Summary.

The macroscopical structure of the kidney has been examined in about 140 species from most mammalian orders. In more than 50 species the microscopical structure has been examined after maceration, and measurements have been made on one or more parts of the nephron.

There are some facts which indicate that a terminal segment, distinct from the rest of the proximal tubule, exists not only in carnivores but probably in all mammals.

The collecting tubules with arcades are shown to be secondarily developed from collecting tubules without such. An explanation of the phylogenetic mode of development is set forth. The arcades are most often developed in herbivores, and have probably developed independently in several groups.

There are several mammals whose kidneys show no long loops (*Hystrix*, *Castor*, *Elephas*, *Hippopotamus*, *Papio*). This is almost certainly a secondary feature, developed independently in several groups of herbivores. This is also the case with the occurrence of numerous cortical nephrons.

The variation of the length of the proximal tubule within the kidney has been studied, as also the relation between the thickness of the cortex and the medulla, and the length of the proximal tubule.

The diameter of the proximal tubule increases relatively rapidly with increasing tubule length, when the latter is small or moderate (up to about 15 mm). When the length of the proximal tubule increases further, the increase in the diameter is slight. Similar circumstances are found with regard to the thick segment and the distal tubule.

The composition of the nephrons is studied in several species. It is shown that there are quantitative differences between carnivores and herbivores. Among the latter a group of 4 desert rodents deviates markedly from the others; the thin and the thick segment are lengthened.

In this connection the problem of the localisation of the water reabsorption in the nephron is discussed. The theory that the hypertonicity of the urine develops in the thin segment is not adequately founded. The comparative study of the nephron composition indicates that, though

a water reabsorption probably occurs in the thin segment, this is also the case in the thick segment, and perhaps in the distal tubule and possibly in the collecting tubules also.

The surface and volume of the segments of the average nephron have been calculated in a few species. v. MÖLLENDORFF's index is discussed.

The simple kidney with a papilla is the primitive kidney type in the mammals. From it the kidneys with crest, with tubi maximi, with papillae and with renculi have developed, each of them independently in several groups. This is not only evident from comparative anatomical facts, but is also entirely in agreement with the embryonic development of the kidneys. The cortex and the zones of the medulla are relatively thinner in kidneys of the secondary types than in the primitive simple kidney. The secondary types usually occur in aquatic or large mammals.

The proximal tubule is relatively shorter in large kidneys than in small. This indicates that the nephrons cannot increase in length as much as the increase in kidney size demands. This is probably the reason why the secondary kidney types have developed in large mammals. In freshwater forms the medullary thickness is decreased (in connection with a shortening of the relative length of the distal parts of the nephron), which seems to be the main cause for the occurrence of modified kidney types in freshwater forms.

An attempt is made to explain the limitation of the length of the proximal tubule as due to the increasing pressure in the capsule required to force the fluid through the nephron when the nephron length increases. If this pressure rises markedly it will interfere with the filtration process in the glomerulus. It seems possible to extend this explanation to the extraordinary shortness of the nephrons in some diving carnivores, and thus to explain the extreme development of the renculi kidney in the marine mammals and *Lutrinae*.

Some evolutionary aspects of the phylogenetic development of the mammalian kidney are discussed. It is concluded that the development may be explained on a selectionist basis, but hardly on an orthogenetic or a Lamarckian one.

Table 47. *Kidney type, kidney size* (= the cube root of the product of the dimensions), *layer thickness, relative layer thickness* $\left(=\frac{\text{layer thickness}}{\text{kidney size}}\right)$ *of mammalian kidneys.*

Z. = ZARNIK 1910, G. = GERHARDT 1914, pap. = papilla, l. pap. = long papilla, s. pap. = several papillae, sh. cr. = short crest, cr.-p. = intermediate between crest and papilla, cr.+t. = crest+tubi maximi; the page numbers refer to descriptions in the special section; the rel. thickness is multiplied by 10.

[1] Forms with arid habitat. [2] Forms with moist habitat.

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Echidna aculeata (Z.)	pap.	(21)	6	7	0	6.2	6.2	3.3
Ornithorhynchus anat.[2]	sh. cr.	19	4	4.5	0	4.5	4.5	2.4
Philander sp.	l. pap.	6.5						
Sminthopsis murina	pap.	5.9	1.0	1.4	2.4	8.1	4.1	6.4
Antechinomys laniger[1]	l. pap.	5.5	1.0	1.5	2.9	9.8	4.5	8.0
Perameles sp.	pap.	8.3						
Sarcophilus satanicus	pap.	31	5	4.5	11	6.6	3.1	5.0
Dasyurus viverrinus	pap.	15		10		6.7		
Didelphys opossum	pap.	23	4	5	8	7.4	3.9	5.7
Acrobates pygmaeus	l. pap.	5.1	1.4	1.2	2.2	9.4	5.1	6.7
Petaurus breviceps	pap.	8.2						
Phascolarctus cinereus	pap.	26	6	10.5		6.3		4.0
Phalangista vulpina	pap.	25	4.5	14		7.4		5.6
Macropus giganteus[1]	pap.	49	8	9	17	6.9	3.5	5.3
Phascolomys mitchelli	crest	35	8	16		6.9		4.6
Tupaia javanica	pap.	8.3	1.5	5		7.8		6.0
Macroscelides sp.[1]	l. pap.	7.0	1.4	2.6	4	11.4	5.7	9.4
Centetes ecaudatus (G.)	pap.	18						
Erinaceus europaeus	pap.	17	2.4	2.3	5.6	6.1	2.8	4.6
Sorex araneus	pap.	5.0	0.9	1.0	1.8	7.6	3.9	5.7
Sorex minutus	pap.	3.9	0.6	0.8	1.1	6.4	3.6	4.9
Neomys fodiens	pap.	5.0	0.7	0.9	1.6	6.4	3.2	5.0
Pachyura etrusca	l. pap.	3.3	0.5	0.75	1.3	7.7	3.8	6.2
Talpa europaea	pap.	8.0						
Desmana moschata[2]	p. 281	11	2.2	2.3	2.0	5.9	4.1	3.9
Galeopithecus (G.)	pap.	(21)						
Pteropus edulis	pap.	14	2.7	5.3	0	5.7	5.7	3.8
Pteropus medius	pap.	13	3	4.5	0	5.8	5.8	3.5

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Pipistrellus nilssoni	l. pap.	5.0	0.85	1.3	2.8	9.9	4.3	8.2
Vespertilio murinus	l. pap.	4.8	0.8	1.3	2.4	9.4	4.4	7.7
Oryctolagus cuniculus . . .	pap.	28	5	5	10	7.1	3.6	5.4
Ochotona alpina	pap.	8.2		6.3		7.7		
Aplodontia rufa	sh. cr.	17	4.2	5		5.4	5.4	2.9
Sciurus vulgaris	pap.	12	1.8	2.6	3.8	6.8	3.7	5.3
Castor fiber[2]	2 pap.	36	7	14	0	5.8	5.8	3.9
Perodipus agilis[1]	l. pap.	7.5	1.5	1.7	4.3	10	4.3	8
Dipodomys m. exilis[1] . . .	l. pap.	5.9	1.0	1.2	3.8	10.2	3.7	8.5
Heteromys adspersus . . .	pap.	6.5		5.5		8.5		
Geomys tuza	pap.	10	2.6	5		7.6		5.0
Pedetes caffer[1]	pap.	22	5	4	9	8.2	4.1	5.9
Jaculus jaculus[1]	l. pap.	8.0	1.4	2.1	5.3	11	4.4	9.3
Spalax typhlus	pap.	7.6		5.5		7.2		
Cricetus cricetus	pap.	12		9		7.5		
Microtus agrestis	pap.	9.0	2.1	2.8	2.4	8.1	5.4	5.8
Evotomys glareolus	pap.	7.0						
Arvicola terrestris	pap.	9.5						
Neofiber alleni[2]	pap.	8.4	2	3		6.0		3.6
Epimys rattus	pap.	14	2.9	2.6	5.4	7.9	3.9	5.8
Mus musculus	l. pap.	6.1	1.3	1.2	3.7	10.2	4.1	8.0
Mus flavicollis	pap.	6.9	1.5	1.3	3.0	8.4	4.1	6.2
Mus sylvaticus	pap.	5.9	1.2	1.8	2.7	8.8	4.2	6.8
Deomys ferrugineus	pap.	7.5		6		8.0		
Gerbillus pyramidum[1] . . .	l. pap.	6.2		7.5		12.1		
Meriones melanurus[1] . . .	l. pap.	9.1		9		9.9		
Psammomys obesus[1]	l. pap.	13	2.1	2.4	11.5	12.3	3.5	10.7
Hydromys chrysogaster[2] . .	sh. cr.	15	2.7	2.1	3.7	5.7	3.2	3.9
Hystrix cristata[(1)]	crest	44	8	12	0	4.5	4.5	2.7
Atherura africana (G.) . .	crest	28						
Erethizon dorsatus (G.) . .	p. 316	33						
Coelogenys paca[2] (G.) . . .	tubi	31						
Dasyprocta aguti	p. 316	23	5	9		6.1		3.9
Hydrochoerus capyb.[2] (G.) .	tubi	53	9	11		3.8		2.1
Dolichotis patagonica[1] . . .	pap.	35	5	7	13	7.1	3.4	5.7

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Chinchilla lanigera	pap.	13	2.5	1.7	7	8.6	3.2	6.7
Myocastor coypus[2]	sh. cr.	24	5.5	8.5		5.8		3.5
Ctenodactylus gundi[1] . . .	l. pap.	6.1		6		9.8		
Manis javanica	pap.	23	4.5	13		7.6		5.7
Bradypus sp.	sh. cr.	23	4	10		6.1		4.3
Cyclopes didactylus	l. pap.	8.3	2	6		9.6		7.2
Dasypus sexcinctus	pap.	32	6	5	10	6.6	3.4	4.7
Felis catus	pap.	30	5.5	4	10.5	6.7	3.2	4.8
Felis leo[1] (HECKING) . . .	sh. cr.	89	7	8	34	5.5	1.7	4.7
Felis tigris (HECKING) . . .	sh. cr.	78	8	6	27	5.3	1.8	4.2
Felis pardus (HECKING) . .	pap.	49	6	6	19	6.3	2.4	5.1
Felis pardalis	pap.	53						
Felis onca	sh. cr.	56	6.5	5	21	5.8	2.1	4.6
Lynx lynx	sh. cr.	45	6.5	6	14.5	6.0	2.8	4.6
Arctitis binturong	cr.-p.	21	5	7	0	5.7	5.7	3.3
Viverra sp.	cr.-p.	21	3	2.5	7	6.0	2.6	4.5
Cryptoprocta ferox	pap.	22	4	5	8	7.7	4.1	5.9
Prionodon linsang	pap.	14	2.7	2.5	6.5	8.4	3.7	6.4
Hyaena sp.[1]	crest	54	7	7	19	6.1	2.6	4.8
Canis lupus	crest	51	7	7	16	5.9	2.7	4.5
Canis familiaris	crest	40	7	6	11	6.0	3.3	4.3
Nasua narica	pap.	26	5.5	3.5	6.5	6.0	3.5	3.8
Potos flavus	pap.	17						
Procyon lotor	sh. cr.	28	5.5	3.5	7.0	5.7	3.2	3.8
Ailurus fulgens (G.)	cr.-p.	29						
Ailuropoda melanoleuca (RAVEN)	6 lob.	57						
Ursus arctos	renc.	73	6	6	8	2.7	1.6	1.9
Mustela erminea	pap.	11	1.5	1.7	4.5	7.0	2.9	5.6
Lutreola vison	pap.	23	3.5	3.5	7	6.1	3.0	4.6
Martes martes	cr.-p.	18	2.5	2.5	4	5.0	2.8	3.6
Gulo gulo	crest	42		26		6.2		
Meles meles	cr.-p.	33	4.5	4	11	5.9	2.6	4.5
Lutra lutra[2]	renc.	38	3.5	4	7.5	3.9	2.0	3.0

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of cortex	Thickness in mm of outer zone	Thickness in mm of inner zone	Relative thickness of cortex + medulla	Relative thickness of cortex + out. zone	Relative thickness of medulla
Phoca hispida[2]	renc.	62	2.2	3	6	1.8	0.8	1.5
Phoca barbata[2]	renc.	97	2.5	4	7	1.4	0.7	1.1
Otaria jubata[2]	renc.	77	2.5	3	6	1.5	0.7	1.2
Phocaena phocaena[2]	renc.	73	1.5	2	3	0.9	0.5	0.7
Balaënoptera musculus[2] . .	renc.		6	9	9			
Procavia capensis	pap.	16	2	4	5	6.9	3.8	5.6
Elephas maximus	renc.	170	20	20	0	2.4	2.4	1.2
Trichechus manatus[2] . . .	p. 346	80	7	20		3.4		2.5
Halicore dugong[2] (RIHA) . .	p. 347	130	8	25		2.5		1.9
Rhytina stelleri[2] (STELLER) .	renc.							
Hippopotamus amphibius[2] .	tubi	160	12	16	0	1.8	1.8	1.0
Sus scrofa domestica . . .	s. pap.	86	20	7.5	6.5	4.0	3.2	1.6
Phacochoerus sp.	p. 359							
Dicotyles sp.	tubi							
Camelus bactrianus[1] . . .	crest	110	15	15	25	5.0	2.7	3.6
Lama lama, young	crest	40		21		5.3		
Tragulus javanicus	tubi	21	4.5	5.5		4.8		2.6
Cervus elaphus	cr. + t.	65	10	15		3.8		2.3
Dama dama	crest	53	9	11	8	5.3	3.8	3.6
Alces alces	crest	93	23	13	12	5.2	3.9	2.7
Rangifer tarandus	tubi	45	15	12	3	6.7	6.0	3.3
Antilope cervicapra[1] . . .	pap.	38	6.5	5.5	12.5	6.4	3.2	4.7
Connochaetes gnu[1]	crest	50	7	21		5.6		4.2
Cephalophus melanorh. . . .	sh. cr.	25		16		6.4		
Ovis aries	crest	50	7	7	10	4.8	2.8	3.4
Ovibos moschatus	crest	79	18	24		5.3		3.0
Anoa depressicornis	s. pap.	54	7	5	8	3.7	2.2	2.4
Bos taurus	lobes	98	9	9	10	2.9	1.8	1.9
Bison bonasus, young . . .	lobes							
Giraffa[1] (GERHARDT 1899) .	l. cr.	110		40		3.6		
Tapirus indicus	tubi	84		42		5.0		
Rhinoceros bicornis	p. 365							
Equus caballus	tubi	110	14	16	21	4.6	2.9	3.4

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of: cortex	outer zone	inner zone	Relative thickness of: cortex + medulla	cortex + out. zone	medulla
Orycteropus (HYRTL 1872) .	pap.							
Lemur catta	pap.	21	5	5.5	2.0	6.0	5.0	3.6
Chiromys madagascar. . . .	pap.	13	2.5	3	5	7.7	4.2	6.2
Galago sp.	cr.-p.	27	6	8		5.2		3.0
Galago sp.	pap.	9.7	2.7	4.6		7.5		4.7
Tarsius spectrum	pap.	9	2	1.5	4.5	8.9	3.9	6.7
Hapale jacchus	pap.	10	2	5		7		5
Macacus sylvanus	tubi	34	8	11	0	5.6	5.6	3.2
Papio sp.	crest	34	8	9	0	5.0	5.0	2.6
Homo sapiens	lobes	64	6.5	19		4.0		3.0

Table 48. *Percentage of long loops, cortical nephrons, kidney size, nephron composition, index and volume index of mammalian kidneys.*

1. Corrected to correspond to the swollen tubules. 2. Corrected for shrinkage. 3. (in the cat). Composition of high nephron from table 26 k. + cortical nephrons. y. = young.

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %: p.t.	t.s.	th.s.	d.t.	"Mean nephron" composition %: p.t.	t.s.	th.s.	d.t.	Prox. tubule / Thick segment	Ind.	Vol. ind.
Sminth. m.	24	5.9	2.0	34	14	35	16	33	28	26	13	1.24	10.8	6.8
Antechin. l.	30	5.5	2.5	35	17	36	12					1.13	10.8	4.7
Macroscel.	34	7.9[1]	4.2	42	11	38	10					1.27	10.2	5.0
Erinaceus e. . . .	39	17	5.0	41	12	33	14					1.38	14.6	7.9
Sorex a. old . . .	12	7.0	2.2	41	12	35	13	40	16	32	12	1.29	17.7	13.3
» » y.	24	5.0	1.6	39	10	36	15						11.5	7.9
» *m.*	16	4.2	1.0	40	14	34	13						11.7	9.1
Neomys f.	21	5.0	1.5	39	11	33	15	38	20	29	14	1.31	9.7	5.7
Pachyura e. . . .	18	3.3	1.1	36	14	35	15	34	23	30	12	1.12	12.9	10.7
Desmana m. . . .	5	11	4.0[2]										13.4	6.0
Pteropus e.	0+	14	3.8	58	2	21	19						15.1	9.5
Pipistr. n.	25	5.0	1.8	33	15	36	17					1.20	6.5	2.9
Vespert. m. y. . .	27	4.8	1.8	36	13	35	17					1.08	6.9	4.0
» » ad. . .	36	5.5	1.8					30	25	31	14	0.96	9.0	5.8

Table 48 (Cont.).

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %				"Mean nephron" composition %				Prox. tubule / Thick segment	Ind.	Vol. ind.
				p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.			
Oryctol. c. ♂ 10 m.	48	27	16.2	55	9	29	7	56	13	25	6	2.25	30.0	14.5
» ♀ 10 m.	46	28	16.7	58	7	27	8	54	16	24	6	2.23	23.0	9.1
Sciurus v.	57	12	6.9	54	9	29	9					2.00	18.9	10.9
Castor f.	0+	36	12[2]										25.6	13.8
Perodipus a.		9.0[1]	4.1	40	16	34	10					1.40	16.4	8.9
Dipodomys m.	27	5.9	2.4[2]	40	18	34	8	38	25	29	7	1.29	14.7	6.9
Jaculus j.	33	8	4.5	37	18	38	7					1.18	18.6	9.5
Microtus a. ♀	14+	7.7	4.1	57	2	30	12	56	8	25	10	2.28	7.9	3.0
» » ♂	8+		4.5	55	3	33	9					1.57	20.0	14.5
Evotomys g.	+	7.0	3.3	61	1	24	13						19.2	12.9
Epimys r.	28	14	10	54	10	30	8					1.87	18.9	8.4
Mus musc.	24	6.1	4.0	56	7	29	8					2.15	16.9	9.9
Mus flavic. ♂	27	7.5	4.0	52	6	32	10	53	11	28	9	1.90	13.9	7.3
» » old ♂	23	8.1	4.7	53	6	31	10	51	11	29	9	1.74	19.2	11.7
Mus sylv.	17	5.9	3.9	51	8	28	13					2.12	15.3	7.8
Hydromys chr.		17	7.5									1.83	28.5	16.4
Psammomys o.	100	13	4.2									0.91	10.5	5.1
Hystrix c.	0+	33[1]	12.6									1.43	17.9	7.7
Felis c. y. ♀ 66 gm[3].	100	24	5.8	44	27	29	7	34	30	27	9	1.30	16.5	8.2
» » ♂ 17 gm.	100	32	18					47	21	24	8	2.00	52.6	37
Arctitis. b.	0+	21	7.1[2]	54	1	30	16					1.63	14.1	5.9
Canis f.	100	40	14.8	44	20	27	9	41	27	23	9	1.78	22.2	9.4
Ursus a.	17	65	11	50	8	28	15	50	13	25	11	2.00	20.1	8.7
Mustela e.	95	11	3.8	42	15	31	12					1.58	15.2	9.1
Lutreola v.	74	23	9.2	40	13	34	13						12.2	4.8
Lutra l. ♀		38	7.4	45	15	32	9						12.0	4.7
» » ♂	46	32	6.8	45	12	32	12						14.8	7.0
Phoca h.	42	62	5.2	42	14	35	9	39	26	28	7	1.38	10.5	4.2
Phoca b.	68	126[1]	10.7	35	21	33	7					1.18	13.5	5.3
Phocaena ph.	34	85[1]	5.1	40	16	35	9					1.28	9.5	4.0
Balaenopt. m.	37		13.3	39	20	35	6					1.15	16.2	6.1
Procavia c.	17	16	9.2[2]										14.1	5.1
Elephas m.	0+	170	19	55	2	23	21						8.2	2.2

Table 48 (Cont.).

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %				"Mean nephron" composition %				Prox. tubule / Thick segment	Ind.	Vol. ind.
				p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.			
Hippopot. a.	0+	160	20	60	0	27	13						12.5	3.6
Sus s. old ♀	3+	86	35	73	0	16	11	68	4	17	12	4.0	20.2	5.3
» » y.	+	66	25										22.4	8.7
Camelus b.	55	110	29	49	11	35	6					1.26	18.7	5.1
Dama d.		53	19										14.7	4.3
Alces a.	+	93	22										17.8	7.4
Rangifer t.	+	45	21[2]										21.9	7.7
Ovis a.	36	50	19	52	10	32	6						18.9	5.6
Bos t.	21	98	27	56	8	25	11	50	13	28	9	1.80	17.7	5.2
Equus. c.	19	110	26[2]	53	10	32	5	51	14	29	6	1.73	19.8	6.3
Chiromys m.	24	13	5.1	43	12	35	12					1.50	12.8	5.9

Table 49.

	Average nephron		Average nephron (excl. capsule)								Total kidney weight gm	Total nephron number n	Author	$\frac{n \times v}{1000}$
	Surface sq. mm	Volume cmm v	Surface of the segments %				Volume of the segments %							
			p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.				
Sorex araneus	0.5015	0.004233	57	4.7	25	13	69	1.1	18	13	0.35	82000	DENZER 1938	0.35
Neomys fodiens . . .	0.2726	0.001729	53	5.8	25	16	64	1.5	19	16	0.19			
Rabbit, male 10 m . .	4.327	0.06258	77	2.7	15	4.8	88	0.5	7.9	3.3	22	315000	NELSON 1922	19.7
» *, female 10 m* .	4.133	0.05179	72	5.5	16	6.1	84	1.6	9.7	5.0	24	315000		16.3
Dipodomys m. exilis			51	12	29	7.8	61	5.5	26	7.4				
Mus flavicoll. male .	0.7764	0.007096	68	3.1	21	8.6	78	0.8	14	7.2	0.42	72000	DENZER 1938	0.51
Dog	4.449	0.05305	60	11	20	8.6	74	3.6	15	7.0	77	800000	KUNKEL 1930	42.4
Cow	7.823	0.1112	69	5.3	19	7.3	82	1.9	11	5.0	1000	8000000	» »	890