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REVIEW

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A listing of human tumor antigens recognized by T cells

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Complete list of abbreviations of tumor antigens *707-AP* 707 alanine proline · AFP *alpha* (α)-*fetoprotein* · *ART-4* adenocarcinoma antigen recognized by T cells 4 · *BAGE* B antigen · *β-catenin/m* β-catenin/mutated · *Bcr-abl* breakpoint cluster region–Abelson · *CAMEL* CTL-recognized antigen on melanoma · *CAP-1* carcinoembryonic antigen peptide-1 · *CASP-8* caspase-8 · *CDC27m* cell-division-cycle 27 mutated · *CDK4/m* cycline-dependent kinase 4 mutated · *CEA* carcinoembryonic antigen · *CT* cancer/testis (antigen) · *Cyp-B* cyclophilin B · *DAM* differentiation antigen melanoma (the epitopes of DAM-6 and DAM-10 are equivalent, but the gene sequences are different; DAM-6 is also called MAGE-B2, and DAM-10 is also called MAGE-B1) · *ELF2M* elongation factor 2 mutated · *ETV6-AML1* Ets variant gene 6/acute myeloid leukemia 1 gene ETS · *G250* glycoprotein 250 · *GAGE* G antigen · *GnT-V* N-acetylglucosaminyltransferase V · *Gp100* glycoprotein 100 kDa · *HAGE* helicose antigen · *HER-2/neu* human epidermal receptor-2/neurological · *HLA-A*0201-R170I* arginine (R) to isoleucine (I) exchange at residue 170 of the α-helix of the α2-domain in the HLA-A2 gene · *HPV-E7* human papilloma virus E7 · *HSP70-2M* heat shock protein 70-2 mutated · *HST-2* human signet ring tumor-2 · *hTERT* or *hTRT* human telomerase reverse transcriptase · *iCE* intestinal carboxyl esterase · *KIAA0205* name of the gene as it appears in databases · *LAGE* L antigen · *LDLR/FUT* low-density lipid receptor/GDP-L-fucose: β-D-galactosidase 2-α-L-fucosyltransferase · *MAGE* melanoma antigen · *MART-1/Melan-A* melanoma antigen recognized by T cells-1/melanoma antigen A · *MC1R* melanocortin 1 receptor · *Myosin/m* myosin mutated · *MUC1* mucin 1 · *MUM-1*, *-2*, *-3* melanoma ubiquitous mutated 1, 2, 3 · *NA88-A* NA cDNA clone of patient M88 · *NY-ESO-1* New York-esophagus 1 · *P15* protein 15 · *p190* minor bcr-abl protein of 190 kDa bcr-abl · *Pml/RARα* promyelocytic leukaemia/retinoic acid receptor α · *PRAME* preferentially expressed antigen of melanoma · *PSA* prostate-specific antigen · *PSM* prostate-specific membrane antigen · *RAGE* renal antigen · *RU1* or *RU2* renal ubiquitous 1 or 2 · *SAGE* sarcoma antigen · *SART-1* or *SART-3* squamous antigen rejecting tumor 1 or 3 · *TEL/AML1* translocation Ets-family leukemia/acute myeloid leukemia 1 · *TPI/m* triosephosphate isomerase mutated · *TRP-1* tyrosinase related protein 1, or gp75 · *TRP-2* tyrosinase related protein 2 · *TRP-2/INT2* TRP-2/intron 2 · *WT1* Wilms' tumor gene

Abbreviations used *ALL* acute lymphoblastic leukemia · *AML* acute myeloid leukemia · *APL* acute promyelocytic leukemia · *CML* chronic myelogenous leukemia · *CTL* cytotoxic T lymphocytes · *Ets* E-26 transforming specific (family of transcription factors) · *H/N* head and neck · *MHC* major histocompatibility complex · *NSCLC* non-small cell lung carcinoma · *ORF* open reading frame · *RCC* renal cell carcinoma · *SCC* squamous cell carcinoma · *TSTA* tumor-specific transplantation antigens

Introduction

Since the cloning of *MAGE-1* [125], the first gene reported to encode a human tumor antigen recognized by T cells, molecular identification and characterization of tumor antigens has mainly been achieved for melanoma. A major reason for this lies in the difficulty of establishing cell lines in vitro from other types of cancer, such lines being necessary to generate tumor-specific CTL

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lines or clones to be used in the genetic or biochemical approach aimed at molecularly identifying new cancer antigens. More recently, however, new approaches have allowed the discovery of new antigens recognized by T cells even in tumors other than melanoma.

It is, then, important to categorize these antigens, particularly for the HLA allele restricting their recognition by T cells and for their tissue distribution. With this purpose, tumor antigens have been collected in the present work and briefly commented.

The list presented in the tables below includes all T-cell-defined epitopes encoded by tumor antigens and published by 31 July 2000. Analogs or artificially modified epitopes are excluded from the list. Only tumor antigens recognized by T cells (either cytotoxic CD8 + or helper CD4 +) are listed, given their potential importance in the control of tumor growth. Other antigens, identified by antibodies, are excluded but a large collection of them, as detected by the Serex technology, can be found in the data base of the Institute for Cancer Research (www.licr.org/SEREX.htm). It is of note that many tumor antigens (e.g. MAGE, NY-ESO-1a) are now known to be recognized by both T cells and antibodies in the same cancer patients [54].

In the tables herein, tumor antigens are listed in alphabetic order along with the epitope sequence and the HLA allele which restricts recognition by T cells. Furthermore, data on the tissue distribution of each antigen are provided, making this listing an important source for easily retrieving data concerning human tumor antigens.

The listing is meant to be a tool for scientists and students who have an interest in the field of tumor immunology and immunotherapy. The bibliography allows a rapid search for more detailed information at the single antigen or epitope level.

We do not ignore, however, the fact that by recent technologies (e.g., subtractive hybridization, representational-difference analysis, microarrays) hundreds of genes are being detected which are preferentially expressed or overexpressed in neoplastic cells as compared with normal counterparts or are expressed in metastatic but not in primary, early lesions (e.g., melanoma, breast cancer, lymphoma). By using appropriate computer algorithms [9], a number of new epitopes will be identified that can bind MHC molecules. By applying such approaches, a large array of gene products can be screened for their potential antigenic function. More cumbersome may be the selection of the most immunogenic epitopes through appropriate functional assays.

Classification of tumor antigens

Group 1: Class I HLA-restricted cancer/testis antigens (Table 1)

A milestone in tumor immunology was certainly the cloning of *MAGE-1* [125] and the subsequent characterization of the first T-cell-defined antigenic epitope a year later [119]. Those findings were rapidly followed by the identification of new members within this group [6, 123]. The *MAGE*, *BAGE* and *GAGE* families of genes were born. The antigens belonging to this group, now including also NY-ESO-1, were called cancer/testis (CT) antigens for their expression in histologically different human tumors and, among normal tissues, in spermatocytes/spermatogonia of testis and, occasionally, in placenta. These antigens now represent one of the main components for antitumor vaccine development. CT antigens result from reactivation of genes normally silent in adult tissues [27], but that are transcriptionally activated in some tumors [30]. Their expression in testis does not provide targets for an immune reaction because cells of testis do not express class I HLA [56]. Despite the fact that the CT genes are probably the most characterized ones, their physiological function remains largely unknown.

Considering that new genes in the group of CT antigens have been cloned (CT9 [105], CT10 [46], LAGE [72], MAGE-B5, –B6, –C2, –C3 and –D [74, 75], HAGE, SAGE [80]), but that no T-cell epitopes have been identified from them yet, the question arises as to how many more genes encoding CT antigens remain to be discovered and how many epitopes exist that could be of use in cancer immunotherapy.

Group 2: Class I HLA-restricted differentiation antigens (Table 2)

These antigens are shared between tumors and the normal tissue from which the tumor arose; most are found in melanomas and normal melanocytes [2]. Many of these melanocyte lineage-related proteins are involved in the biosynthesis of melanin. Epitopes recognized by both CD8 + and CD4 + T cells can be derived from melanosome proteins [8, 118, 135, 136].

Group 3: Class I HLA-restricted widely expressed antigens (Table 3)

Genes encoding widely expressed tumor antigens have been detected in many normal tissues as well as in histologically different types of tumors with no preferential expression on a certain type of cancer. It is possible that the many epitopes expressed on normal tissues are below the threshold level for T-cell recognition, while their overexpression in tumor cells can trigger an anticancer response even by breaking a previously established tolerance. These widely expressed gene products have revealed a broad spectrum of mechanisms that are involved in generating T-cell-defined epitopes through alterations in gene transcription and translation. To highlight some examples, the epitope of CEA is derived from a non-AUG-defined alternative ORF [1], while the RU2 gene creates its epitope by reverse strand transcription [124].

Table 1 Class I HLA-restricted cancer/testis antigens. All these antigens were found to be expressed by normal spermatocytes and/or spermatogonia of testis. Occasionally *MAGE-3*, *MAGE-4* and the *GAGE* genes were found to be expressed also in placenta [26, 24]. The NY-ESO-1 antigen was found to be expressed in normal ovary cells [18]

Gene	HLA allele	Peptide epitope	Authors [ref.]	Tissue distribution among tumors[a]
MAGE-A1	A1	EADPTGHSY	Traversari et al. 1992 [119]	Melanoma, breast carcinoma, SCLC [27, 29, 125] – sarcoma, NSCLC [27, 29] – thyroid medullary carcinoma [125] – colon carcinoma [27] – laryngeal tumors [29]
MAGE-A1	A3	SLFRAVITK	Chaux et al. 1999a [16]	
MAGE-A1	A24	NYKHCFPEI	Fujie et al. 1999 [37]	
MAGE-A1	A28	EVYDGREHSA	Chaux et al. 1999a [16]	
MAGE-A1, -A2, -A3, -A6	B37	REPVTKAEML	Tanzarella et al. 1999 [113]	Melanoma, colon and breast carcinomas, SCLC [27, 29, 125] – sarcoma, NSCLC [27, 29] – thyroid medullary carcinoma, H/N tumors, bronchial SCC [125] – laryngeal tumors [29] – leukemias [27]
MAGE-A1	B53	DPARYEFLW	Chaux et al. 1999a [16]	Melanoma, breast carcinoma, SCLC [27, 29, 124] – sarcoma, colon carcinoma, NSCLC [27, 29] – thyroid medullary carcinoma [125]
MAGE-A1	Cw2	SAFPTTINF	Chaux et al. 1999a [16]	
MAGE-A1	Cw3	SAYGEPRKL	Chaux et al. 1999a [16]	
MAGE-A1	Cw16	SAYGEPRKL	van der Bruggen et al. 1994b [127]	
MAGE-A2	A2	KMVELVHFL	Visseren et al. 1997 [128]	Melanoma, colon and breast carcinomas, SCLC [27, 29, 125] – sarcoma, NSCLC [27, 29] – thyroid medullary carcinoma [125] – laryngeal tumors [77] – leukemias [27]
MAGE-A2	A2	YLQLVFGIEV	Visseren et al. 1997 [128]	
MAGE-A2	A24	EYLQLVFGI	Tahara et al. 1999 [110]	
MAGE-A3	A1	EADPIGHLY	Gaugler et al. 1994 [40]	Melanoma, colon and breast carcinomas [27, 125] – H/N tumors [18] – bronchial SCC, thyroid medullary and bladder carcinoma, sarcomas, SCLC, NSCLC [125] – leukemias [29]
MAGE-A3	A2	FLWGPRALV	van der Bruggen et al. 1994a [126]	
MAGE-A3	A24	TFPDLESEF	Oiso et al. 1999 [89]	
MAGE-A3	A24	IMPKAGLLI	Tanaka et al. 1997 [111]	
MAGE-A3	B44	MEVDPIGHLY	Herman et al. 1996 [48], Fleischhauer et al. 1996 [35]	
MAGE-A3	B52	WQYFFPVIF	Russo et al. 2000 [103]	
MAGE-A4	A2	GVYDGREHTV	Duffour et al. 1999 [33]	Melanoma, NSCLC, sarcomas, esophageal, colon and breast carcinomas [27]
MAGE-A6	A34	MVKISGGPR	Zorn and Hercend, 1999b [147]	Melanoma, NSCLC, colon carcinoma, leukemias [27]
MAGE-A10	A2	GLYDGMEHL	Huang et al. 1999 [52]	Not defined
MAGE-A12	Cw7	VRIGHLYIL	Panelli et al. 2000 [91], Heidecker et al. 2000 [47]	Melanoma, myeloma, brain tumors, sarcoma, leukemias, SCLC, NSCLC, H/N tumors, bladder, lung, esophageal, breast, prostate and colorectal carcinoma [27]
BAGE	Cw16	AARAVFLAL	Boël et al. 1995 [6]	Melanoma, bladder and mammary carcinomas, H/N SCC, NSCLC, sarcoma
DAM-6, -10	A2	FLWGPRAYA	Fleischhauer et al. 1998 [36]	Melanoma, skin tumors, mammary and ovarian carcinomas [77] – lung carcinoma [25, 77] – seminomas [25]
GAGE-1, -2, -8	Cw6	YRPRPRRY	Van den Eynde et al. 1995 [123], De Backer et al. 1999 [26]	Melanoma, sarcoma, NSCLC, SCLC, mesothelioma, sarcoma, seminoma, leukemias, lymphomas, H/N tumors, bladder, esophageal, mammary, colon, prostate carcinomas
GAGE-3, -4, -5, -6, -7B	A29	YYWPRPRRY	De Backer et al. 1999 [26]	Melanomas, H/N tumors, leukemias, esophageal, lung and bladder carcinomas
NA88-A	B13	MTQGQHFLQKV	Moreau-Aubry et al. 2000 [82]	Melanoma
NY-ESO-1	A2	SLLMWITQCFL	Jäger et al. 1998 [54]	Melanoma, sarcoma, B-lymphomas, hepatoma, H/N tumors, bladder, lung, prostate, ovarian, thyroid and breast carcinoma [18]
NY-ESO-1a (CAG-3)	A2	SLLMWITQC	Jäger et al. 1998 [54]	
	A2	QLSLLMWIT	Jäger et al. 1998 [54]	
	A31	ASGPGGGAPR	Wang et al. 1998b [134]	

[a] Tissue distribution among tumors as described in the given references when different from the paper first reporting the sequence of the epitope

Group 4: Class I HLA-restricted, tumor-specific antigens (Table 4)

Unique tumor antigens arise from point mutations of normal genes (like β-catenin, CDK4) [98, 137], whose molecular changes often accompany neoplastic transformation or progression. These antigens are thus expressed only in the individual tumor where they were identified, since it is unlikely that the same mutation may occur in two different neoplasms unless it involves genes (e.g. RAS) whose alteration is an obligatory step in neoplastic transformation.

Table 2 Class I HLA-restricted melanocyte differentiation antigens. These antigens can only be expressed in normal and neoplastic cells of the same lineage (namely melanocytes, skin, retina, peripheral ganglia) or in normal cells of the prostate gland

Gene	HLA allele	Peptide epitope	Authors [ref.]
MART-1/Melan-A[a]	A2	AAGIGILTV	Coulie et al. 1994 [22], Kawakami et al. 1994a [58]
	A2	EAAGIGILTV	Schneider et al. 1998 [106]
	A2	ILTVILGVL	Castelli et al. 1995 [14]
	B45	AEEAAGIGIL	Schneider et al. 1998 [106]
	B45	AEEAAGIGILT	Schneider et al. 1998 [106]
MC1R	A2	TILLGIFFL	Salazar-Onfray et al. 1997 [104]
	A2	FLALIICNA	Salazar-Onfray et al. 1997 [104]
Gp100	A2	KTWGQYWQV	Bakker et al. 1995 [3]
	A2	AMLGTHTMEV	Tsai et al. 1997 [120]
	A2	MLGTHTMEV	Tsai et al. 1997 [120]
	A2	SLADTNSLAV	Tsai et al. 1997 [120]
	A2	ITDQVPFSV	Kawakami et al. 1995 [61]
	A2	LLDGTATLRL	Kawakami et al. 1994b [59]
	A2	YLEPGPVTA	Cox et al. 1994 [24]
	A2	VLYRYGSFSV	Kawakami et al. 1995 [61]
	A2	RLMKQDFSV	Kawakami et al. 1998 [62]
	A2	RLPRIFCSC	Kawakami et al. 1998 [62]
	A3	LIYRRRLMK	Kawakami et al. 1998 [62]
	A3	ALNFPGSQK	Kawashima et al. 1998 [65]
	A3	SLIYRRRLMK	Kawashima et al. 1998 [65]
	A3	ALLAVGATK	Skipper et al. 1996 [108]
	A24	VYFFLPDHL	Robbins et al. 1997 [99]
	Cw8	SNDGPTLI	Castelli et al. 1999 [15]
PSA	A1	VSHSFPHPLY	Corman et al. 1998 [20]
	A2	FLTPKKLQCV	Correale et al. 1997 [21]
	A2	VISNDVCAQV	Correale et al. 1997 [21]
PSM	A1	HSTNGVTRIY	Corman et al. 1998 [20]
Tyrosinase	A1	KCDICTDEY	Kittlesen et al. 1998 [68]
	A1	SSDYVIPIGTY	Kawakami et al. 1998 [62]
	A2	YMDGTMSQV	Wölfel et al. 1994 [137]
	A2	MLLAVLYCL	Wölfel et al. 1994 [137]
	A24	AFLPWHRLF	Kang et al. 1995 [57]
	B44	SEIWRDIDF	Brichard et al. 1996 [10]
TRP-1 (or gp75)	A31	MSLQRQFLR	Wang et al. 1996b [132]
TRP-2	A2	SVYDFFVWL	Parkhurst et al. 1998 [92]
	A2	TLDSQVMSL	Noppen et al. 2000 [86]
	A31	LLGPGRPYR	Wang et al. 1996a [131]
	A33	LLGPGRPYR	Wang et al. 1998a [133]
	Cw8	ANDPIFVVL	Castelli et al. 1999 [15]

[a] Two different groups simultaneously discovered this gene and gave it two different names, MART-1 and Melan-A respectively

Table 3 Class I HLA-restricted widely expressed antigens

Gene	HLA	Peptide epitope	Tissue distribution		Reference
			Tumors	Normal tissues	
ART-4	A24	AFLRHAAL DYPSLSATDI	SCC, SCLC, H/N tumors, leukemia, lung, esophageal, gastric, cervical, endometrial, ovarian and breast carcinomas	Testis, placenta, fetal liver	Kawano et al. 2000 [64]
CAMEL	A2	MLMAQEALAFL	Melanoma	Testis, placenta, heart, skeletal muscle, pancreas	Aarnoudse et al. 1999 [1]
CEA	A2	YLSGANLNL (CAP-1)[a]	Melanoma	Testis, placenta, heart, skeletal muscle, pancreas	Tsang et al. 1995 [121]
CEA	A3	HLFGYSWYK	Colon, rectum, pancreas, gastric, breast and lung carcinomas	Gastrointestinal embryonic tissue	Kawashima et al. 1999 [66]
Cyp-B	A24	KFHRVIKDF DFMIQGGDF	Lung adenocarcinoma, T cell leukemia, lymphosarcoma – bladder, ovarian, uterine and esophageal SCC	Ubiquitously expressed in normal tissues	Gomi et al. 1999 [42]

Table 3 (Continued)

Gene	HLA	Peptide epitope	Tissue distribution		Reference
			Tumors	Normal tissues	
HER2/neu	A2	KIFGSLAFL	Melanoma – ovarian and breast carcinomas	Epithelial cells	Fisk et al. 1995 [34]
HER2/neu	A2	IISAVVGIL	Melanoma, ovarian, pancreatic [96][b] and breast carcinomas	Epithelial cells	Peoples et al. 1995 [95]
HER2/neu	A2	RLLQETELV	Melanoma, ovarian, gastric, pancreatic [96] and breast carcinomas	Epithelial cells	Kono et al. 1998 [71]
HER2/neu	A2	VVLGVVFGI ILHNGAYSL YMIMVKCWMI	Melanoma, ovarian, gastric, pancreatic [96] and breast carcinomas	Epithelial cells	Rongcun et al. 1999 [101]
HER2/neu	A3	VLRENTSPK	Melanoma, ovarian, gastric, pancreatic [96] and breast carcinomas	Epithelial cells	Kawashima et al. 1999 [66]
hTERT[c]	A2	ILAKFLHWL	Lung and ovarian carcinomas – multiple myeloma, melanoma, sarcoma, acute leukemias, non-Hodgkin's lymphomas	Hematopoietic stem cells and progenitors; germinal center cells; basal keratinocytes; gonadal cells; certain proliferating epithelial cells	Vonderheide et al. 1999 [131]
hTRT[c]	A2	ILAKFLHWL RLVDDFLLV	Lung, prostate and ovarian carcinomas, multiple myeloma, melanoma, sarcoma, acute leukemias, non-Hodgkin's lymphomas	Circulating B cells; germinal center B cells; thymocytes; CD34+ progenitor hemopoietic cells	Minev et al. 2000 [81]
iCE	B7	SPRWWPTCL	RCC	Kidney, colon, small intestine, liver, heart, pituitary gland, adrenal gland, prostate, stomach	Ronsin et al. 1999 [102]
MUC1	A11	STAPPAHGV	Breast and ovarian carcinomas, multiple myeloma, B-cell lymphoma	None[d]	Domenech et al. 1995 [31]
MUC1	A2	STAPPVHNV	Breast and ovarian carcinoma, multiple myeloma, B-cell lymphoma	None[d]	Brossart et al. 1999 [11]
MUC2	A2	LLNQLQVNL MLWGWREHV	Ovary, pancreas and breast mucinous tumors, colon carcinoma of non-mucinous type	Colon, small intestine, bronchus, cervix and gall bladder	Böhm et al. 1998 [7]
PRAME	A24	LYVDSLFFL	Melanoma, H/N and lung SCC, NSCLC [122], RCC, adenocarcinoma, sarcoma, leukemias [122]	Testis, endometrium, ovary, adrenals, kidney, brain, skin	Ikeda et al. 1997 [53]
P15	A24	AYGLDFYIL	Melanoma	Testis, spleen, thymus, liver, kidney, adrenal tissue, lung tissue, retinal tissue	Robbins et al. 1995 [97]
RU1	B51	VPYGSFKHV	Melanoma, renal and bladder carcinomas	Testis, kidney, heart, skin, brain, ovary, liver, lung, lymphocytes, thymus, fibroblasts	Morel et al. 2000 [83]
RU2	B7	LPRWPPPQL	Melanoma, sarcomas leukemia – brain, esophageal and H/N tumors – renal, colon, thyroid, mammary, bladder, prostatic and lung carcinomas	Testis, kidney, liver, urinary bladder	Van den Eynde et al. 1999 [124]
SART-1	A24	EYRGFTQDF	Esophageal, H/N and lung SCC – adenocarcinoma, uterine cancer	Testis, fetal liver	Kikuchi et al. 1999 [67]
SART-1	A*2601	KGSGKMKTE	Esophageal, H/N and lung SCC, adenocarcinoma, uterine cancer	Testis, fetal liver	Shichijo et al. 1998 [107]
SART-3	A24	VYDYNCHVDL AYIDFEMKI	H/N, esophageal and lung SCC, adenocarcinoma, leukemia, melanoma	Lymphoid cells, fibroblasts, testis, fetal liver	Yang et al. 1999 [139]
WT1	A2	RMFPNAPYL	Gastric, colon, lung, breast, ovary, uterine, thyroid and hepatocellular carcinomas – leukemia (including AML, ALL and CML)	Kidney, ovary, testis, spleen	Oka et al. 2000 [90]

[a] CAP-1 is an alternative name of this peptide
[b] Tissue distribution among tumors as described in the given references when different from the paper first reporting the sequence of the epitope
[c] Telomerase is expressed in most human tumors: those listed were shown to be susceptible to lysis by cytotoxic T lymphocytes
[d] All epithelial tissues express mucin-like hyperglycosylated molecules

Table 4 Class I HLA-restricted tumor-specific antigens, including both unique (CDK-4, MUM-1, MUM-2, β-catenin, HLA-A2-R170I, ELF2 m, myosin-m, caspase-8, KIAA0205, HSP70-2m) and shared (CAMEL, TRP-2/INT2, GnT-V, G 250) antigens

Gene	HLA allele	Peptide epitope	Tissue distribution		Reference
			Tumors	Normal tissues	
AFP	A2	GVALQTMKQ	Hepatocellular carcinoma	Fetal liver	Butterfield et al. 1999 [12]
β-Catenin/m	A24	SYLDSGIHF	Melanoma	None	Robbins et al. 1996 [98]
Caspase-8/m	B35	FPSDSWCYF	H/N tumors	None	Mandruzzato et al. 1997 [78]
CDK-4/m	A2	ACDPHSGHFV	Melanoma	None	Wölfel et al. 1995 [138]
ELF2 M	A68	ETVSEQSNV	Lung SCC	None	Hogan et al. 1998 [50]
GnT-V	A2	VLPDVFIRC(V)[a]	Melanoma, brain tumors, sarcoma	Breast and brain (low expression)	Guilloux et al. 1996 [45]
G250	A2	HLSTAFARV	RCC, colon, ovarian and cervical carcinomas	None	Vissers et al. 1999 [129]
HSP70-2M	A2	SLFEGIDIY	RCC, melanoma, neuroblastoma	None	Gaudin et al. 1999 [39]
*HA-A*0201-R170I*	A2	CVEWLRIYLENGK	RCC	None	Brändle et al. 1996 [9]
HST-2	A31	YSWMDISCWI	Gastric signet cell carcinoma	None	Suzuki et al. 1999 [109]
KIAA0205	B44*03	AEPINIQTV	Bladder cancer	None	Gueguen et al. 1998 [44]
MUM-1	B44	EEKLIVVLF	Melanoma	None	Coulie et al. 1995 [23]
MUM-2	B44	SELFRSGLDY	Melanoma	None	Chiari et al. 1999 [19]
MUM-2	Cw6	FRSGLDSYV	Melanoma	None	Chiari et al. 1999 [19]
MUM-3	A28	EAFIQPITR	Melanoma	None	Baurain et al. 2000 [4]
Myosin/m	A3	KINKNPKYK	Melanoma	None	Zorn and Hercend, 1999a [146]
RAGE	B7	SPSSNRIRNT	Melanoma, sarcomas, mesotheliomas, H/N tumors, bladder, renal, colon and mammary carcinomas	Retina only	Gaugler et al. 1996 [41]
SART-2	A24	DYSARWNEI	H/N and lung SCC, lung adenocarcinoma, RCC, melanoma, brain tumors, esophageal and uterine cancers	None	Nakao et al. 2000 [85]
		AYDFLYNYL			
		SYTRLFLIL			
TRP-2/INT2	A68	EVISCKLIKR	Melanoma	None	Lupetti et al. 1998 [76]
707-AP	A2	RVAALARDA	Melanoma	None[b]	Morioka et al. 1995 [84]

[a] VLPDVFIRC(V) = nonamer and decamer peptides are both recognized by CTLs
[b] This antigen is not expressed in normal cells but, as the tissue of the testis was not tested, it will not become clear to which category the antigen may belong until more information is available

In mouse models unique antigens have been shown to be more immunogenic than the other groups of shared antigens [32]; since unique antigens are responsible for the rejection of tumor transplants in mice, they have been defined as tumor-specific transplantation antigens (TSTA). The unique antigens are the most specific targets for immunotherapy, but this potential advantage must be balanced against the almost total impossibility of their clinical use, as they can induce an immune response only against the original tumor on which they were found.

Other tumor-specific but shared antigens have been described which are generated by alteration in splicing mechanisms and which occur in tumor but not in normal cells, as in the case of TRP-2/INT2 [76].

Group 5: Class II HLA-restricted antigens (Table 5)

Stimulation of the CD4+ T helper cells by tumor antigens is considered to be impaired or absent in cancer patients and this may be the reason of an insufficient immune response to tumors. Therefore the identification of tumor antigen epitopes recognized by such lymphocytes is a crucial step in the long sought improvement of antitumor immune response that may result into clinical efficacy. The first epitope presented by a class II HLA and capable of provoking a CD4+ T-cell response was identified in 1994 in melanoma tyrosinase [117]. Then a gap of 4 years followed during which only one additional epitope was characterized [118], before other genes encoding class II-restricted peptides were discovered. However, as the technical and methodological approaches for identifying CD4+ T-cell epitopes of tumor antigens have become available, an exponential increase in reporting such epitopes has been seen. In fact, since 1998 as many as 27 new class II HLA-restricted epitopes from 14 antigens have been molecularly identified using, among others, Ii-cDNA fusion libraries [135], immunized transgenic mice [145] and biochemical approaches [96].

Table 5 Class II HLA-restricted antigens

Gene	HLA allele	Peptide epitope	Tissue distribution		Reference
			Tumors	Normal tissues	
Epitopes from normal protein antigens					
Annexin II	DRB*0401	DVPKWISIM-TERSVPH	Melanoma	Not done	Li et al. 1998 [73]
Gp100	DRB1*0401	WNRQLYPE-WTEAQRLD	Melanoma	Melanocytes	Li et al. 1998 [73]
MAGE-1, -2, -3, -6	DRB*1301 DRB*1302	LLKYRAREP-VTKAE	Melanoma, lung and breast carcinomas, H/N SCC	Testis, placenta	Chaux et al. 1999a [16]
MAGE-3	DR*1101	TSYVKVLHHM-VKISG	Melanoma, lung and breast carcinomas, H/N SCC	Testis, placenta	Manici et al. 1999 [79]
MAGE-3	DRB*1301 DRB*1302	AELVHFLLLK-YRAR	Melanoma, lung and breast carcinomas, H/N SCC	Testis, placenta	Chaux et al. 1999b [17]
MART-1/Melan-A	DRB1*0401	RNGYRALMDKS-LHVGTQCALTRR	Melanoma	Melanocytes	Zarour et al. 2000 [143]
MUC1	DR3	PGSTAPPAHGVT	Breast and ovarian cancers, multiple myeloma, B-cell lymphoma	None[a]	Hiltbold et al. 1998 [49]
NY-ESO-1	DRB4*0101	VLLKEFTVSG	Melanoma, B-lymphoma, hepatoma [18][b], sarcoma, H/N tumors, – bladder, lung, prostate, ovarian, thyroid and breast carcinomas	Testis	Zeng et al. 2000 [145]
NY-ESO-1	DRB4*0101–0103	PLPVPGVLLK-EFTVSGNI VLLKEFTVSG-NILTIRLT AADHRQLQL-SISSCLQQL	B-lymphoma, melanoma, sarcoma, H/N tumors, hepatoma [18] – bladder, lung, prostate, ovarian, thyroid and breast carcinomas	Testis	Jäger et al. 2000 [55]
PSA	DR4	ILLGRMSLFM-PEDTG SLFHPEDTGQVFQ QVFQVSHSFPHPLYD NDLMLLRLSEPAELT KKLQCVQLHVISM GVLQGITSMGSEPCA	Melanoma	Melanocytes	Corman et al. 1998 [20]
Tyrosinase	DRB1*0401	QNILLSNAPLGPQFP DYSYLQDSDPD-SFQD SYLQDSDPDSFQD	Melanoma	Melanocytes	Topalian et al. 1994 [117], Topalian et al. 1996 [118]
Tyrosinase	DRB1*1501	RHRPLQEVYP-EANAPIGHNRE	Melanoma	Melanocytes	Kobayashi et al. 1998a [69]
Tyrosinase	DRB1*0405	EIWRDIDFAHE	Melanoma	Melanocytes	Kobayashi et al. 1998b [70]
Epitopes from mutated protein antigens					
HPV-E7	DR*0401 DR*0407	LFMDTLSFVCPLC LFMDSLNFVCPWC	Cervical carcinoma	None	Höhn et al. 1999 [51]
CDC27/m	DRB1*0401	FSWAMDLDPKGA	Melanoma	None	Wang et al. 1999a [135]
TPI/m	DRB1*0101	GELIGILNAAKVPAD	Melanoma	None	Pieper et al. 1999 [96]

[a] All epithelial tissues express highly glycosilated mucins whereas tumor cells often show hypoglycosilated mucins with a normal protein sequence

[b] Tissue distribution among tumors as described in the given references when different from the paper first reporting the sequence of the epitope

It is of note that even class II-restricted antigens include a subgroup of mutated proteins which, therefore, represent truly tumor-specific antigens.

Group 6: Fusion proteins (Table 6)

In several malignancies, particularly in some forms of leukemia, the molecular mechanism of carcinogenesis involves translocation of chromosomes which results in fusion of distant genes. This often causes the synthesis of fusion proteins which characterize each type of disease (e.g., bcr-abl and pml-RARα in CML and APL, respectively) and generate new epitopes that can be recognized by T cells, either CD8+ or CD4+ in class I or class II HLA restriction, respectively. Although these epitopes appear to be weakly immunogenic in leukemia patients [28], some of these peptides or proteins

Table 6 Epitopes derived from fusion proteins (fusion proteins are never found in normal tissues)

Gene	HLA allele	Peptide epitope	Tissue distribution among tumors	Reference
HLA class I restricted epitopes				
bcr-abl[a]	A2	FMVELVEGA KLSEQESLL MLTNSCVKL	CML	Buzyn et al. 1997 [13]
bcr-abl p210(b3a2)	A2	SSKALQRPV	CML	Yotnda et al. 1998a [141]
bcr-abl (b3a2)	A3	ATGFKQSSK KQSSKALQR	CML	Greco et al. 1996 [43]
bcr-abl p210 (b3a2)	A3, A11	HSATGFKQSSK	CML	Bocchia et al. 1996 [5]
bcr-abl p210(b3a2)	A3	KQSSKALQR	CML	Norbury et al. 2000 [87]
bcr-abl p210(b3a2)	B8	GFKQSSKAL	CML	Norbury et al. 2000 [87]
ETV6/AML	A2	RIAECILGM	ALL	Yotnda et al. 1998b [142]
HLA class II restricted epitopes				
bcr-abl p190 (e1a2)	DRB1*1501	EGAFHGDAEALQRPVAS	ALL	Tanaka et al. 2000 [112]
bcr-abl p210 (b2a2)	DRB5*0101	IPLTINKEEALQRPVAS	CML	ten Bosch et al. 1999 [116]
bcr-abl p210 (b3a2)	DRB1*0401	ATGFKQSSKALQRPVAS	CML	ten Bosch et al. 1996 [115]
bcr-abl p210 (b3a2)	DRB1*1501	ATGFKQSSKALQRPVAS	CML	ten Bosch et al. 1996 [115]
bcr-abl (b3a2)	DRB1*0901	ATGFKQSSKALQRPVAS	CML	Yasukawa et al. 1998 [140]
bcr-abl (b3a2)	DRB1*1101	LIVVIVHSATGFKQSS-KALQRPVA	CML	Pawelec et al. 1996 [93]
bcr-abl (b3a2)	DR11	IVHSATGFKQSSKALQRP-VASDFEP	CML	Bocchia et al. 1996 [5]
Dek-cain	DRB4*0103	TMKQICKKEIRRLHQY	AML	Ohminami et al. 1999 [88]
LDLR/FUT	DRB1*0101	GGAPPVTWRRAPAPG WRRAPAPGAKAMAPG	Melanoma	Wang et al. 1999b [132]
Pml/RARα	DR11	NSNHVASGA-GEAAIETQSSSSEEIV [28]	APL	Gambacorti-Passerini et al. 1993 [38]
p190 minor bcr-abl (e1a2)	DRB1*1501	EGAFHGDAEALQRPVAS	AML	Tanaka et al. 2000 [112]
TEL/AML1	DP5, DP17	IGRIAECILGMNPSR	AML	Yun et al. 1999 [143]

[a]These bcr-abl epitopes are not true fusion proteins generated-epitopes, because they derive from outside the bcr-abl junction

Table 7 Frequency of epitopes recognized by a given HLA allele

Antigen	No. of epitopes	HLA-A	HLA-B	HLA-C
MAGE-1, -2, -3, -4, -6, -10, -12	24	13 (54%)	7 (29%	4 (17%)
GAGE-1, -2, -3, -4, -5, -6, -7B, -8	8	5 (62.5%)	0	3 (37.5%)
MART-1	6	4 (67%)	2 (33%)	0
Gp100	12	11 (92%)	0	1 (8%)
Tyrosinase	6	5 (83%)	1 (17%)	0

can nevertheless be used to pulse dendritic cells for vaccination.

Frequency of epitopes recognized by a given HLA allele (Table 7)

In Table 7 we have summarized, for those antigens from which a high number of epitopes have been described (e.g., CT and differentiation antigens of melanoma) the distribution of epitopes recognized in the context of different HLA loci. This table shows that the majority of epitopes are seen as restricted by HLA-A in all the three groups of antigens considered. Whether this reflects a bias caused by the fact that most of the studies have been carried out with HLA-A-restricted T cells or is mediated by the immunodominant role of the HLA locus in recognition of tumor antigens remains to be established.

Conclusions

Several excellent and timely reviews on tumor antigens have been published periodically during the past few years [8, 63, 100]. However, to our knowledge a comprehensive list of all available tumor antigens and their epitopes and HLA restriction has never been reported, despite the fact that the features of each antigen can be easily found in data bases. We hope that our work may be of interest for many tumor immunologists and students. Needless to say, we may have inadvertently missed information on some antigens despite our careful scrutiny of the published literature; therefore, we will be grateful to any readers who provide us with any missing information. We now plan to update these tables bimonthly in order to keep our data base as informative as possible. The antigen list can also be found at the INT website (www.istitutotumori.mi.it).

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