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Checklist: Vertebrate homeobox genes

Stefan Stein, Rüdiger Fritsch, Lydia Lemaire, Michael Kessel*

Max-Planck-Institut für biophysikalische Chemie, D-37077 Göttingen, Germany

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Abstract

Up to now around 170 different homeobox genes have been cloned from vertebrate genomes. A compilation of the various isolates from mouse, chick, frog, fish and man is presented in the form of a concise checklist, including the designations from the original publications. Putative homologs from different species are aligned, and key characteristics of embryonic or adult expression domains, as well as mutant phenotypes are briefly indicated.

Keywords: Homeobox genes; Homeodomain; Vertebrate

Many developmental control genes are characterized by a common sequence motif, a homeobox, encoding a homeodomain. The high degree of conservation throughout the animal and plant kingdom has allowed the isolation of homeoboxes by screening or PCR procedures. Subfamilies of highly related genes were recognized by sequence comparisons of the homeodomains, and homologies between genes from different species could be assigned. The homeobox has proved a unique entry site for the study of vertebrate development. Expression analyses, overexpression in transgenic mice and inactivation via homologous recombination in embryonic stem cells have allowed the unravelling of major steps in development. As a common denominator, homeobox genes appear to be involved in the specification of cellular identity in the widest sense.

The number of isolated homeoboxes has increased dramatically over the last years. Multiple isolations and a non-standardized nomenclature have further contributed to a growing confusion concerning the identity of a given box in relation to those of the same or other species. This large amount of primary data has been dealt with in a number of excellent reviews (Duboule, 1994; Gehring et al., 1994; Kappen et al., 1993; Laughon, 1991; Schubert et al., 1993; Scott, 1989). Based on published communications and EMBL/Genebank entries we have assembled a checklist of the currently identified homeobox genes in vertebrates. Our current database contains about 650 boxes or domains from animal and plant sources. In order to summarize our current knowledge in a concise, but still informative pattern, we have condensed the available information in one large table. Our aim was to allow a quick placement of a gene into its context, cross-reference its potential homologs from other species to provide key information, and allow the reader to proceed from here to the primary publications. The emphasis of our checklist lies in the direct comparison of vertebrate homologs, which allows the fast checking for specific genes in different species. The checklist indicates that so far a total of around 170 different vertebrate homeobox sequences have been identified. Although realistic estimations are difficult at the present time, this may represent more than half of the homeobox genes actually present in a given vertebrate genome. Thus, more than 0.1% of the estimated 100 000 genes per genome may possess a homeobox.

The table lists on the left hand pages the published homeobox genes from the five major experimental systems in vertebrates, namely mouse *(Mus musculus)*, chick *(Gallus gallus)*, frog *(Xenopus laevis)*, zebrafish *(Danio rerio)* and man *(Homo sapiens)*. Genes from the five species aligned horizontally are suspected homologs based mainly on sequence comparisons. Such homology relationships cannot, however, readily be extended to homeobox genes of the fruitfly *(Drosophila melanogas*

* Corresponding author. Tel.: +49 551 2011560; fax: +49 551 2011504.

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mouse	chick	frog	zebrafish	man	fruitfly
Atbf1=zfh4				ATBF1 <a-d>	zfh-2 <a-c> (159)
Tcf8=bzp	∂EF1			TCF8=NIL2A =BZP=AREB6	zfh-1 (159)
Barx1					BarH1/BarH2 (215) bsh (252)
Cdx1				CDX1	caudal (331)
Cdx2				CDX2	
Cdx3*				CDX3=JRX	
Cdx4	CHOXCAD2		Zf-cad1	CDX4	
	CDXA =CHOXCAD	Xlcad2			
		Xcad1			
		Xcad3			
Cutl=Cux=Clox				CUTL=CUT=CDP	cut=bk88 (41)
Dlx1=Dll				DLX1	distal-less (80)
Dlx2=Tes1=Gsh3		Xdll1/Xdll4	zdlx2	DLX2	
Dlx3=Dlx7		Xdll2	zdlx3		
Dlx4					
Dlx5	DLX5	Xdll3	zdlx4	DLX5	
Dlx6		xdll		DLX6	
		Xdll5			
Emx1			emx1	EMX1	empty spiracles=e4 (95)
Emx2			emx2	EMX2	e5 (95)
En1	EN1	En1=En1a/En1b	En1=Eng1	EN1	engrailed/ invected (83, 156)
En2	EN2	En2	En2=Eng2	EN2	
			En3=Eng3		
Evx1		Evx1=Xhox3	eve1	EVX1	evenskipped (312)
Evx2				EVX2	
Gbx1=Gst1 =MMoxA	CHOX7=OVX1	XGst1	G9*	GBX1	unplugged (72)
Gbx2=Gst2 =MMoxB		Xlhox7A/B =XGstA		GBX2	
gsc	GSC	gsc	gsc	GSC	goosecoid (186) =60Mun2 (116)
Gsh1				HPX15	
Gsh2					
Gtx					
Hesx1=Hes1					
Rpx		Xanf1			
		Xanf2			
Hhex=Hex	PRH=PROBOX			PRHX=HEX=PRH	
m1234					
Hlx				HLX1=HB24	H2.0 (26)
Dbx=Gsh5	ChoxE=cHLX-A		Hlx1		
				HLXB9=HB9	66Dem (116)
				Homeb	
				Homec	
				HPX2	

Embryonic or adult expression in vertebrates (EE, AE), knock out phenotype (KO), comments (C)	references
EE: skeletal muscle, midbrain, hindbrain, differentiated EC cells C: zfh-2 contains three, ATBF1 four homeodomains	(232, 278, 341, 523)
EE: notochord, somites, nephrotomes; lens C: diverged homeobox, several zinc fingers	(160, 170, 504, 512, 513)
EE: craniofacial ectomesenchyme, stomach, 1st, 2nd branchial arch	(487)
EE: intestine, primitive streak. KO: homeotic transformation of vertebra	(135, 229, 327, 469)
AE: intestine, reduced in later stages of human colorectal carcinogenesis	(137, 244, 245)
AE: intestine, tumor cell lines. C: *only hamster gene described	(183, 234)
EE: primitive streak, neuroectoderm, presomitic mesoderm, hindgut endoderm	(173, 225, 251, 443)
EE: primitive streak, definitive endoderm, intestine	(44, 120, 166-168, 316)
EE: dorsal blastopore lip	(44)
EE: marginal zone	(356)
EE: entire neural axis, heart, cartilage. C: repression of Myc and Ncam	(13, 134, 293, 347, 496)
EE: forebrain, branchial arches, facial and limb primordia, otic vesicle, retina	(56, 127, 383, 384, 409, 508)
EE: similar to Dlx1, but lower level. C: Dlx1 +2 clustered KO: abnormal forebrain and branchial arch derivatives	(5, 55, 368, 371, 379, 380, 387, 406, 441)
EE: not in CNS; 1st, 2nd branchial arch, otic vesicle, limb bud, epidermis	(5, 117, 138, 337, 338, 371, 406)
C: only PCR fragment	(407)
EE: forebrain, preskeletal structures; branchial arches; auditory vesicle; fin fold	(5, 150, 371, 452)
EE: similar to Dlx5, but lower level. AE: ovary, testis. C: Dlx5 + 6 clustered	(14, 49, 452)
C: PCR fragment most similar to Xdll4	(371)
EE: forebrain	(48, 264, 342, 450, 454)
EE: forebrain	(48, 264, 342, 450, 454)
EE: mid-hindbrain junction, hindbrain, spinal cord, dermamyotome, sclerotome, limbs KO: lethal, no cerebellum, limb abnormalities	(97, 101, 139, 204, 221, 256, 306, 324, 505, 517)
EE: see En1, myoblasts, first branchial arch KO: viable, abnormal foliation pattern in the cerebellum	(97, 100-102, 139, 154, 157, 211, 221, 255, 257, 306, 328, 351)
C: possibly recent duplication of En2	(139, 221)
EE: primitive streak, neural tube, limb buds. KO: postimplantation lethality	(32, 136, 143, 250, 320, 416, 458)
C: located 5' of the HoxA cluster	(415, 417, 418)
EE: CNS, limb buds, genitalia (similar to Hoxd13). C: located 5' of the HoxD cluster	(32, 94, 123)
AE: haematopoetic cell lines. C: *only goldfish gene described	(145, 320, 321)
EE: forebrain, hindbrain, spinal cord	(56, 67, 320)
EE: blastopore lip, primitive streak, prechordal and head mesoderm, limb KO: normal gastrulation, craniofacial defects	(42-44, 74, 177, 237, 349, 350, 482) (401, 521)
EE: forebrain, midbrain, spinal cord	(339, 455, 497)
EE: forebrain, hindbrain	(227, 455)
AE: glial cells of brain, germ cells. C: Similar to Nkx6.1 from hamster	(274)
EE: ES cells, liver, lung	(483, 484, 506)
EE: anterior neural folds	(212, 423, 529, 530)
EE: anterior neural folds, pituitary	(285, 318)
AE: haematopoetic cells, lung, liver	(35, 91, 226, 315)
C: PCR-fragment	(108)
EE: haematopoetic cells, gut, liver, dermamyotome, endothelia, extraembryonic tissues	(7, 8, 111, 345)
EE: CNS, prechordal plate	(155, 307, 308, 392)
AE: B lymphocytes; pancreas, small intestine, colon, tonsils	(110, 112, 205, 345)
C: both Homeb/c boxes are part of the D4Z4 tandem repeat sequence associated with facioscapulohumeral muscular dystrophy; not very similar to each other	(214, 516) (214, 516)
C: PCR fragment from haematopoietic progenitor cells; most similar to Homeb	(339)

mouse	chick	frog	zebrafish	man	fruitfly
Hoxa1		Hoxa1		HOXA1	labial
Hoxa2	HOXA2			HOXA2	proboscipedia
Hoxa3			Hoxa3	HOXA3	
Hoxa4	HOXA4			HOXA4	Deformed
Hoxa5				HOXA5	Sex combs reduced
Hoxa6				HOXA6	Antennapedia
Hoxa7		Hoxa7		HOXA7	Ultrabithorax
Hoxa9	HOXA9			HOXA8	abdominal-A
Hoxa10	HOXA10			HOXA10	Abdominal-B
Hoxa11	HOXA11			HOXA11	Abdominal-B
Hoxa13	HOXA13			HOXA13	Abdominal-B
Hoxb1	HOXB1	Hoxb1		HOXB1	labial
Hoxb2				HOXB2	proboscipedia
Hoxb3	HOXB3	Hoxb3		HOXB3	
Hoxb4	HOXB4	Hoxb4	Hoxb4	HOXB4	Deformed
Hoxb5	HOXB5	Hoxb5	Hoxb5	HOXB5	Sex combs reduced
Hoxb6	HOXB6	Hoxb-6	Hoxb6	HOXB6	Antennapedia
Hoxb7		Hoxb7a		HOXB7	Ultrabithorax
Hoxb8	HOXB8	Hoxb8		HOXB8	abdominal-A
Hoxb9	HOXB9	Hoxb9		HOXB9	Abdominal-B
Hoxc4	HOXC4			HOXC4	Deformed
Hoxc5	HOXC5	Hoxc5	Hoxc5	HOXC5	Sex combs reduced
Hoxc6	HOXC6	Hoxc6	Hoxc6	HOXC6	Antennapedia
Hoxc8	HOXC8			HOXC8	abdominal-A
Hoxc9	HOXC9			HOXC9	Abdominal-B
Hoxc10	HOXC10			HOXC10	Abdominal-B
Hoxc11	HOXC11			HOXC11	Abdominal-B
Hoxd12				HOXC12	Abdominal-B
Hoxc13				HOXC13	Abdominal-B
Hoxd1		Hoxd1		HOXD1	labial
Hoxd3				HOXD3	
Hoxd4	HOXD4			HOXD4	Deformed
Hoxd8	HOXD8			HOXD8	abdominal-A
Hoxd9				HOXD9	Abdominal-B
Hoxd10	HOXD10			HOXD10	Abdominal-B
Hoxd11	HOXD11			HOXD11	Abdominal-B
Hoxd12	HOXD12			HOXD12	Abdominal-B
Hoxd13	HOXD13			HOXD13	Abdominal-B
Lbx1=Hesx2				LBX1=HPX6	ladybird early=d125 (243) ladybird late=nkch4 (243)
Lhx1=lim1	LIM1	lim1	lim1	LIM1	
		lim5=lim2	lim5		
Lhx4=gsh4	LIM3	lim3			bk64, bk87 (259)
Lhx3=lim3=PLim					
Isl1	ISL1		isl1	ISL1	
Isl2*	ISL2		isl2		
			isl3		
Lhx2=LH2=PB36	LH2			HLH2	apterous (52, 79)
Lmx1*	LMX1			LMX1	
		mix.1			

Embryonic or adult expression in vertebrates (EE, AE), knock out phenotype (KO), comments (C)	references
EE: hindbrain, spinal cord, occipital somites. KO: deficiencies in hindbrain, ear	(1, 28, 73, 126, 272, 286, 309)
EE: hindbrain, spinal cord, occipital somites. KO: transformation of 2nd branchial arch	(162, 182, 231, 346, 385, 399, 478)
EE: hindbrain, spinal cord, cervical somites. KO: no thymus, throat abnormal	(1, 73, 144, 175, 176, 333)
EE: hindbrain, spinal cord, cervical somites. KO: transformation of cervical vertebrae	(1, 172, 223, 224, 277, 413, 427, 439, 480)
EE: spinal cord, cervical somites, lung. KO: transf. of cervical and thoracic vertebrae	(1, 82, 132, 151, 246, 358)
EE: spinal cord, thoracic somites. KO: transf. of cervical and thoracic vertebrae	(1, 82, 130, 277)
EE: spinal cord, thoracic somites, kidney, stomach	(1, 22, 81, 87, 268)
EE: spinal cord	(1, 58, 411, 412, 426)
EE: spinal cord, lumbar vertebrae, urogenital tract, limb buds KO: transformation of lumbar vertebrae. cryptorchidism	(1, 37, 58, 200, 428, 525, 526)
EE: spinal cord, sacral vertebrae, urogenital tract, limb buds KO: transformation of lumbar and sacral vertebrae, limb defects	(1, 58, 200, 228, 456, 525, 526)
EE: limb buds, caudal vertebrae	(1, 58, 200, 525, 526)
EE: hindbrain, spinal cord, occipital somites	(1, 114, 164, 187, 206, 344, 472)
EE: hindbrain, spinal cord, occipital somites, visceral arches	(1, 231, 445)
EE: hindbrain, spinal cord, visceral arches, cervical somites, kidney, lung, stomach	(1, 114, 231, 439, 444)
EE: hindbrain, spinal cord, kidney, stomach, lung. KO: transformation of axis to atlas	(1, 194, 208, 223, 353, 391, 425)
EE: spinal cord, lung stomach, kidney. KO: rostral shift of shoulder	(1, 193, 208, 220, 282, 351, 507)
EE: hindbrain, spinal cord,somites. KO: missing first rib, transformation C6-T1	(1, 352, 435, 507, 514)
EE: spinal cord, somites, kidney	(1, 207, 281, 332, 352, 499, 514)
EE: spinal cord, dorsal root ganglia, somites	(1, 58, 68, 207, 275, 377, 439, 535)
EE: spinal cord	(1, 47, 58, 76, 187, 514)
EE: hindbrain, spinal cord, somites, oesophagus	(1, 58, 180, 367)
EE: hindbrain, spinal cord, somites, oesophagus, stomach	(1, 58, 140, 163, 178)
EE: spinal cord, somites	(1, 58, 62, 75, 84, 352, 434, 447)
EE: spinal cord, somites. KO: vertebral transformations in the thoracic region	(1, 16, 53, 58, 176, 291, 495)
EE: spinal cord, somites, kidney, hindlimb bud. KO: vertebral transformations	(1, 15, 53, 58, 141, 470)
EE: spinal cord, somites, hindlimb bud	(58, 373)
EE: spinal cord, somites, hindlimb bud	(58, 373)
EE: spinal cord, somites	(1, 373)
EE: spinal cord, somites	(1, 373)
EE: lateral, extraembryonic mesoderm, neural crest, dermatome	(165, 272, 346)
EE: spinal cord, somites. KO: transf. of cervical vertebrae (C1, C2)	(1, 39, 54, 85, 86, 381, 466)
EE: spinal cord, somites	(1, 58, 148, 179, 223, 310, 323)
EE: spinal cord, somites, gonads, limb buds	(1, 58, 92, 122, 238, 363, 420)
EE: spinal cord, somites, gonads, limb buds	(1, 58, 122, 133, 240, 395)
EE: spinal cord, somites, limb bud. KO: lethal chimaeras, vertebral abnormalities	(1, 58, 122, 125, 133, 398)
EE: spinal cord, somites, limb bud. KO: transf. of sacral vertebrae, limb abnormalities	(1, 58, 99, 125, 147, 239, 240)
EE: spinal cord, somites, limb bud	(58, 124, 125, 239, 279, 284)
EE: spinal cord, somites, gut, limb bud. KO: skeletal transformations and defects	(58, 121, 124, 240, 279)
C: human PCR clone from haematopoetic cells	(242, 339)
EE: dorsal blastopore lip, primitive streak, motor neurons, interneurons, dorsal mesoderm, mesonephros, diencephalon, hindbrain AE: cerebellum, medulla, kidney KO: loss of anterior head structures, some homozygous embryos with secondary axis	(27, 169, 448, 474, 490, 493)
EE: ectoderm, anterior region of neural plate/keel, brain	(103, 474, 490)
EE: motor neurons. EE: ventrolateral regions of the neural tube and hindbrain KO: postnatal death resulting from immature lungs	(259, 298, 493)
EE: Rathke's pouch, neural tube, oral ectoderm, hindbrain, spinal cord. AE: pituitary	(20, 440, 531, 532)
EE: motor neurons, interneurons. AE: pancreatic islet cells, brain, pituitary, kidney	(128, 262, 276, 485, 493, 503)
EE: motor neurons. C: *only rat gene described	(189, 493)
C: only partial cds, isolated of a salmon pituitary cDNA library	(189)
AE: B-and T-lymphoid cell lines, brain, spinal cord, liver, ventral myotome	(488, 520)
EE: dorsal limb mesenchyme. C: *hamster gene expressed in insulinoma cell line	(183, 184, 397)
EE: presumptive endoderm, part of marginal zone. C: rapidly induced by activin	(408)

mouse	chick	frog	zebrafish	man	fruitfly
Meis1					
	AKR				
Mox1				MEOX1=MOX1	94Che (116)
Mox2		Mox2		MEOX2=MOX2	btn (71)
Mox3				=GAX	
Msx1=Hox7	MSX1=Ghox7	msx1=Xhox7.1	MsxA	MSX1=HOX7	msh (402)
=Hox7.1					
Msx2=Hox8	MSX2=Ghox8	Xhox7.1'		MSX2=HOX8	
=Hox8.1					
msx3					
			MsxB		
			MsxC=msh-C		
			MsxD=msh-D		
				HPX5	
Nkx1.1				HPX153	NK1/S59 (269)
Sax1	SAX1=Chox3			HPX134	
Nkx2-1=TTF-1				NKX2A=TTF-1	
Nkx2-2		XeNK-2	nk2.2		nk2=vnd (248, 269)
Nkx2-3		XNkx-2.3			
Nkx2-4					
Nkx2-5=Csx	NKX2.5	Nkx2.5		CSX	nk4=msh-2
					=tinman (17, 46, 269)
Nkx2-6					
					nk3=bagpipe (17, 269)
Nkx5.1=Hmx3	HMX3=GH6				(H6) (459)
Nkx5.2=Hmx2	HMX2			HMX2	
Hmx1				HMX1=H6	
	SOHO1				
	CNOT=GNOT1	Xnot/Xnot2			90Bre (116)
	GNOT2		flh		
otp	OTP				orthopedia=w26 (330, 453)
Otx1			z-otx1	OTX1	orthodenticle (otd) (153)
Otx2	OTX2=c-otx2	Xotx2	z-otx2	OTX2	
			z-otx3		
Pax3=Sp	PAX3			PAX3=HUP2=WS1	paired (50)
					gooseberry dist. (33, 90)
					gooseberry prox. (33, 90)
Pax4				PAX4	
Pax6=Sey	PAX6		pax-6=pax-zfa	PAX6=AN	eyeless (ey) (201, 388)
					bk27 (259)
Pax7				PAX7=HUP1	
Pbx1				PBX1=PRL	extradenticle=Dpbx
				PBX2=HOX12=G17	(372)
Pbx3				PBX3	
Pdx1=Ipf1=Stf1		Xlhbox8		IPF1	
Pem					
Pmx1=Mhox	PRX1=gMHOX			PMX1=PHOX1	aristaless (430)
=K2=Prx1				=PHBX1	repolarity (203, 519)
Pmx2=Phox2					bk36 (259)
					bk50 (259)

Embryonic or adult expression in vertebrates (EE, AE), knock out phenotype (KO), comments (C)	references
C: involved in myeloid leukemia	(343)
EE: liver	(419)
EE: mesoderm, somites, similar, but different from Mox2	(60, 171)
EE: mesoderm, somites, similar, but different from Mox1	(60, 61, 195, 294)
	(410)
EE: visceral arches craniofacial mesenchyme, heart, eye, tooth, limb, fin	(77, 98, 213, 217, 219, 236, 314, 402, 468)
KO: cleft palate, defects of tooth development	(6, 78, 355, 524)
EE: visceral arches craniofacial mesenchyme, heart, eye, tooth, limb	(6, 36, 65, 77, 98, 241, 313, 334, 355)
EE: dorsal neural tube, excluding the roof plate	(96, 219, 222)
EE: fin	(6)
EE: fin	(6, 138)
EE: fin	(6, 138)
C: PCR fragment from human haematopoietic progenitor cells	(339)
	(45, 119, 339)
EE: pretectum, rhombomere 1, spinal cord	(339, 432, 457)
EE: thyroid, lung; di-, telencephalon. AE: thyroid, lung. C: transactivated by HOXB3	(197, 198, 233, 289, 382, 383)
EE: fore- , hindbrain; in fish also midbrain. AE: pancreatic islet cells (in hamster)	(30, 382, 383, 421)
EE: early cardiac primordia; partially overlapping with Nkx2-5	(88, 303, 383)
EE: posterior hypothalamus	(382, 383)
EE: precardiac mesoderm, myocardium; pharyngeal endoderm;	(142, 273, 303, 311, 436, 449, 489)
AE: heart; spleen, tongue. KO: heart defects; growth retardation, lethal at d 9-10 pc	
AE: neonatal brain	(88, 303)
EE: forebrain, ear, eye, 2nd visceral arch	(45, 459, 461)
EE: forebrain, ear, eye. C: similar, but later than Nkx5.1	(45, 400, 459)
	(459, 460)
EE: anterior neural tube, retina, ear, dorsal root ganglia, 2nd visceral arch	(113)
EE: organizer (node, blastopore lip), notochord, epiphysis, limbs, tailbud	(190, 271, 393, 462, 500)
EE: marginal cells, embryonic shield, notochord. C: GNOT1 + GNOT2 clustered	(393, 476)
KO (floating head): no notochord; somites fused	(202, 476)
EE: forebrain, hindbrain, spinal cord. C: complementary to Dlx1 in diencephalon	(453)
EE: forebrain, midbrain	(264, 301, 340, 450, 451)
EE: epiblast, forebrain, midbrain, 1st branchial arch.	(2, 23, 40, 264, 301, 340, 370, 450, 451)
KO: gastrulation, early brain, and axial mesoderm defect	
EE: embryonic shield	(340)
EE: somites, spinal cord, forebrain, midbrain, hindbrain, neural crest	(21, 29, 59, 191, 192, 464, 479)
KO (Splotch): Spina bifida, pigmentation defect, limb muscle defect;	
Waardenburg syndrome, rhabdomyosarcoma	
	(477, 502)
EE: spinal cord, forebrain, hindbrain, eye, nose, pituitary, pancreas	(192, 216, 280, 299, 386, 464, 501)
KO (Small eye): no eyes, no nose, brain defects; Aniridia, Peter's anomaly, keratinitis	
EE: somites, muscle, spinal cord, forebrain, midbrain hindbrain, neural crest; rhabdomyosarcoma	(59, 254, 429, 446, 464)
EE: most fetal tissues. C: protooncogene, cooperation with Hox proteins	(66, 109, 158, 230, 258, 260, 357, 378, 405)
EE: most fetal tissues	(4, 335, 471)
EE: most fetal tissues	(335, 376)
EE: pancreas anlage, intestine.KO: no pancreas	(152, 174, 199, 253, 329, 359, 463, 515)
EE: only extraembryonic, tumor cell lines	(302, 394, 424)
EE: craniofacial, limb, pericardial, primitive dermal, prevertebral mesenchyme	(93, 266, 267, 283, 317, 354)
KO: defect in formation and growth of chondrogenic and osteogenic precursors	
EE: sympathetic and cranial sensory ganglia, hindbrain	(196, 486, 496)
C: Pmx1 and Pmx2 not very similar	

mouse	chick	frog	zebrafish	man	fruitfly
S8=Prx2	PRX2				60Mun1 (116)
Chx10=Hox-10			Vsx2*=g10		57San (116)
			Vsx1*		
alx3*					
Cart1		Xcart1			
Drg11*					
Pit1=Ghf-1=dw				POU1F1=PIT1	
				=GHF-1	
Pit1-rs1					
Pou2f1=Oct-1	OCT1	oct1		POU2F1=OCT1	pdm-1=pou19 (38, 305)
=Otf-1				=OTF1	miti-mere=pdm-2=pou28
Pou2f2=Oct-2				POU2F2=OCT2	(38, 305, 522)
=Otf-2				=OTF2	
Pou2f3=Oct-11a=Otf-11		nrl-16/21			
=Epoc-1=Skn-1					
Pou3f1=Oct-6=Otf-6		pou1=nrl-19/22/34		POU3F1=OCT6	drifter=cf1a=bk54
=Tst-1=Scip				=OTF6	(12, 38, 249)
Pou3f2=Brn-2		pou3=nrl-20	zfpou1	POU3F2=BRN2	
=Otf-7				=N-OCT3=OTF7	
Pou3f3=Brn-1				POU3F3=BRN1	
=Otf-8				=OTF8	
Pou3f4=Brn-4		pou2		POU3F4=BRN4	
=Otf-9=RHS2				=OTF9=DFN3	
Pou3f-rs1					
=MM-POU-III-A					
Pou4f1=Brn-3				POU4F1=BRN3A	ipou (491, 492)
=Brn-3.0=Brn-3a				=RDC-1	
Pou4f2=Brn-3.2				POU4F2=BRN3B	
=Brn-3b					
Pou4f3=Brn-3.1		Brn3		POU4F3	
=Brn-3c					
Pou4f-rs1=mBrn-3R					
Pou5f1=Oct-3				POU5F1=OCT3	
=Oct-4=Otf-3=Otf-4				=OTF3	
			pou2		
		oct25			
		oct60=pou60			
		oct91/oct92			
Sprm1					
Pou6f1=Brn-5			pou-c	POU6F1=BRN5	
=Cns-1=Emb				=MPOU=TCFB1	
Prox1					prospero (118)
		siamois			
Six1					sine oculis (70, 442)
Six2					
Six3					
Dmahp				DMAHP	
Tcf1=Hnf1=Hnf1a		Lfb1		TCF1=HNF1=LFB1	
Tcf2=vHnf1=Hnf1ß		Lfb3		TCF2=VHNF1=LFB3	
Tlx1=Hox11				HOX11=TCL3	C15=93Bal (116)
Tlx2=Mur10f				HPX204	
=Hox11L1					
Tlx3=Hox11L2					

Embryonic or adult expression in vertebrates (EE, AE), knock out phenotype (KO), comments (C)	references
EE: mesenchyme craniofacial, limb, heart, somites	(104, 295, 354, 366)
EE: thalamus, hindbrain, ventral spinal cord, eye, neuroretina	(296, 304)
EE: neuroretina. C:*only goldfish gene described	(297)
AE: pancreatic cell lines, testis. C:*only hamster gene described	(414)
EE: prechondrogenic mesenchyme	(533, 534)
EE: dorsal root ganglia, spinal cord. C:*only rat gene described	(422)
EE: pituitary, pituitary hormone deficiency, dwarfism	(63, 235, 300, 375, 389)
AE: mammary gland, muscle, brain, liver. C: PCR fragment	(247)
EE: ubiquitous	(374, 467, 498)
EE: CNS. AE: lymphoid cells. KO B cell maturation	(89, 149, 209, 210, 465)
EE: skin, thymus, stomach, testis	(25, 188, 527)
EE: forebrain, midbrain, epidermis, testis	(3, 9, 146, 161, 210, 325, 336, 473)
EE: forebrain, spinal cord	(9, 24, 210, 322)
EE: forebrain, spinal cord	(9, 210)
EE: forebrain. KO: deafness	(3, 9, 105, 129, 290, 319)
AE: mammary gland, muscle, kidney, spleen. C: PCR fragment	(247)
EE: midbrain, hindbrain, spinal cord, retina, pituitary	(185, 270)
EE: midbrain, hindbrain, spinal cord, retina	(494, 518) (270, 481)
AE: mammary gland, brain, heart, lung, kidney, spleen, liver. C: PCR fragment	(247)
EE: cleavage stage, inner cell mass, primordial germ cells	(360, 369, 431)
EE: cleavage stage, epiblast during gastrulation, tailbud	(475)
EE: oocytes, cleavage stages. AE: kidney, ovary	(218)
EE: oocytes, cleavage stages. AE: kidney, ovary	(218, 511)
EE: oocytes, cleavage stages. AE: brain, ovary	(218, 270)
AE: male germ cells	(10)
AE: brain, spinal cord, kidney, lung, heart, skin, testis, lymphoid cells	(11, 57, 326, 361, 510)
EE: CNS, pancreas, liver, heart, skeletal muscles	(364)
EE: dorsal-vegetal cells, dorsal endoderm	(292)
EE: phalangal tendons, skeletal muscles. C: complementary to Six2 in tendons	(365)
EE: phalangal tendons, smooth muscles. C: complementary to Six1 in tendons	(365)
EE: anterior neural plate, eye	(362)
C: associated with a myotonic dystrophy; unstable (CTG) repeat	(51)
EE: yolk sac, liver, intestine, kidney. AE: liver, intestine, kidney	(18, 19, 31, 34, 64, 288, 348, 528)
EE: yolk sac, liver, intestine, kidney. AE: liver, intestine, kidney	(64, 106, 115, 263, 396)
EE: branchial arches, motor neurons, spleen anlage. KO: no spleen.	(69, 107, 265, 390, 403, 404, 509)
EE: not expressed in branchial arches	(69, 108, 265, 339, 509)
EE: not expressed in branchial arches	(69, 108)

ter), which often seem to represent tentative subfamily prototypes (Dessain and McGinnis, 1993). One or more such 'prototype' fly genes are indicated with references in the sixth column of the left hand pages. We have attempted to list all the published designations, and combined synonyms with '='. Putative pseudoallelic genes of the tetraploid frog are separated by '/'. No intentions were made to involve matters of nomenclature, even if the sequence of appearance may reflect a hierarchy in terms of current preferences or names suggested by the various nomenclature committees (for references, see Mouse locus catalog: The Jackson Laboratory, Bar Harbour <http://www.informatics.jax.org>; and The Human Genome Data Base: Johns Hopkins University, Baltimore <http://gdbwww.gdb.org/gdb/browsers/docs/topq.html>). Since the nomenclature of Hox genes is finally settled in a generally accepted, systematic way, we decided not to repeat the numerous laboratory names used in older papers (for a summary, see Scott, 1993). Subfamilies of homeobox genes are listed alphabetically following the names of mouse genes. Subfamilies are separated by horizontal lines; Hox and Pou genes are further subdivided by dashed lines.

On the right hand pages we give some keywords on the embryonic (EE) or adult (AE) expression, we occasionally add comments (C), and mention the knock-out phenotypes (KO) when available. We should emphasize that in the extremely limited space of one or two lines only a minimum of information can be presented. Thus, EE, AE, C, and KO should serve as memo technical keywords, rather than as gene descriptions. In general we tried to cite most of the published information. In several cases, however, only an arbitrary selection of major references is given, which should allow access to further publications.

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