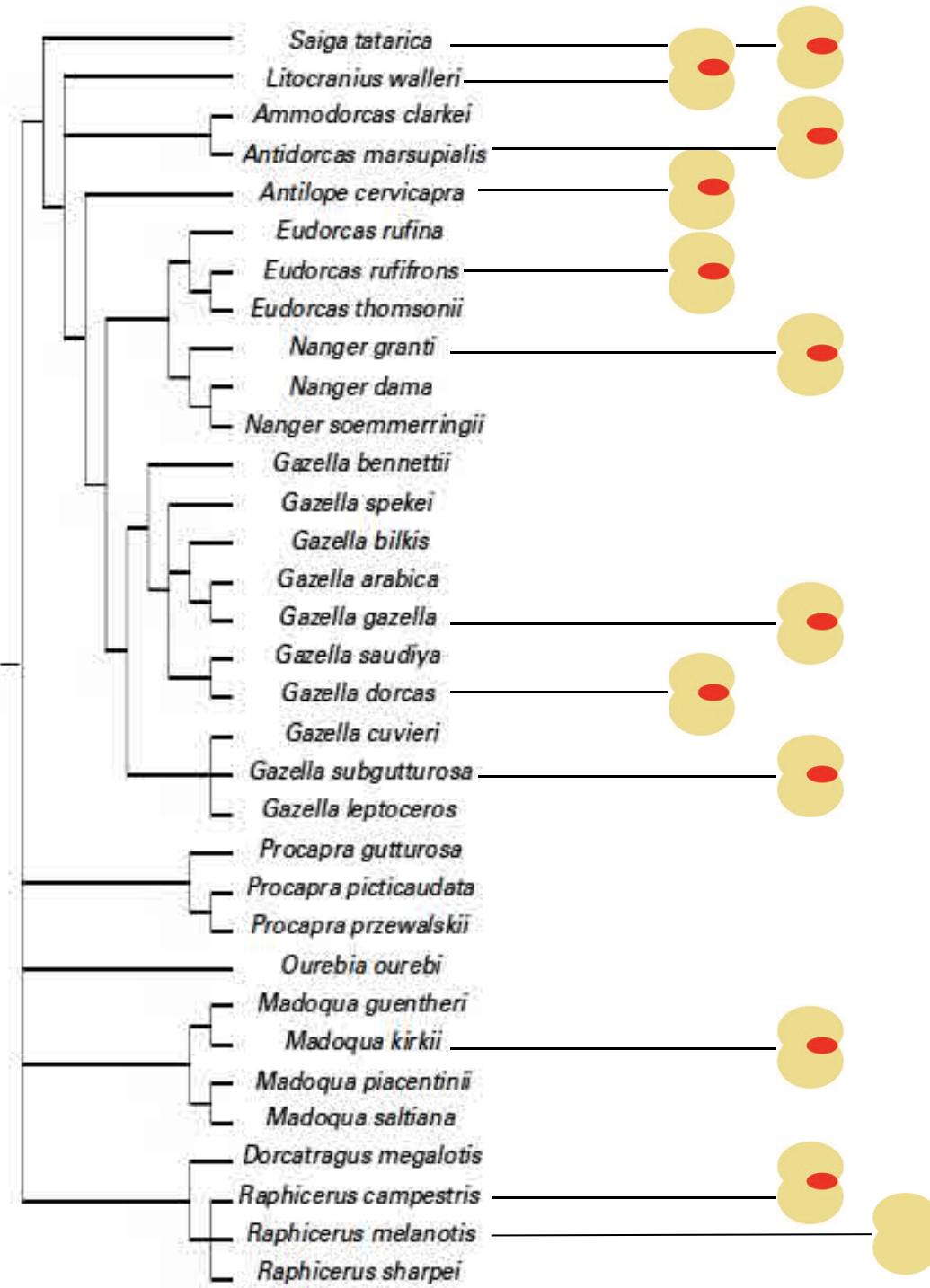
Lönnberg E (1900) On the soft anatomy of the musk-ox (*Ovibos moschatus*). Proceedings of the Zoological Society of London, pp 142-167

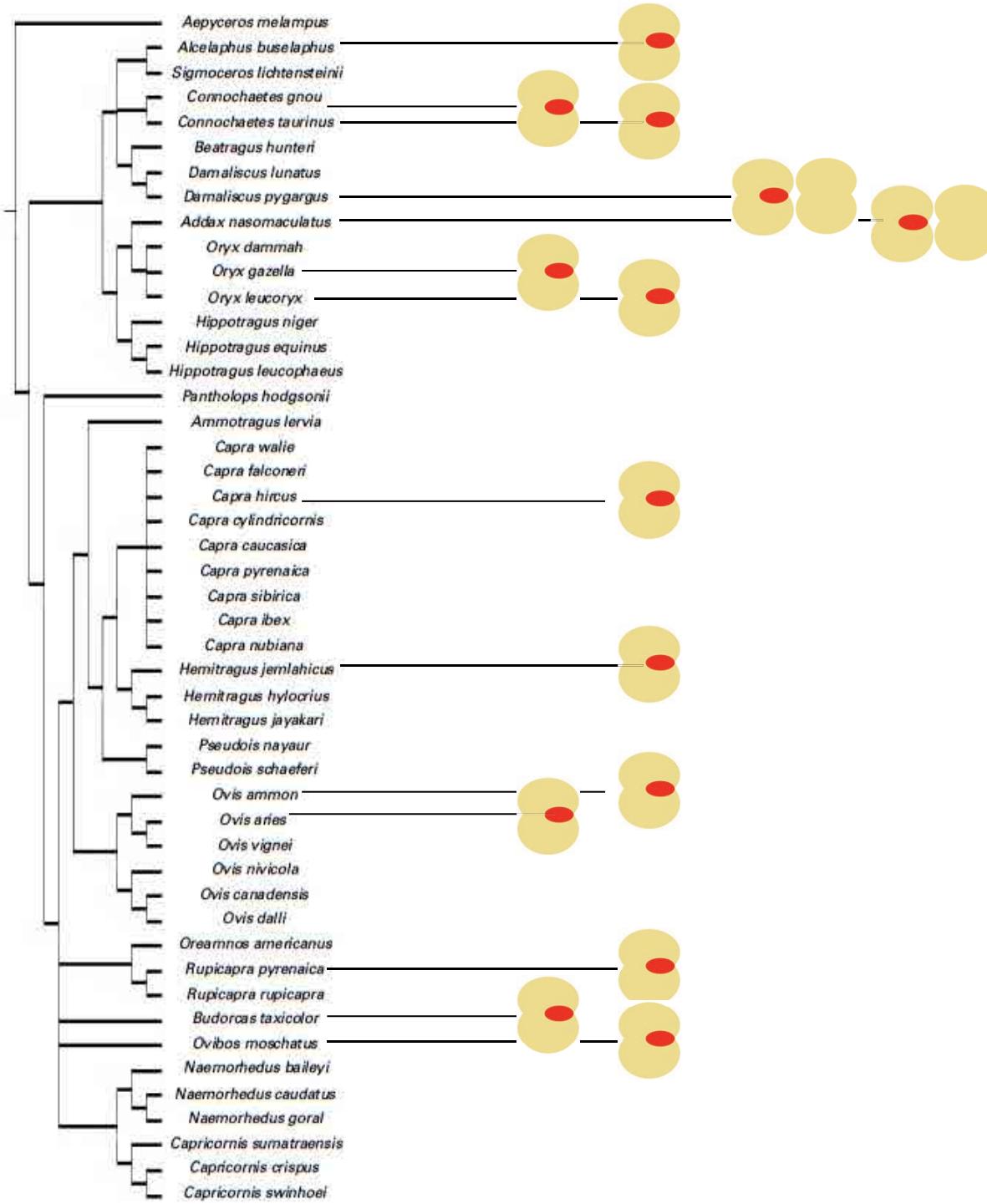
Nickel R, Schummer A, Seiferle E (2004) Lehrbuch der Anatomie der Haustiere. Band II: Eingeweide. Parey, Stuttgart (Domestic ruminants)

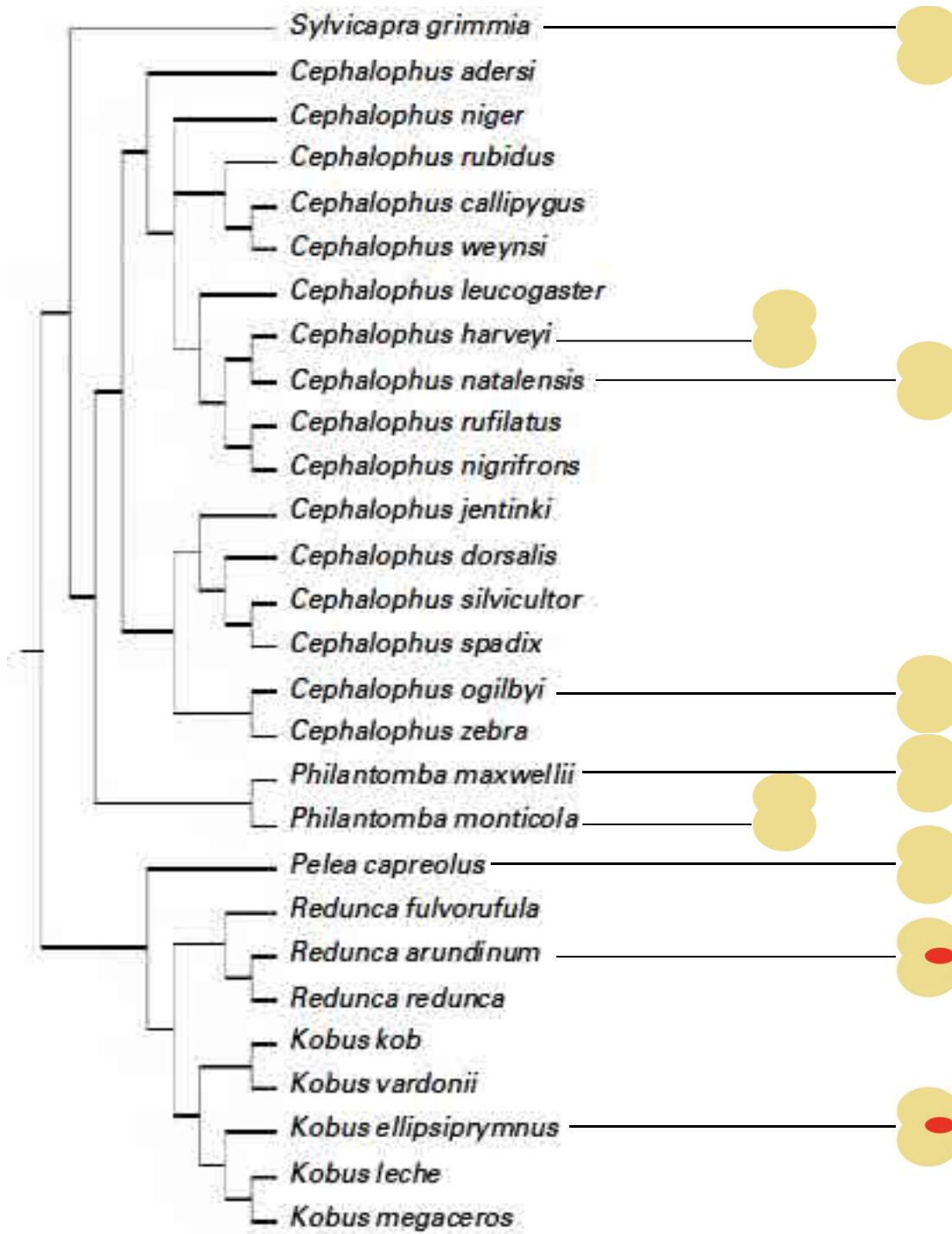














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Sources (gall bladder)

Cave AJE (1950) On the liver and gall-bladder of the giraffe. Proceedings of the Zoological Society of London 120:381-393

Crisp MD (1862) On the situation, form, and capacity of the gall-bladder in the vertebrata; on its absence in certain animals; and on the colour of the bile. Proceedings of the Zoological Society of London:132-139 (for conflicting cases)

Gorham FW, Ivy AC (1938) General function of the gall bladder from the evolutionary standpoint. Zoological Series, Field Museum of Natural History Chicago 22:159-213



Personal conclusion I

Those existing datasets on soft tissue biology that I consider most reliable reflect current phylogenetic concepts and might contribute little to the resolution of uncertain relationships.

For that aim, in my view, new, detailed and systematic studies are required and would be well worthwhile (e.g. kidneys in tragelaphini).



Morphological vs. molecular phylogeny

Morphological studies require much more samples (volume), expertise in trait evaluation, consistency of various methods –

which makes them tedious, and data collated from different sources difficult to use.

as well as checks for covariation ('logical independence'), relationship with body mass, threshold decisions, convergence control

(for which concepts/methods might still have to be established).



Personal conclusion II & outlook

The availability of data on hard and soft tissue, life history, behaviour and ecology as well as phylogenetic hypotheses presents an enormous opportunity

- for ancestral state reconstructions
- to simulate evolutionary sequences.

The stages of vertebrate evolutionary radiation

J. Todd Streelman¹ and Patrick D. Danley²

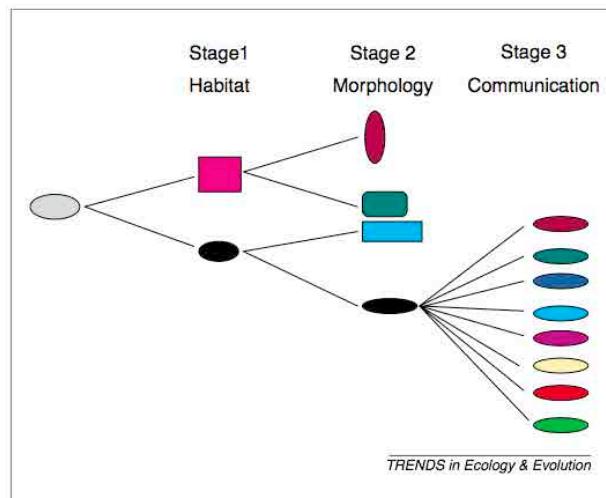
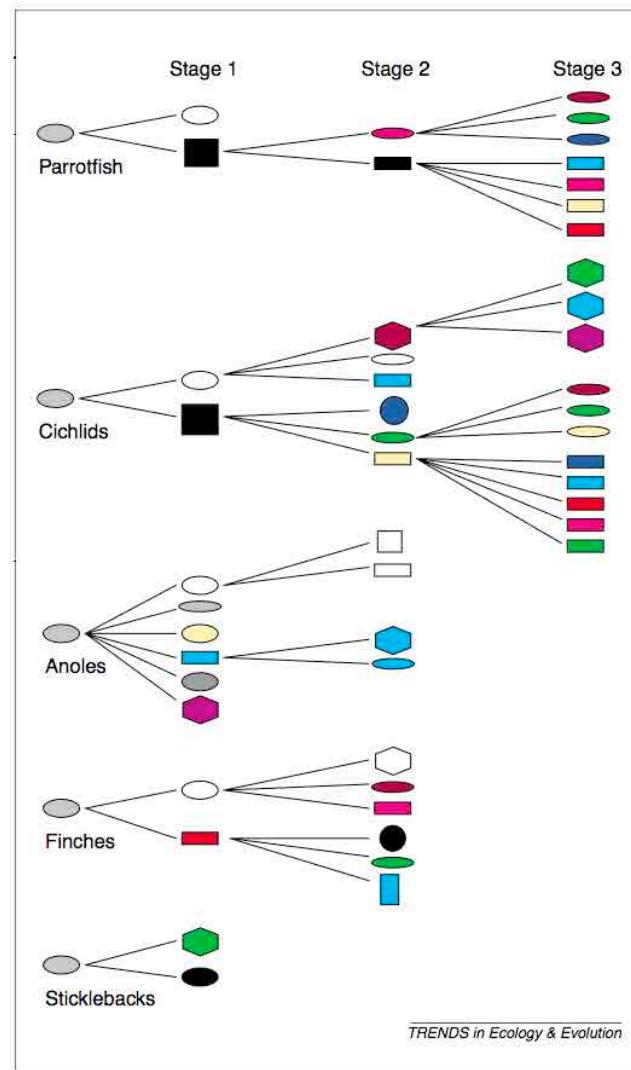


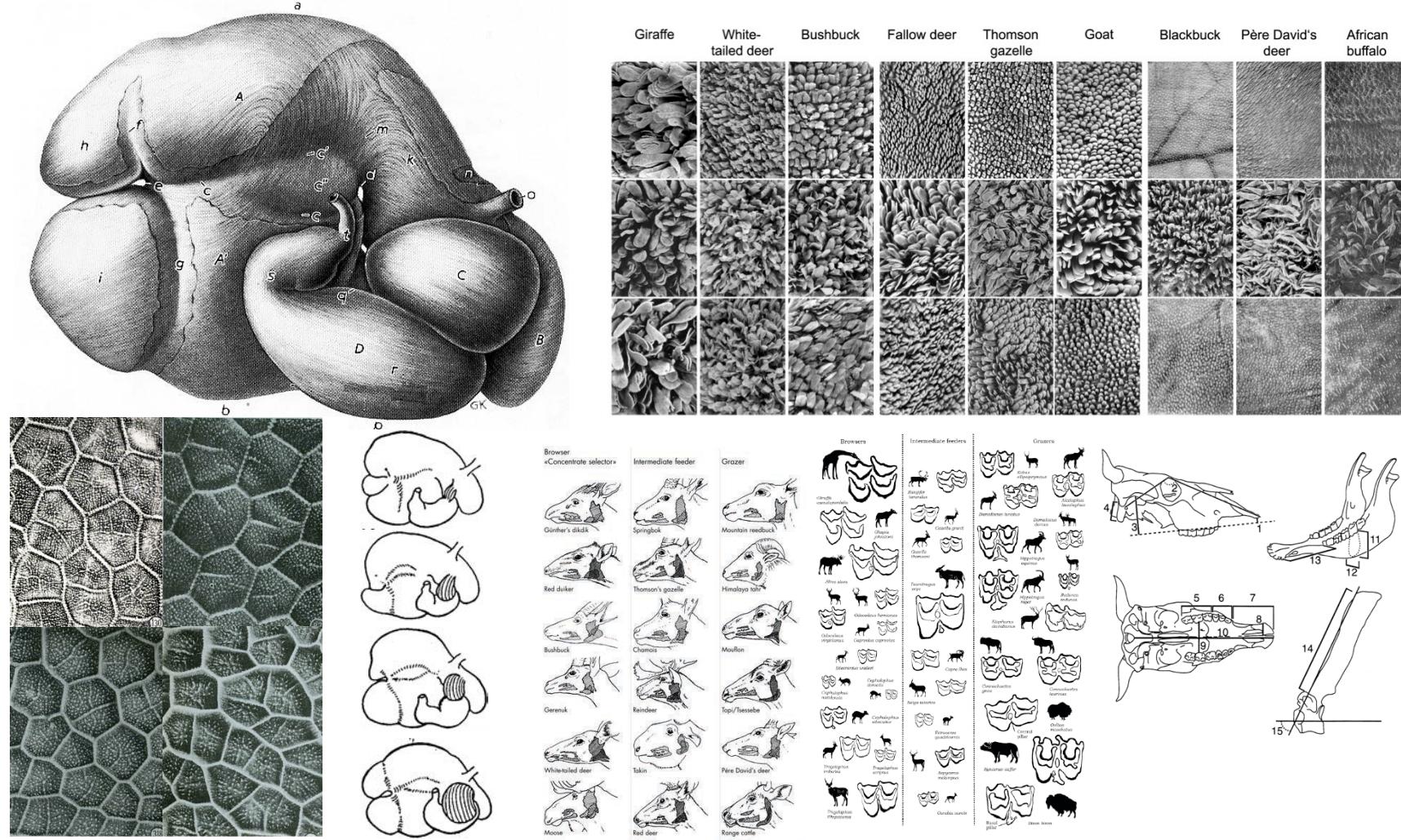
Table 1. Comparison of evolutionary radiations featured in this review

Radiation	Age (years)	No. of species	Habitat
Malawi cichlids	500 000	>500 per lake	Tropical, lacustrine
Sticklebacks	10 000	2/lake	Temperate, lacustrine
Parrotfish	40 million	100	Tropical, marine
Anoles	30 million	2–6 per island	Tropical, terrestrial
Finches	3 million	14 in Galápagos	Tropical, terrestrial





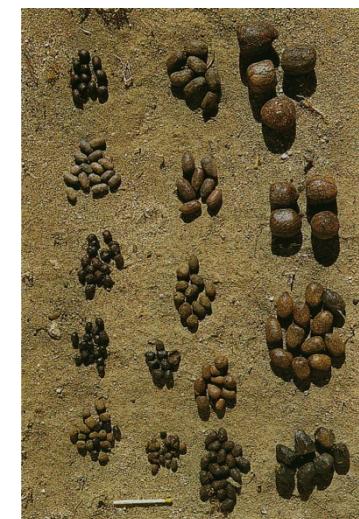
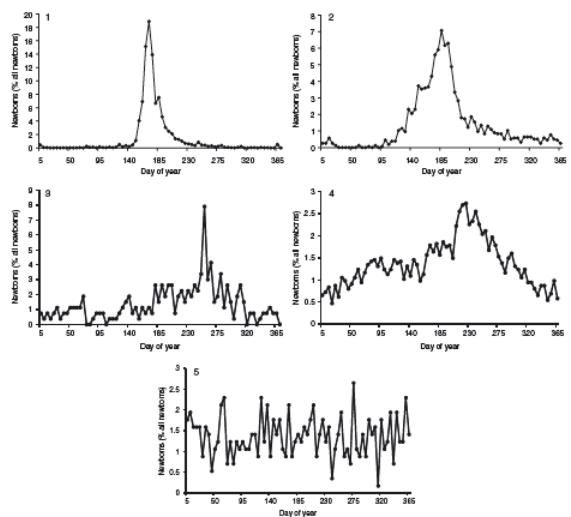
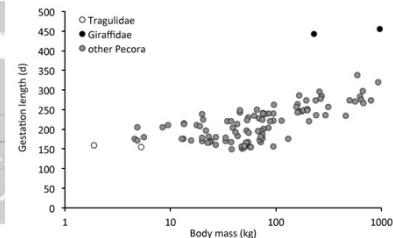
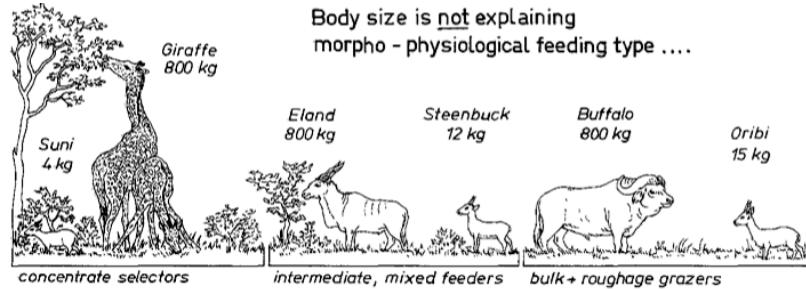
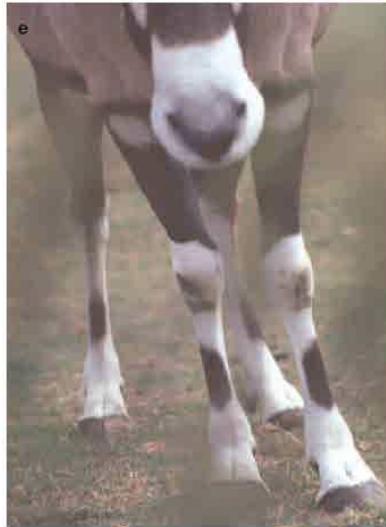
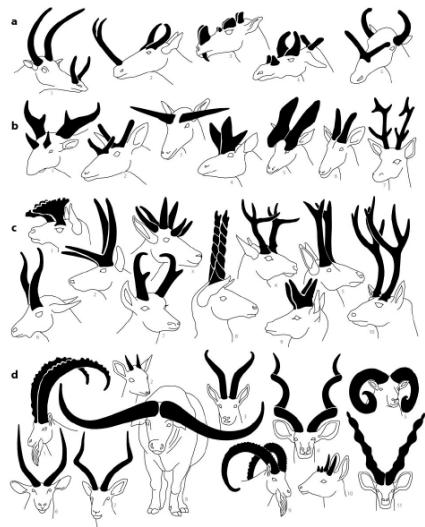
The ruminant digestive tract – an ideal model



(from Nickel-Schummer-Seiferle 1967, Hofmann 1969, Spencer 1995, Clauss et al. 2009, 2010, Kaiser et al. 2010)



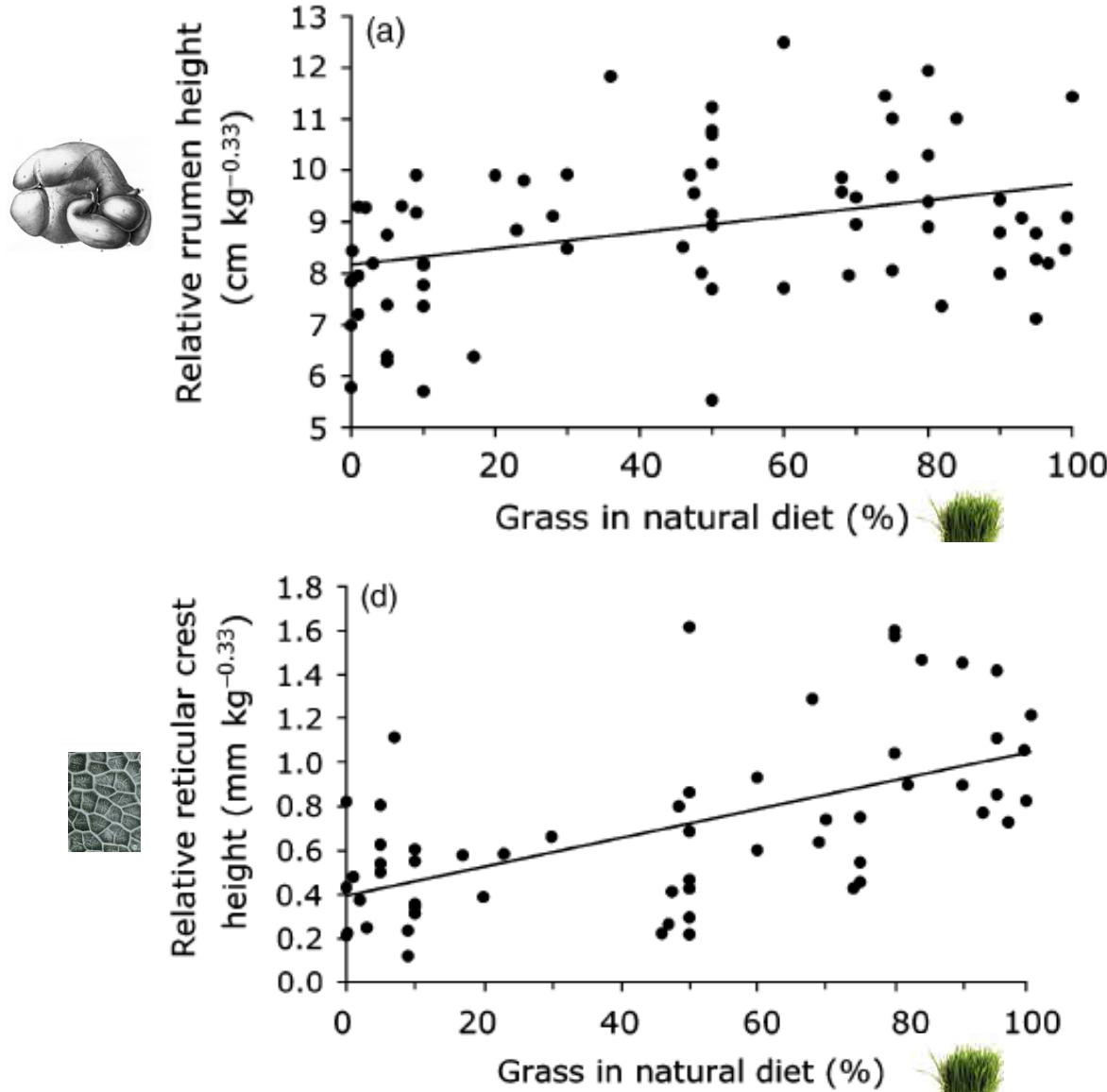
The ruminant group – an ideal model



(from Hofmann 1989, Emerle et al. 2003, Caro 2005, Zerbe et al. 2012)



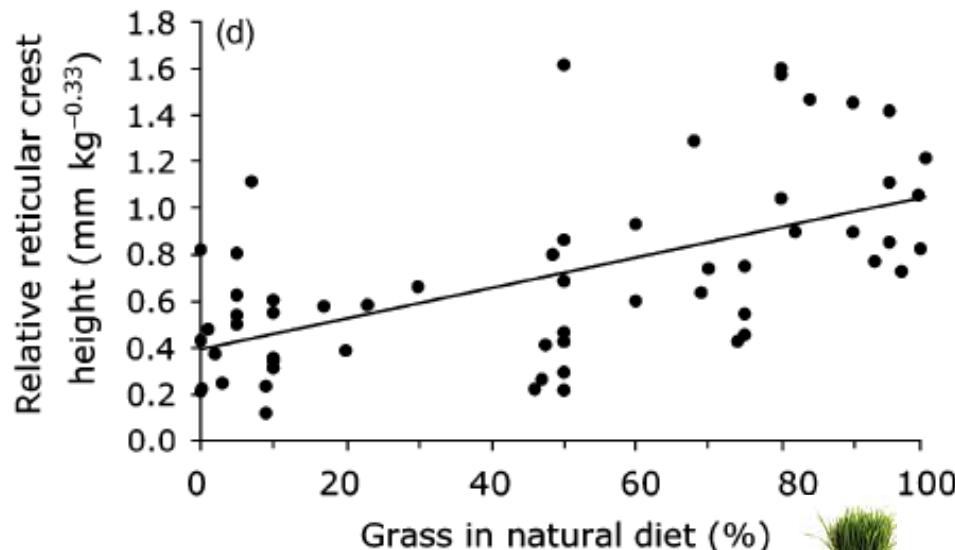
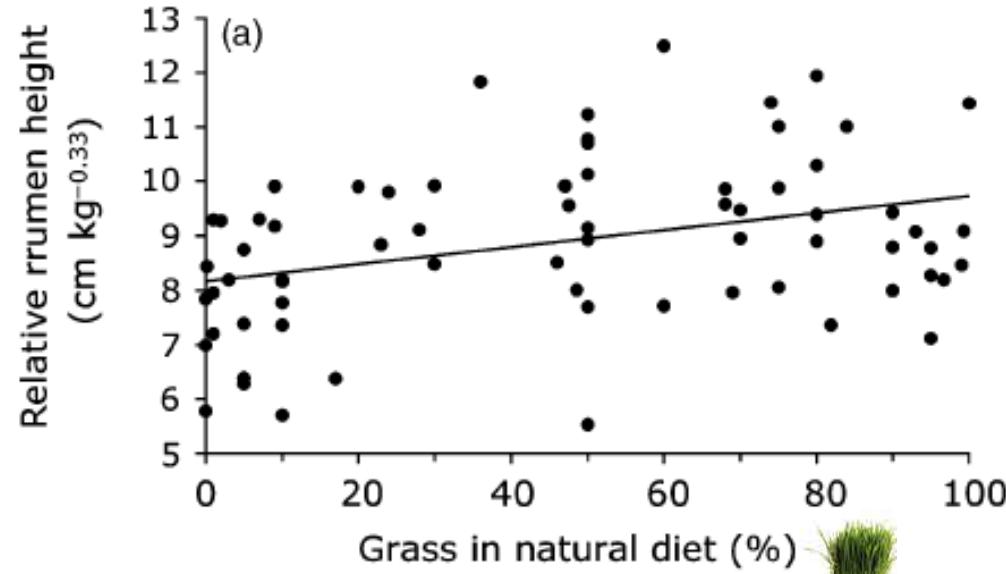
Reconstructing ruminant evolution



Clauss et al. (2010)



Reconstructing ruminant evolution

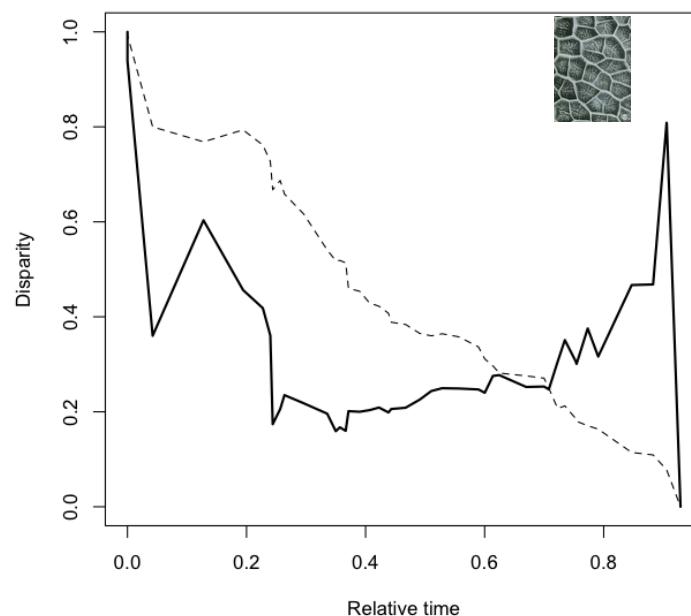
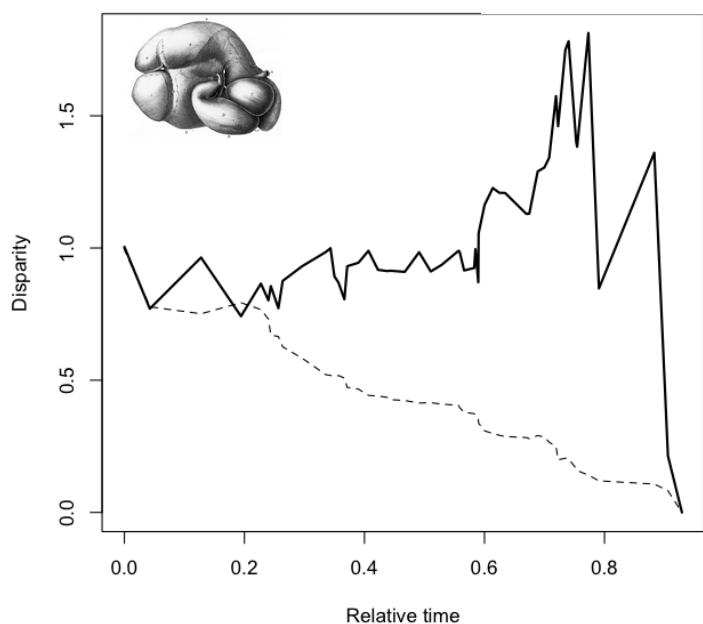
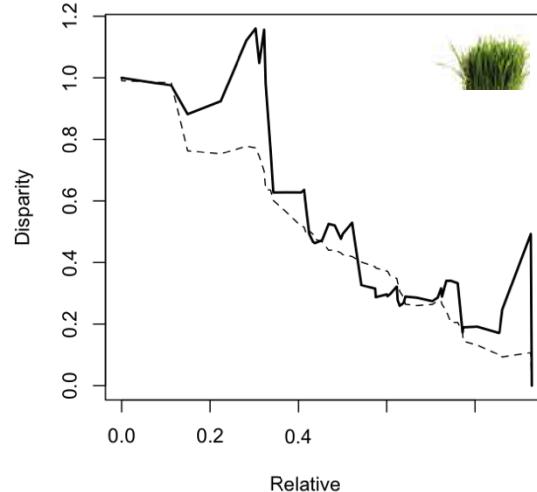


Evidence for convergence: correlation of form and 'function' (here: a niche proxy)

Clauss et al. (2010)



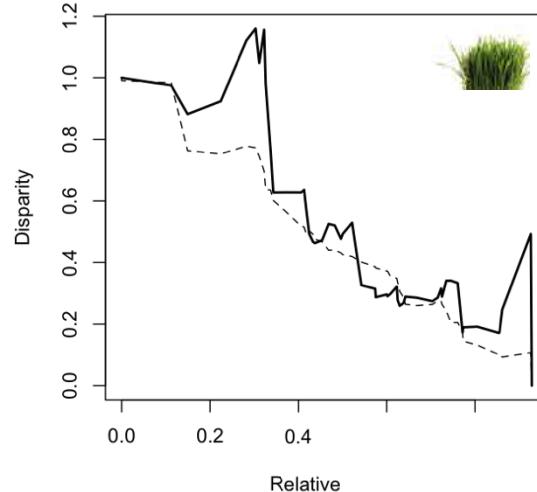
Reconstructing ruminant evolution



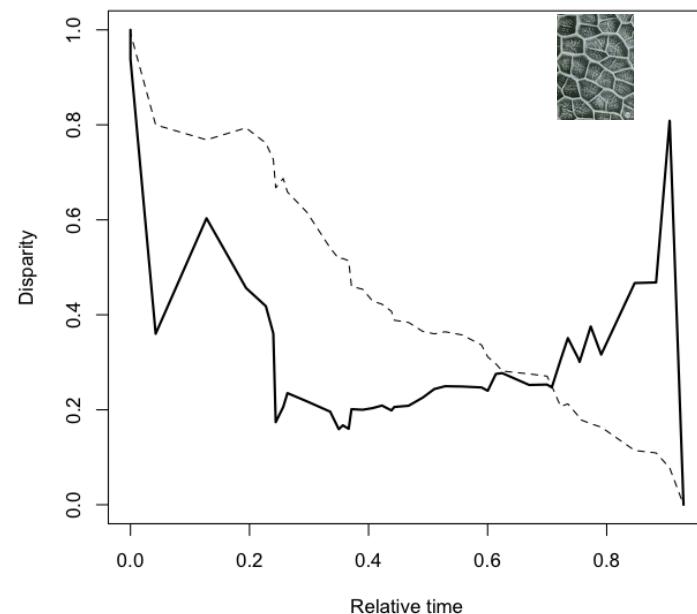
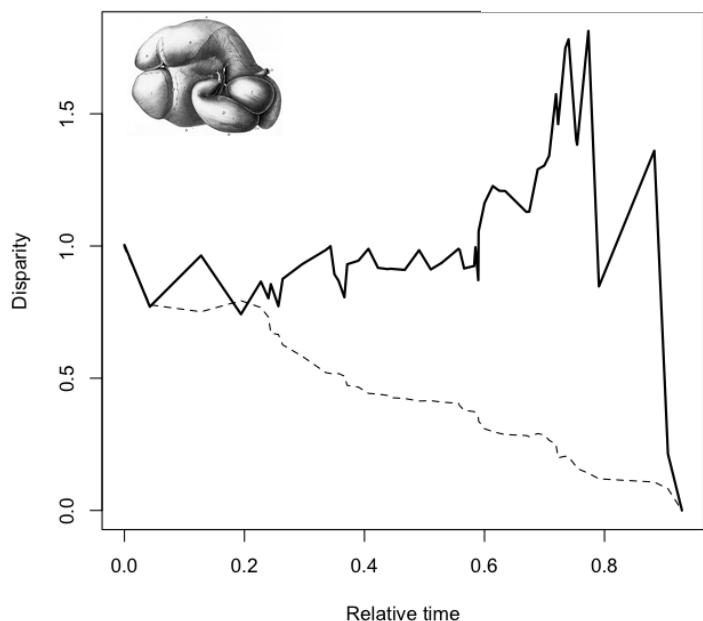
M. Dittmann (pers. obs.)



Reconstructing ruminant evolution



Anatomical traits linked to grazing did not evolve in synchrony with each other, and not with grazing (!?)



M. Dittmann (pers. obs.)



