25 inbred strains of mice as possible candidates for a multi-strain carcinogenesis bioassay

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Choice of strains

Strains have been chosen on which there is some published work on lifespan and tumor incidence, and the strain does not have any obvious characteristics which would make it totally unsuitable (e.g. a high incidence of one particular type of tumor and a short lifespan). Note that this list was last up-dated in 1998 and there may be some strains not listed here which would also be potential candidates. Only data on lifespan and spontaneous disease is shown. References in the bibliography to other characteristics have not been removed.

Note that a more radical choice of strains would be to choose a set of recombinant inbred strains such as the BXD set. This comprises 35 new inbred strains derived from a cross between C57BL/6 and DBA/2. Choice of such a set for carcinogenesis testing would have the benefit of indicating in many cases which genes confer susceptibility/resistance to any given carcinogen. The use of such a set deserves careful consideration.

INTRODUCTION

Note that the strains are listed in order according to the ASCII code, with strains having a numerical designation such as 129 listed before strains with an alphabetic designation such as A. Special characters such as a slash (/) also come before alphabetic ones.
Some of the more widely used strains have become divided into substrains among which there are detectable genetic differences. This is likely to accelerate as we learn more about such differences using the very wide range of genetic markers which are now available. Two extensive studies on the 129 strain have recently been published, and the nomenclature of this family has been revised, but this is not shown here.
Some of the strains are related, having come from the same outbred colony, or having some other form of common ancestry. Other strains are derived directly from wild mice. There is good evidence that laboratory mice have been developed with contributions from more than one species/subspecies of wild mouse. For example, some strains carry the *Mus musculus domesticus* Y-chromosome, while others have the *M.m. musculus* type. Thus, Nishioka (1987) found the following:

M.m. musculus type

A/J, AEJ/Gn, AU/SsJ, BALB/cJ, BDP/J, BXSB/MpJ, CBA/J, CE/J, C3H/HeJ, C57BL/6J, DA/HuSn, DBA/2J, HRS/J, HTG/Go,, I/Ln, LP/J, NZB/BlN, NZW/Lac, P/J, RIIIS/J, SB/Le, SEA/Gn, SEC/1ReJ, SF/Cam, SK/Cam, SM/J, WB/ReJ, WC/ReJ, YBR/Ei, 129/J.

M.m. domesticus type
AKR/J, BUB/J, MA/MyJ, PL/J, RF/J, SJL/J, ST/bJ, SWR/J, SWV.

NOTES ON THE LISTINGS

The number of generations of full-sib mating is given for each strain, but this should be regarded as an approximate figure, as it varies considerably between colonies, and it is very difficult to keep it updated. In any case it is doubtful whether the exact figure has much significance once 30-40 generations have been completed, except possibly in studies of substrain differentiation.
In the case of quantitative characteristics strains have been ranked, and approximately the top and bottom quarter of the strains have been ranked as `high' and `low' ,respectively. Thus, `low intra strain aggression (13/14)' indicates that in a study of intra-strain aggression the strain in question ranked thirteenth out of fourteen strains being tested. These strain rankings should be treated with some caution, as they depend on exactly which strains happened to be chosen for the study, and the rankings could be altered by environmental influences. In some cases it will be noted that studies by different workers are contradictory. In the case of qualitative characteristics a `cf'. (compare) precedes the number responding out of the number tested. Thus good immune response to X antigen (cf. 4/8) means that the strain was one of four responders out of eight tested. Several papers describe pairs of strains which are known from previous work to differ. In this case the paper is quoted and the contrasting strain is noted in parenthases.
Where a substantial amount of information is available for a given strain this has been classified into `*Behaviour*', `*Life-span and spontaneous disease*', etc. The heading `*Drugs*' refers to response to any xenobiotic such as chemicals and drugs, and also includes response to irradiation. Only *Lifespan and spontaneous disease* and *Drugs* are shown in this abbreviated listing.

In compilations of this sort, substrain differences present a problem. Where there are major substrains of an inbred strain, an attempt has been made to show which one was involved in each study. However, references have been given, and where necessary the original article should be consulted.

The full listing is available on-line in a searchable database which can be accessed via the Jackson Laboratory, www.informatics.jax.org. I would like to take this opportunity of thanking the Jackson Laboratory for providing this service.

INBRED STRAINS AND THEIR CHARACTERISTICS

129

Inbr and colour depends on substrain (see below). Origin: Dunn 1928 from crosses of coat colour stocks from English fanciers and a chinchilla stock from Castle. This strain has a common origin with strain 101. Most substrains carry the white-bellied agouti gene

A^W though only a subset have the agouti pattern as many carry albino or chinchilla and/or the pink-eyed dilution gene, *p*, which is derived from Asian mice of the *Mus musculus* type (see also strains SJL, P/J and FS/Ei) (Brilliant et al, 1994).
It is known for the high incidence of spontaneous testicular teratomas, though the incidence differs between substrains, but more recently it has been the most widely used strain in the production of targeted mutations due to the availability of several lines of embryonic stem cells. Two recent studies show that there is major genetic variation within the 129 "family", at least some of which must be attributed to genetic contamination (Threadgill et al, 1997,Simpson et al, 1997). Strain 129/SvJ was genetically contaminated in about 1978 by an unknown strain, and differs from other 129 substrains at about 25% of SSLP genetic markers. Threadgill et al suggest that it is equivalent to a recombinant congenic strain and suggest that it is designated 129cX/Sv. Simpson et al recognised three major groups of substrains: parental substrains, steel substrains and "ter" substrains. Threadgill et al identified substrains 129/Ola, 129/J, 129/Sv, 129/ReJ and 129/RrRk, and the associated embryonic stem cells.
Clearly, major revision of the nomenclature of this group of strains is necessary. This will be undertaken in the next revision. In the mean time, people doing targeted mutagenesis should take special care to ensure that the genotype of their embryonic stem cell culture matches the substrain of mice which they use.
"Parental" substrains
129/J
129/ReJ
$129/ReJ\text{-}Lama2^{dy}$
129/OlaHsd
129/Sv
129/SvJ

129/Re

Inbr (J) 89. Pale yellow: A^w,c^{ch},*p*. Non-dystrophic substrain of 129/Re-*dy*. Maint. by Ola.

129/RrJ

Inbr (J) 97. Pale yellow, or albino. A^w, c^{ch} (or *c*),*p*. Origin: Jackson Laboratory 1948. Maint. by J.

129/Sv-*ter*/+

Inbr (Sv) N8 F49. Agouti with light belly: A^w, c^{ch}, p^+. Also carries a gene *ter* causing a high incidence of testicular teratomas. Origin: A substrain to determine the effect of the *W* gene on incidence of testicular teratomas. The *W* gene was backcrossed repeatedly to 129, and at generation N8 a female produced 38 male offspring of which 8 had testicular teratomas. All subsequent members derived from that mating. The *W* gene has been eliminated. Incidence of testicular teratomas now 30% (Stevens, 1973). Maint. by J.

Life-span and spontaneous disease
Long life-span in conventional conditions (18/22 = 679 days in males, 15/22 = 648 days in females) (Storer, 1966). Long life-span in SPF fostered conditions (16/17 = 699 days in males, 11/1 7 = 666 days in females) (Festing and Blackmore, 1971). Low overall tumour incidence (7% in males, 21% in females), including lymphoma 2% in males and 7% in females, soft tissue sarcomas 2% in males and 1% in females and benign tumours 2% in males and 3% in females (Smith *et al*., 1973). Lung tumours 4-46% (Festing and Blackmore, 1971). Testicular teratomas about 1% in most substrains, but 30% in the terSv substrain (Stevens, 1973). Incidence of teratomas increased in p53-deficient mice (Harvey et al, 1993). The Ter gene has been mapped to chromosome 18 (Asada et al, 1994). Congenital malformations about 4% in RrSvKt-*jt* substrain (Kalter, 1968). High incidence of urinary calculi (Russell and Meier, 1966).

A

Inbr: More than F150. Albino. Genet: *a, b, c.* Origin: Dr L. C. Strong, 1921, from a cross between the Cold Spring Harbor and Bagg albino random-bred stocks (and therefore relavted to BALB/c). Internationally distributed, Strain A was the third most widely used strain in cancer and immunology research (Festing, 1969), though its popularity has probably declined recently. Although it may be classified as a general-purpose strain, it is well known for a high susceptibility to induction of congenital cleft palate by cortisone and a high spontaneous incidence of lung adenomas, as well as developing a high incidence of lung tumours in response to carcinogens. Shimkin and Stoner (1975) suggest that this response may be used as a rapid in *vivo* assay for carcinogenesis. The strain also suffers from a defect in macrophage function somewhat resembling the mutant *lps* found in C3H/HeJ (Vogel et al 1981).
The following main substrains are recognised, though they have not been defined by genetic markers:

A/St

Maintained by Strong.

A/He

Strong to Heston, 1938.

A/GrFa

Main British substrain, Strong to Gruneberg 1932, and mainly distributed by Falconer.

A/WySn

Strong to Bittner 1927, to Wooley, to Snell, 1951.

A/J

Strong to Cloudman 1928, to Jackson Laboratory 1947, now widely distributed.

Life-span and spontaneous disease
Primary lung tumours 6% in male, 32% in female and 26% in virgin females in J substrain; 44% in males, 23% in females and 30% in virgin females in He substrains (Hoag, 1963). Zero incidence of lymphatic leukaemia in He substrain, 1% in J substrain. Mammary adenocarcinomata zero in males, 1% in virgin females, 28% in breeding females of J substrain and 54% in breeding females of He substrain (Hoag, 1963). Pulmonary tumours 90% in mice at 18 months (Heston, 1963). Leukaemia 3% in HeJ substrain (Myers *et al*., 1970). A high proportion of the mammary tumours are of the

acinar type (3/7) (Tengbergen, 1970). Lung adenomas 53-64% in BrA and A substrains, but mammary tumours zero (Muhlbock and Tengbergen, 1971). Lung tumours 4-31% and lymphatic leukaemia 10-43% (Festing and Blackmore, 1971). Spontaneous lung tumours occur at rate of 0.21 tumours/mouse at 24 weeks (Poirier *et al*., 1975). Rare spontaneous myoepitheliomas arising from myoepithelial cells of various exocrine glands have been observed in the J and HeJ substrains (Sundberg et al 1991)

Life-span in conventional conditions intermediate in both sexes (9/22 = 490 days in males, 13/22 = 590 days in females (Storer, 1966). Life-span in SPF fostered conditions intermediate (8/17 = 512 days) in males and short (3/17 = 558 days) in females (Festing and Blackmore, 1971). Life-span 662 days in males and 688 days in females (Goodrick, 1975). Median life-span 400 days in HeJ substrain (Curtis, 1971).
Spontaneous congenital cleft palate 4% and high susceptibility to teratogenic effects of cortisone, which may be associated with the $H2^a$ allele, (Bonner and Slavkin, 1975). Congenital malformations in new-born mice 10% (1/9), including cleft lip and palate and polydactyly (Kalter, 1968). WySn substrain has 20% cranofacial defects due to the action of two genetic loci with unequal duplicate epistasis (Juriloff, 1995). Cleft palate is a function of foetal genotype rather than maternal factors (Yoshida et al, 1996). An exclusion map for the major gene causing nonsyndromic cleft lip with or without cleft palate has swept 40% of the mouse genome, with candidate regions on chromosomes 12, 18 and 19 with a few candidate loci (Juriloff, 1993).
Low incidence of virus-like particles in chemically induced sarcomas (6/6) (Liebelt *et al*., 1970). Can be made obese by a suitable diet (Fenton and Dowling, 1953). Does not develop non-insulin-dependent diabetes mellitus and hypertension when fed a high fat-high simple carbohydrate diet, whereas C57BL/6 mice do (Mills et al 1993). Blood glucose levels and insulin insensitivity in crosses between diet-induced type II diabetes sensitive C57BL/6 and resistant A/J are genetically independent (Surwit et al 1991)
High incidence of amyloidosis (Russell and Meier, 1966). No amyloidosis found by Powers *et al*. (1976) in He and HeJ substrains, in contrast to previous reports. About 4% incidence of congenital open eyelids (Dagg, 1966). High incidence of cannibalism of young restricted to anatomically defined mutilation and amputation, particularly of neck, lower jaw and digits in Ha substrain (Hauschka, 1952).
Relatively resistant to secondary amyloidosis which does not appear to be associated with variation in the serum amyloid A gene cluster (Butler and Whitehead, 1994).

Drugs
Susceptible to urethane-induced lung tumours (1/6) (Falconer and Bloom, 1962). Sensitive to induction of pulmonary tumours (1/6) but resistant to leukaemia and liver tumour induction by DMBA given neonatally (6/6 and 5/6, respectively) (Flaks, 1968). Susceptible to the induction of lung tumours by cyclopenta(cd)pyrene (Nesnow et al, 1994). Most benzo(a)pyrine-induced lung tumours had K-ras oncogenes inherited from the A/J parent with mRNA transcribed from the allele inherited from strain A/J being 5-20 times more abundant than that from C3H in crosses involving strain C3H (Chen et al, 1994) The A/J mouse lung can be used as a model to study the effectiveness of new chemical intervention therapies for controlling malignant tumor growth (Belinsky et al, 1993), and in the study of chemopreventive agents such as dietary and green tea

polyphenols (Castonguay and Packer, 1993, Katiyar et al, 1993), isothiocyanates (AdamRodwell et al, 1993, Hecht, 1995), vitamin E (Yano et al, 1994) and other substances (Yun et al, 1995). No glycerol-associated effect on active oxygen formation and thiobarbituric acid reactive substances was observed in the lungs of A/J mice treated with 4-nitroquinoline 1-oxide, in contrast with outbred ddY strain mice (Yano et al, 1993, 1994).
Nicotine decreases shock avoidance learning in J substrain (7/9), but increases it in He substrain (2/9) (Bovet *et al*., 1966). Low ED50 to behavioural effects of nicotine (2/19). Resistant to seizures induced by nicotine (2/19) (Marks et al 1989) Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Not sensitive to histamine (8/9) (Brown, 1965). Susceptible to the teratogenic effect (cleft palate) of cortisone acetate (1/4) (Dostál and Jelínek, 1973; Kalter, 1965, Kalter 1981). There appears to be a threshold dose of cortisone needed to induce cleft palate (Fawcett et al, 1996). Sensitive to teratogenic effect (malformed ribs and vertebrae) of hypoxia on ninth day of gestation (1/5) (Dagg, 1966). Sensitive to X-irradiation (22/27 in He substrain, 20/27 in J substrain) (Roderick, 1963), 9/10 in males, 8/10 in females of J substrain (Storer, 1966). Highly susceptible to endotoxin lipopolysaccharide (1/5) (Heppner and Weiss, 1965). Resistant to hyperbaric oxygen (15/18 in J substrain, 12/18 in He substrain) (Hill *et al*., 1968). Susceptible to pulmonary hyaline-membrane formation in 90% oxygen (3/10) (Lieberman and Kellog, 1967). Low LD_{50} to X-irradiation (7/9) (Yuhas and Storer, 1969). Interstitial tumours of testis readily induced with oestrogens (Heston, 1963). Sensitive to chloroform toxicity (cf. 4/9) (Deringer *et al*., 1953). Thalidomide increases congenital malformations such as cleft lip and palate (Szabo and Steelman, 1967)..High bronchial reactivity (1/6) to methacholine and serotonin (Konno et al 1993). Susceptible (1/8) to daunomycin-induced nephorsis (Kimura et al 1993). Resistant to hepatotoxic effects of cadmium (Shaikh et al, 1993). Airways hyperreactive to acetylcholine (c.f. 3/7) (Zhang et al, 1995). Susceptible (cf 5/8) to ozone-induced decreases of tracheal potential (Takahashi et al, 1995). Clonidene failed to produce an aggressive behavioural response (cf 3/9) (Nikulina and Klimek, 1993). A diet containing 15% dairy fat, 1% cholesterol and 0.5% cholic acid caused a high incidence of cholesterol gallstones (like SWR, C57L, contrast SM, AKR, DBA/2) (Faulkner et al, 1995).

A2G

Inbr: F 101. Albino. Genet: *b*, c. Originated as an illegitimate mating of strain A at Glaxo Laboratories, UK, in 1942-50, followed by b x s mating. Should not be considered as a substrain of A. Distributed mainly in European laboratories, and best known for its unique resistance to myxovirus (influenza) infections.

Life-span and spontaneous disease

Long life-span in males (13/17 = 640 days) but intermediate in females (8/17 = 644 days), and lung tumours 17-65% in SPF fostered conditions (Festing and Blackmore, 1971).

Drugs

Sensitive to insulin (2/9) but insensitive to histamine (7/9) (Brown, 1965). Long survival on Warfarin (9/12) (Lush and Arnold, 1975). Long sleeping time under hexobarbital anaesthetic (13/15) (Lovell, 1976), long sleeping time under pentobarbitone anaesthetic

(18/23), Lovell (1986). Highly susceptible to lung tumour induction by urethane (cf. strain A) (Festing 1980).

BALB/c

Albino: *A,b,c*. Origin: Stock acquired by H.Bagg in 1913, to MacDowell, to Snell in 1932 (who added the /c). Now widely distributed and among the top 2-3 most widely used inbred strains. The strain is particularly well known for the production of plasmacytomas on injection with mineral oil. These tumours form the basis for the production of monoclonal antibodies. Used as a general-purpose strain in many different disciplines. Good breeding performance and long reproductive life-span. Normally has low mammary tumour incidence but can be infected with the mammary tumour virus by fostering to C3H (which carries the virus), and it then gets a high incidence of mammary tumours.

The history and characteristics of the strain have been reviewed by Potter (1985). Three major substrains trace back to before 1940, and are listed separately below. Data on genetic markers suggest that these substrains have diverged largely through mutation or residual heterozygosity rather than genetic contamination. Hilgers et al (1985) have shown that the substrains differ as a result of mutations at the *Raf1* locus (controlling the expression of alpha-fetoprotein), the *Qa2* locus (governing cell surface antigens), the *Gdc1* locus (governing L-glycerol 3-phosphate dehydrogenas activity in the liver) and the PR1 repetative sequence. There is no evidence for genetic contamination during the early history of the strain. A fourth substrain, BALB/cWt is also listed as it has a high incidence of hermaphroditism.

BALB/cHeAn

Inbr ?.To Snell circa 1932, to He circa 1935. Now widely distributed (including the By, AnN, HeA and AnPt substrains). This substrain is much less aggressive than the J substrain. Maint. by A, N.

BALB/cJ

Inbr 150 +?.Snell to Jackson Laboratory after 1940. Males of this substrain are extremely aggressive and will fight if housed together once mature. The Lac substrain separated in 1952 is non-aggressive. Maintained by J, Ola (JLac substrain).

BALB/cRl

Inbr ?. Snell to Green circa 1937, to W.L. and L.B.Russell c1948.

BALB/cWt

Inbr. ?. Has about a 3% incidence of true hermaphroditism, which significantly distorts the sex ratio (Eicher et al 1980)

Life-span and spontaneous disease

Life-span intermediate in both sexes in conventional conditions (12/22 = 539 days in males, 11/22 = 575 days in females) (Storer, 1966). Life-span intermediate in males (7/17 = 509 days) and short in females (4/17 = 561 days) in SPF fostered conditions (Festing

and Blackmore, 1971). Life-span 648 ± 20.6 days in females and 816 32.4 days in males (Goodrick, 1975). Life-span 20 months in females and 13 months in males. Amyloidosis 40% in males. Reticular neoplasms 23% females and 3% males (Ebbesen, 1971). Primary lung tumours 32% in males, 30% in breeding females and 14% in virgin females in Scott substrain. Leukaemia 5% (Myers *et al*., 1970). Zero incidence of lymphatic leukaemia. Mammary adenocarcinomas zero in males, 5% in breeding females and 1% in virgin females (Hoag, 1963). Mammary tumours 30% at 2 years (3/7) (Bentvelzen *et al*., 1970). Mammary tumours 20% in females at 16.7 months, but 100% at 7.1 months in BALB/cfC3H (Heston and Vlahakis, 1971). Mammary tumours 10% at 14 months (Schlom *et al*., 1973). Low gross tumour incidence in males (20/22) (Storer, 1966). Renal tumours 25-48%, mammary tumours 3-13%, reticuloendothelial tumours 11-20%, lung tumours 10-16%, synoviomas 2-8%, depending on substrain (Sass *et al*., 1976). Low incidence of virus-like particles in chemically induced sarcomas (5/6) (Liebelt *et al*., 1970). Frequency of rhabdomyosarcomas was calculated to be 2.4/100,000 mice retained as breeders, and 10/14 mice found with these tumours were of the BALB/cJ substrain (Sundberg et al 1991). Rare spontaneous myoepitheliomas arising from myoepithelial cells of various exocrine glands have been observed in the J and ByJ substrains (Sundberg et al 1991)

Gross tumour incidence in germ-free mice 43%, with lung tumours 21%, angiomas 6%, lymphosarcomas 5% and other tumour types less than 3% each (Smith and Pilgrim, 1971). Pulmonary tumours 26-29% (Heston, 1968).

Left auricular thrombosis occurs in 66% of older breeding females. This is associated with reduced levels of the prothrombin complex factors such as factor IX (40% of normal), factor XIII (60% of normal), factor X (50% of normal) and prothrombin (about 33% of normal). These deficiencies occur slightly before parturition (Meier and Hoag, 1966). High incidence of epicardial mineralisation (11% in males, 4% in females), which increases slightly with age (Frith *et al*., 1975). Heart defects, including cardiac calcinosis 17-62% (Festing and Blackmore, 1971). Spontaneous myocardial lesions of right ventricle found in 60% of females and 30% of males. These macroscopically visible degenerative fibrosclerotic lesions may represent a last phase of myocarditis of the inflammatory type found in apparently normal mice (Bellini *et al*., 1976).
Carry a single recessive gene different from that found in C57BL/6J and WB/ReJ, causing age-related hearing loss (Willott et al, 1995).
Zero incidence of spontaneous congenital malformations (cf. 2/9) in GrKt-*tk* substrain (Kalter, 1968).

Drugs
Susceptible to skin ulceration by 7,12-dimethylbenz(a)anthracene (DMBA) (cf. 13/23) (Thomas *et al*., 1973). Sensitive to the development of uterine tumours following treatment with DMBA at 4-weeks of age (cf 3/6) (Tsubura et al, 1993). Sensitive to the induction of skin tumours by methylnitrosourea in methanol (1/4) (Lijinsky et al 1991). Susceptible to tumour induction by 3-methylcholanthrene (3/12) (Whitmire *et al*., 1971). Susceptible to induction of leukaemia (1/6) but resistant (6/6) to induction of liver tumours by neonatally administered DMBA (Flaks, 1968). High incidence of interstitial tumours of testis induced by stilboestrol, high incidence of haemangioendotheliomas,

particularly in interscapular fat pad and lung in mice treated with O-aminoazotoluene (Heston, 1963). High incidence of lung tumours after administration of methycholanthrene by gavage (1/5) (Akamatsu and Barton, 1974). Injection of mineral oil i.p. induces a high incidence of transplantable plasmacytomas (myelomas). Bence Jones proteins include kappa and lamda light chains and the two-chain IgA protein. 60% of tumours are of the IgA type (Potter, 1972). Susceptibility appears to be mediated by two genes on chromosome 4 (Potter et al, 1994). Susceptible (2/8) to daunomycin-induced nephorsis (Kimura et al 1993).
Sensitive to X-irradiation (26/27) (Roderick, 1963), (10/10) (Storer, 1966); low LD_{50} to X-irradiation (9/9) (Yuhas and Storer, 1969).
Nicotine increases shock avoidance learning (3/9) (Bovet *et al.*, 1966). Sensitive to insulin (3/9) (Brown, 1965). Poor ovulatory response to PMS at both 3 IU (6/6) and 7 IU (5/6), but response increased by exposure to males (Zarrow *et al*., 1971). Low locomotor excitation after treatment with D-amphetamine (6/6) (Babbini *et al*., 1974). Resistant to hyperbaric oxygen (16/18) (Hill *et al*., 1968). Insensitive (eosinophil response) to cortisone acetate (cf. 3/6) (Wragg and Speirs, 1952). Low sensitivity to induction of malformed ribs and vertebrae by hypoxia on ninth day of gestation (5/5) (Dagg, 1966). Sensitive to chloroform toxicity (cf. 5/10) (Christensen *et al*., 1963). Resistant to toxic effects of isoniazid (1/10) (Taylor, 1976b). Resistant (3/3) to neurotoxic effects of monocrotophos (Rao et al 1991). High transient increase in renal lipid peroxidation following treatment with nickel (1/4) (Misra et al 1991). Resistant to biliary tract injury following oral dosing with 500 micrograms of the fungal toxin sporidesmin (3/4), but the injury is much more persistent than in SJL and was accompanied by periductal fibrosis and occasionally by obliteration of ducts typical of sclerosing cholangitis (Bhathal et al 1990). High LD50 following injection of butylated hydroxytoluene (BHT) (1/4) (Kehrer and DiGiovanni 1990). High histamine release from peritoneal mast cells induced by compound 48/80, a calcium dependent histamine releaser (1/8) (Toda et al 1989). High histamine release from peritoneal mast cells induced by Ca2+ ionophore A23187 (c.f. 7/8, contrast C57BL/6) (Toda et al 1989). Cultured mast cells grow more slowly and release less histamine and TNF-alpha following anti-DBN IgE antibody treatment than those of strain SJL (Bebo et al, 1996). Highly sensitive to the induction of catalepsy by haloperidol (1/8) associated with midbrain dopamine D2 receptor density levels (Kanes et al, 1993). Resistant to both acute and chronic cadmium toxicity (contrast NFS) (Abshire and Waalkes, 1994). However, cadmium can induce hematopoetic and suppress pulmonary tumours in these mice (Waalkes and Rehm, 1994). Resistant to weight loss induced by cocaine (1/7) (Shimosato et al, 1994). Clonidene induces a strong aggressive behavioural response (1/9) (Nikulina and Klimek, 1993). More resistant to acute toxic effects of aflatoxin B-1 than C57BL/6 (Almeida et al, 1996).
The IgE response following topical application has been used to predict which chemicals may have the potential to cause sensitization of the respiratory tract (Hilton et al, 1996). More susceptible to the development of micronuclei than C57BL/6 or DBA/2 following treatment with clastogenic base analogues and nucleosides (Sato et al, 1993). Estrogen does not induce an increase in VLDL and LDL-cholesterol (like C3H contrast C57BL/6 and C57L)) (Srivastava, 1995).

C3H

Inbr: F130 to F170 depending on substrain. Agouti. Genet: +, *rd*. Developed by Strong 1920 from a cross of Bagg albino with DBA male (see CBA) with selection for a high incidence of mammary tumours. Now among the most widely used of all mouse strains. Most substrains have a good reproductive performance. Unfostered substrains (which are now relatively rare since 'SPF' animals have become popular) have a high incidence of mammary tumours (usually > 90% at one year) caused by a virus which is passed from mother to offspring through the milk. Fostering of the young or transfer of fertilised ova to a mammary tumour virus-free strain eliminates the virus, and substantially reduces the incidence of mammary tumours. Note that all `SPF' stock will be free of this virus.

The unfostered substrains are widely used in cancer research for the sake of their mammary tumours. Fostered stock are widely used as a general-purpose strain which is readily available and well known. The strain should be used with care in behavioural studies, since it carries the *rd* (retinal degeneration) gene and is blind after about 6 weeks.

Some substrain differences are large, and can not be accounted for solely on the basis of mutation, and must be ascribed either to substantial residual heterozygosity or genetic contamination (McLaren and Tait, 1969), though C3H/HeJ is known to differ from C3H/He as a result of a mutation at the *lps* (lipopolysaccharide) locus.

The following major substrains are recognised:

C3H/Bi

Strong to Bittner 1931, to Kirschbaum 1952. Has 83% mammary tumours in unfostered breeders. Low leukaemia.

C3H/Fg

Origin not known, but has a very high incidence of lymphatic leukaemia (over 90%) (Fuchs, 1962).

C3H/He

This substrain was passed to Heston in 1941,and is now the most widely distributed of all. Non-fostered substrains have more than 90% mammary tumours by about 11 months. Fostered substrains have a high incidence of hepatomas (Festing and Blackmore, 1971).

C3H/HeJ

Heston, to Jackson Laboratory in 1947, and now widely distributed. Has poor immune response to endotoxic lipopolysaccharide due to a B-cell deficit (Rosenstreich and Glode, 1975; Coutinho, 1976).

C3HeB/De

A substrain developed by transfer of fertilised ova to strain C57BL by Deringer. This substrain lacks the mammary tumour virus and therefore has a lower incidence of mammary tumours (4% in virgin females and 55% in breeding females and 74% in force-bred females) (Deringer, 1959a).

C3HeB/FeJLe-*a/a*

Inbr. N10F12 (1993). The a allele transferred from C57BL/6J. Now used to create a B6C3Fe-a/a non-agouti hybrid as a coat colour marker for stocks maintained by ovarian transfer.

C3HeB/Fe (syn: TC3H)

Developed by Fekete in 1948 by transfer of fertilized ova of C3H/HeJ to C57BL/6. Lacks mammary tumour virus.

C3H/He-mg

`Mahogany' coat colour mutation occurred spontaneously in C3H/He stock held at Laboratory Animals Centre, Carshalton, in 1967. The strain has been propagated because authenticity can be guaranteed by the colour of the coat.

C3H/He-A^{vy}

Congenic line developed by backcrossing the A^{vy} to the C3H background. Has an exceptionally high mammary tumour incidence, virtually 100% at 7-8 months. The fostered substrain C3H-A^{vy}f*B* has a 90% incidence of mammary tumours transmitted by either parent (Vlahakis *et al*., 1970).

C3H.PRI-Flv^r (formerly C3H.RV) and C3H.M.Dom-Flv^r

Congenic line resistant to flavivirus (arbovirus) infection, developed by Groschel and Koprowski (1965) by backcrossing the resistance gene from PRI to C3H, and by Shallam by backcrossing the resistance gene from wild *M.m. domesticus* to C3H.

Life-span and spontaneous disease

Almost 100% of mammary tumours in females of unfostered substrains (Heston, 1963). Mammary adenocarcinomas in unfostered substrains less than 1% in males, 95% in breeding and 88% in virgin females. Lymphatic leukaemia zero incidence (Hoag, 1963). Mammary tumours 100% at 6.8 months in C3H-A^{vy}, 90% in C3H- A^{vy}fC57BL at 15.3 months. Mammary tumours 40% at 18.8 months in C3HfC57BL, but 99% at 7.2 months in unfostered C3H (Heston and Vlahakis, 1971). Mammary tumours 37% at 2 years in fostered substrain (Bentvelzen *et al*., 1970). Median latent period to develop mammary tumours in unfostered substrains ranged from 276 to 566 days, depending on breeding status and environmental stress (Riley, 1975). A high proportion of the mammary tumours are of the acinar type (2/7) (Tengbergen, 1970). Incidence of mammary tumours reduced by bromocriptine and interferon Stravoravdi et al, 1993).

Hepatomas 72-91% in males at 14 months, 59% in virgin females, 30-38% in breeding females (Heston, 1963). Hepatomas have eosinophilic cytoplasmic inclusion bodies (Liebelt *et al*., 1971). Good model of genetic predisposition to hepatocellular tumours, susceptibility being associated with six chromosomal regions (Dragani et al, 1995). Point mutations in H-ras do not generally play a major or initiating role in spontaneous hepatocarcinogenesis in this strain (Enomoto et al, 1993).

Lung adenomas 2-10% in fostered A substrain, leukaemia 6-30% (Muhlbock and Tengbergen, 1971). Occasional Harderian gland tumours (Heston, 1963). Rare "lipomatous" hamartomas or choristomas have been noted (Adkison et al 1991).

Life-span in SPF fostered conditions intermediate in both sexes (11/17 = 590 days in males, 12/17 = 676 days in females). Liver tumours 9-23%, lung tumours 2-10% and mammary tumours 21-36%. Heart defects 13-26% and cystic ovaries 13-26% (Festing and Blackmore, 1971). Tail lesions similar in appearance to bit wounds were found in grouped C3H/HeJ by Les (1972). Develop dystrophic cardiac calcification which may be related to disturbed myocyte calcium metabolism (Brunnert, 1997).
Can be made obese by a suitable diet (Fenton and Dowling, 1953). Resistant to the development of aortic cartilaginous metaplasia (contrast C57BL/6) (Qiao et al, 1995). Resistant to diet-induced aortic fatty streak lesions which correlates with a high level of paroxinase mRNA (contrast C57BL/6) (Shih et al, 1996).

C3HeB/FeJ

Primary lung tumours 8% in males, 4% in breeding females and 10% in Virgin females. Lymphatic leukaemia zero. Mammary adenocarcinomas zero in males, 12% in breeding females, 2% in virgin females (Hoag, 1963). Ovarian tumours 47% in Virgin and 37% in breeding females, 29% in force-bred females (Heston, 1963). Hepatomas 91% in breeding males, 58% in Virgin and 30% in breeding females (Murphy, 1966). Life-span above average in both sexes (16/22 = 652 days in males, 17/22 = 657 days in females). High gross tumour incidence in males (5/22) (Storer, 1966).

Drugs

Susceptible to skin ulceration to DMBA (cf. 13/22) (Thomas *et al*., 1973). Sensitive to the development of uterine tumours following treatment with DMBA at 4-weeks of age (cf 3/6) (Tsubura et al, 1993). Susceptible to induction of subcutaneous tumours by 3-methylcholanthrene (1/14 to 4/14, depending on substrain) (Kouri *et al*., 1973). Susceptible to tumour induction by 3-methylcholanthrene in fostered and unfostered substrains (1/8 to 2/8) (Whitmire and Salerno, 1972), (2/12) (Whitmire *et al*., 1971). Susceptible to induction of liver (1/6) but resistant to pulmonary (5/6) tumours by neonatally administered DMBA (Flaks, 1968). High susceptibility to tumour induction by 3,4-benzpyrene (1/6) (Liebelt *et al*., 1970). High susceptibility to induction of mammary tumours by urethane (2/7) (Bentvelzen *et al*., 1970). High incidence of gastric tumours after administration of methylcholanthrene by gavage (2/5) (Akamatsu and Barton, 1974). Susceptible to fibrosarcoma induction by methylcholanthrene (2/15 male, 1/15 female) (Strong, 1952). Highly susceptible to the induction of hepatocellular tumours by various carcinogens, with the volume of hepatic lesions being >100-fold greater than in more resistant strains. Susceptibility is linked to at least six chromosomal regions (Dragani et al, 1995). C3HxMSM F1 hybrids treated with N-methyl-N-nitrosourea (MNU) develop squamous cell carcinomas of the forestomach with about 20% and 15% having mutations in H-*ras* and p53, respectively (Masui et al, 1997).
Phenobarbitone in the diet to give an intake of 85mg/kg per day resulted in 70% of animals developing basophilic nodules by 91 weeks of age (contrast 4% in C57BL/6), but no increase in liver carcinomas (Evans et al, 1992). However, there was a two-fold greater level of DNA synthesis in C3H mice relative to C57BL/6 mice after partial hepatactomy, though partial hepatectomy is a tumour promoter in C57BL/6 but not in C3H mice (Bennett et al, 1995).
Insensitive to histamine (9/9) (Brown, 1965). Airways of C3H/HeJ hyporeactive to acetylcholine (c.f. 3/7) (Zhang et al, 1995). Resistant to teratogenic effect of acetazolamide (5/6) (Green *et al*., 1973). Pentobarbital i.p. induces hepatic epoxide

hydrase (cf. 4/7) (Oesch *et al*., 1973). Sensitive to X-irradiation (25/27) (Roderick, 1963). Long survival on Warfarin (12/12) (Lush and Arnold, 1975). Sensitive to hyperbaric oxygen (2/18) (Hill *et al*., 1968). Sensitive uterine response to oestrogens (5/5) (Chai and Dickie, 1966). Short hexobarbital sleeping time (3/9) (Vesell, 1968). Long survival in 90% oxygen (1/10) and highly susceptible to pulmonary hyaline-membrane formation (1/10) (Lieberman and Kellog, 1967). Resistant to the induction of pulmonary fibrosis by bleomycin (contrast C57BL/6) (Haston et al, 1996), and irradiation though the sensitivity of lung fibroblasts to irradiation *in-vitro* does not correlate with *in-vivo* sensitivity (Dileto and Travis, 1996). Sensitive to chloroform toxicity (cf. 4/9) (Deringer *et al*., 1953). Susceptible to toxic effects of isoniazid (10/10) (Taylor, 1976b). High ED50 to behavioural effects of nicotine (17/19) (Marks et al 1989). Low self-selection of nicotine (5/6) which is inversely correlated with sensitivity to nicotine-induced seizures (Robinson et al, 1996).
Low bronchial reactivity (5/6) to methacholine and serotonin (Konno et al 1993). No increase in renal lipid peroxidation following treatment with nickel (4/4) (Misra et al 1991). Susceptible to biliary tract injury following oral dosing with 500 micrograms of the fungal toxin sporidesmin (2/4) (Bhathal et al 1990). Low histamine release from peritoneal mast cells induced by compound 48/80, a calcium dependent histamine releaser (c.f. 5/8) (Toda et al 1989). High histamine release from peritoneal mast cells induced by Ca2+ ionophore A23187 (c.f. 7/8, contrast C57BL/6) (Toda et al 1989). Cadmium highly hepatotoxic (1/5) (Shaikh et al, 1993). Resistant (cf 3/8) to ozone-induced decreases of tracheal potential (Takahashi et al, 1995, Kleeberger et al, 1993). Susceptible to weight loss induced by cocaine, but this is attenuated by anisomycin (cf SJL, CBA) (Shimosato et al, 1994). Estrogen does not induce an increase in VLDL and LDL-cholesterol (like BALB/c, contrast C57BL/6 and C57L)) (Srivastava, 1995).

C3HeB/FeJ

Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Sensitive to X-irradiation (23/27) (Roderick, 1963). Good ovulatory response (94%) to 3 I.U. PMS (1/6), but poor response (33%) to 7 I.U. PMS. Response facilitated by exposure to males (Zarrow *et al*., 1971). Susceptible (cf 5/8) to ozone-induced decreases of tracheal potential (Takahashi et al, 1995).

C57BL

Black, a. Origin: Little 1921 from the mating of female 57 with male 52 from Miss Abbie Lathrop's stock. The same cross gave rise to strains C57L and C57BR. Female 58 mated with the same male gave rise to strain C58. C57BL is probably the most widely used of all inbred strains, (substrain C57BL/6 alone accounts for over 14% of occasions on which an inbred strain is used) though in many ways it seems to be atypical of inbred strains of laboratory mice. In contrast to 36 other standard inbred strains, it carries a Y chromosome of Asian *Mus musculus* origin (c.f. AKR and SWR) (Tucker et al 1992), and a LINE-1 element derived from *Mus spretus* the frequency of which suggests that up to 6.5% of the genome may be of *M. spretus* origin (Rikke et al, 1995). A probe designated B6-38 to the pseudoautosomal region of the X and Y chromosome has a characteristic Pst I pattern of fragment sizes which is present only in the C57BL family of strains (Kalcheva et al, 1995).
It usually has a good breeding performance, depending on substrain, and has been used as the genetic background for a large number of congenic strains covering both

polymorphic and mutant loci. Four major substrains A, GrFa, 6 and 10 appear to be quite similar, and any differences are consistent with what might be expected from the accumulation of new mutations and a small ammount of residual heterozygosity, though McClive et al (1994) have found that B6 and B10 differ at multiple loci on chrosome 4 including the microsatellite markers D4Mit69, D4Mit71 and D4Mit72. Additional microsatellites which distinguish between B6, B10 and C57BLKS are given by Slingsby et al (1996). The former Ks substrain differs at several loci probably as a result of genetic contamination with a DBA substrain. This has been re-named C57BLKS, and is listed separately. The seven major substrains existing in 1935 are listed below.

C57BL/A

Inbr(A) ?+142. Origin. Little to A c1932. Maint. by A.

C57BL/An

Little to Andervont 1932. Differs from B6 and B10 at the *Ce1* locus.

C57BL/GrFa.

Origin: Little to Gruneberg 1932, to Falconer 1947. Most British substrains derived from this stock, though 6 and 10 substrains have been imported more recently. This substrain seems to resemble the 6 rather than the 10 substrain. Maint. by Ola

C57BL/KaLwN.

To N 1965 from Lw at F35. Maint. by N.

C57BL/Ks see C57BLKS

C57BL/6

Inbr (J) 150. Origin: substrains 6 and 10 were separated prior to 1937. This substrain is now probably the most widely used of all inbred strains. Substrain 6 and 10 differ at the *H9, Igh2* and *Lv* loci. Maint. by J,N, Ola.

C57BL/10

Inbr (J) 158. Origin: see C57BL/6. Maint. by J.

C57BL/10ScSn.

Inbr (J) ? +136. Little to W.L.Russell to J.P.Scott at F26 as a separate substrain. To Snell at F35-36. Behaviour differs from C57BL/10J. Maint. by J,N, Ola.

C57BL/10Cr

Carries spontaneous lipopolysaccharide mutation *lps* which appears to resemble that found in C3H/HeJ (Vogel et al 1981).

C57BL/Ola

Carries a spontaneous mutation, Wld^S, causing a marked slowing of axonal degeneration during Wallerian degeneration (Tsao et al, 1994).

Life-span and spontaneous disease

Substrain unspecified:

Mammary tumours less than 1% (Heston and Vlahakis, 1971). Lung adenomas 0-9% in LiA substrain (Mühlbock and Tengbergen, 1971). Zero incidence of mammary tumours at 2 years (cf. 3/7) (Bentvelzen *et al*., 1970).

Mean life-span 800 days in males and 750 days in females according to Rowlatt *et al*. (1976), who also give details of pathology in a large aging colony of C57BL/Icrf-*a*^{t} mice. Hyperphalangy and polydactyly occur with a low incidence in all C57BL strains and substrains (Dagg, 1966). Hydrocephalus 4.1% (Mori, 1968). Type B reticulum cell neoplasms 75% at about 20 weeks in HeDe substrain (Dunn and Deringer, 1968).

C57BL/Ka

Median life-span 23 months in males. Main autopsy findings include reticulum cell sarcoma type B (29%), testes interstitial tumour (13%), thyroid follicular adenoma (9%), unclassified lymphoreticular tumours (9%). Nine other tumour types found. Non-neoplastic lesions include amyloid (83%), Sendai virus pneumonia (20%), periarteritis nodosa (16%), mesenteric disease (10%). Several other lesions noted. (Zurcher *et al*., 1975). About 50% of mice develop homogeneous immunoglobulins resembling idiopathic paraproteinaemia in man by 24 months (Radl and Hollander, 1974).

C57BL/Fa

Long life-span in males (14/17 = 645 days), but intermediate in females (5/17 = 580 days) in SPF fostered conditions (Festing and Blackmore, 1971). Hydronephrosis 0.5% in females, 1.5% in males (Taylor and Fraser, 1973).

C57BL/6

Primary lung tumours 1% in males, 3% in breeding females and zero in virgin females. Lymphatic leukaemia less than 2%, mammary adenocarcinomas less than 1% (Hoag, 1963). Leukaemia 7% (Myers *et al*., 1970). Rare "lipomatous" hamartomas or choristomas have been noted (Adkison et al 1991).

Susceptible to the development of atheromatous lesions on wall of aorta after 20 weeks on a high-fat diet (Thompson, 1968; Roberts and Thompson, 1976). Develop fatty streak-like lesions in the valve sinus region of the ascending aorta after 10-20 weeks on a diet enriched in saturated fat and cholesterol. After a further 15 weeks fibro-fatty lesions with many of the characteristics of human atheromatous plaques are found (Stewart-Phillips and Lough 1991). Exhibit aortic cartilaginous metaplasia (contrast C3H) (Qiao et al, 1995). Susceptible to diet-induced aortic fatty streak lesions which correlates with a low level of paroxinase mRNA (contrast C3H) (Shih et al, 1996).

Develops non-insulin-dependent diabetes mellitus and hypertension when fed a high fat-high simple carbohydrate diet, whereas A/J mice do not (Mills et al 1993). Susceptible to the development of atherosclerosis on a semi-synthetic high fat diet (1/9) (Nishina et al, 1993). Blood glucose levels and insulin insensitivity in crosses between diet-induced type II diabetes sensitive C57BL/6 and resistant A/J are genetically independent (Surwit et al 1991). High simple carbohydrate diet for five months induced hyperglycemia, hyperinsulinemia and hypercholesterolemia and non-insulin-dependent diabetes mellitus

which appeared to be associated with the metabolic characteristics of visceral fat (Rebuffe-Scrive et al, 1993). Gain more weight on high fat diets without consuming more calories than A/J mice and develop adipocyte hyperplasia. However, animals fed a low fat, high sucrose diet were leaner than those fed a high-complex-carbohydrate diet. These results suggest that genetic differences in metabolic response to fat is more important in the development of obesity and diabetes than caloric intake (Surwit et al, 1995). Loci on chromosomes 1, 3, 5 and 11 are associated with variation in high density lipoprotein levels with coordinate expression of cholesterol-7-alpha hydroxylase in a cross involving atherosclerosis resistant C3H/HeJ mice (Machleder et al, 1997). Hepatic stearoyl CoA desaturase mRNA levels significantly elevated compared with atherosclerosis-resistant BALB/c mice, and was reduced in mice fed a high fat diet (Park et al, 1997).
Congenital abnormalities 10%, including eye defects, polydactyly and otocephaly (Kalter, 1968). Microphthalmia and anophthalmia 8-20% and hydrocephalus 1-3% (Dagg, 1966). Occular defects appear to be due to defects in development of the lens (Robinson et al, 1993).
Develop spontaneous auditory degeneration with onset during young adulthood, with enhanced susceptibility to acoustic injury and delayed effects of toluene (contrast CBA/Ca) (Li, 1992, Willott et al, 1993, Li et al, 1993, Li and Borg, 1993). This is associated with early hair cell changes including bent and fused stereocillia, bulging of the cuticle plates, hair cell loss and swelling of affected dendrites (Hultcrantz and Li, 1993). Carry a single recessive gene different from that found in BALB/cBy and WB/ReJ, causing age-related hearing loss (Willott et al, 1995). Hearing loss is caused by degeneration of the organ of Corti, originating in the basal, high frequency region and then proceeding apically over time. This results in a severe sensorineural hearing loss by 14 months of age (Walton et al, 1995). More susceptible to noise-induced hearing loss than CBA/J (Erway et al, 1996).
Life-span above average in both sexes in conventional conditions (17/22 = 676 days in males, 18/22 = 692 days in females) (Storer, 1966). Life-span 827 ± 34 days in males, 818 ± 21 days in females (Goodrick, 1975). Life-span 878 ± 10 days in males and 794 ± 6 days in females (Kunstyr and Leuenberger, 1975). Median life-span 600 days (Curtis, 1971). Gross tumour incidence 70%, maximum life-span about 1200 days in SPF conditions (Mewissen, 1971).

Dermatitis with intense pruritis leading to self-mutilation and death, and sometimes associated with the mite *Myobia musculi* appears to be more severe in this strain than others (Csiza and McMartin, 1976). Impaired axonal regeneration involving multiple genetic loci (Lu et al, 1994)

C57BL/10

Long life-span (826±29 days in males, 693±31 days in females). Overall tumour incidence 33% in males and 31% in females, most of which is due to lymphoma (31% in males, 29% in females) (Smith *et al*., 1973). Microphthalmia and anophthalmia 8-20% and hydrocephalus 1-3% (Dagg, 1966). Dermatitis leading to self-mutilation as described in C57BL/6 is also common in this substrain. Incidence may reach 4% (Sparrow, personal communication).

Drugs

Substrain unspecified

Resistant to induction of adenocarcinomas of the colon by 1, 2-dimethylhydrazine (cf. 2/4) (Evans *et al*., 1974). Resistant to induction of pulmonary tumours (6/6) and leukaemia (5/6) by neonatal administration of DMBA (Flaks, 1968). Susceptible to the induction of pulmonary fibrosis by bleomycin (contrast C3Hf/Kam) (Haston et al, 1996) and irradiation, though the sensitivity of lung fibroblasts to irradiation *in-vitro* does not correlate with *in-vivo* sensitivity (Dileto and Travis, 1996).
Sensitive to the development of uterine tumours following treatment with DMBA at 4-weeks of age (cf 3/6) (Tsubura et al, 1993). Resistant to induction of mammary tumours by urethane (7/7) (Bentvelzen *et al*., 1970). Pituitary adenoma induced in most mice by oestrogens (Heston, 1963). Resistant to skin tumour induction by methylcholanthrene (5/5) (Andervont and Edgcomb, 1956). Susceptible to fibrosarcoma induction by methylcholanthrene (4/15 males, 3/15 females) (Strong, 1952).
Resistant to chloroform toxicity (cf. 5/9) (Deringer *et al*., 1953). Resistant to induction of cleft palate by cortisone (4/5) (Kalter, 1965).

Resistant to lethal effects of ozone (22/22) (Goldstein *et al*., 1973). Resistant to colon carcinogenesis by 1,2-dimethylhydrazine (cf. 4/7) (Evans *et al*., 1977).

C57BL/Fa

Resistant to induction of lung tumours by urethane (6/6) (Falconer and Bloom, 1962). Insensitive to insulin (8/9), sensitive to histamine (2/9) (Brown, 1965).

C57BL/6

Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Susceptible to induction of subcutaneous tumours by 3-methylcholanthrene (3/14) (Kouri *et al*., 1973), (1/12) (Whitmire *et al*., 1971). High incidence of lymphomas after methylcholanthrene administration by gavage (2/5) (Akamatsu and Barton, 1974). Susceptible to toxic effects of DMBA (6/6) (Schmid *et al*., 1966). Pre-treatment with beta-naphthoflavone 48 hr. before administration of N-nitrosoethylurea (ENU), once weekly for 4 weeks caused a significant doubling in the number of lung tumor bearers (contrast 4 strains) (Anderson et al 1990). Phenobarbitone in the diet to give an intake of 85mg/kg per day resulted in 4% of animals developing basophilic nodules by 91 weeks of age (contrast 70% in C3H/He), but no increase in liver carcinomas (Evans et al, 1992). However, there was a two-fold lower level of DNA synthesis in C57BL/6 mice relative to C3H mice after partial hepatactomy, though partial hepatectomy is a tumour promoter in C57BL/6 but not in C3H mice (Bennett et al, 1995).
Sensitive to teratogenic effects of acetazolamide (2/6) (Green *et al*., 1973). Resistant to teratogenic effect (cleft palate) by cortisone acetate (2/6) (Kalter 1981). Hepatic epoxide hydrase activity induced by pentobarbital i.p. (cf. 4/7) (Oesch *et al*., 1973). Resistant to teratogenic effects of cortisone acetate (4/4) (Dostal and Jelinek, 1973). Resistant to lethal effects of ozone (16/21) (Goldstein *et al*., 1973), but susceptible (cf 5/8) to ozone-induced decreases of tracheal potential (Takahashi et al, 1995) and to airway inflammation (contrast C3H/He) (Kleeberger et al, 1993). Susceptible to ozone-induced lung inflammation, which is exacerbated by vitamin A deficiency (Paquette et al, 1996).

High incidence of convulsions induced by flurothyl (1/5) (Davis and King, 1967). Susceptible to hyperbaric oxygen (4/18) (Hill *et al*., 1968). Resistant to chloroform toxicity (cf. 5/9) (Hill *et al*., 1975; Deringer *et al*., 1953). Resistant to toxic effects of isoniazid (2/10) (Taylor 1976b). Sensitive, as judged by eosinophil response, to cortisone acetate (cf. 3/6) (Wragg and Speirs, 1952). High (89%) ovulatory response to 3 I.U. of PMS in immature mice (2/6), but only a 56% response to 7 I.U. No facilitation by exposure to males at these doses (Zarrow *et al*., 1971). High locomotor activity after treatment with D-amphetamine (1/6) (Babbini *et al*., 1974). Nicotine increases learning ability (1/9) (Bovet *et al*., 1966). Resistant to colon carcinogenesis by 1,2-dimethylhydrazine (cf. 4/7) (Evans *et al*., 1977). Low ED50 to behavioural effects of nicotine (3/19) (Marks et al 1989). High self-selection of nicotine (1/6) which is inversely correlated with sensitivity to nicotine-induced seizures (Robinson et al, 1996). Low bronchial reactivity (6/6) to methacholine and serotonin (Konno et al 1993). Resistant (6/8) to daunomycin-induced nephorsis (Kimura et al 1993). Low (10/10) neural sensitivity to pentylenetetrazol convulsions (Kosobud et al 1992). Susceptible to biliary tract injury following oral dosing with 500 micrograms of the fungal toxin sporidesmin (1/4) (Bhathal et al 1990). Low histamine release from peritoneal mast cells induced by compound 48/80, a calcium dependent histamine releaser (c.f. 5/8) (Toda et al 1989). Low histamine release from peritoneal mast cells induced by Ca2+ ionophore A23187 (c.f. 1/8, contrast BALB/c, C3H/He, DBA/2 etc.) (Toda et al 1989). Carries gene (*Tpmt*) for low levels of thiopurine methyltransferase activity, catalyzing the *S*-methylation of 6-mercaptopurine and other heterocyclic and aromaticthiol compounds (like AKR, unlike DBA/2) (Otterness and Weinshilboum 1987a,b). More sensitive to acute toxic effects of aflatoxin B-1 than strains CBA/J or BALB/c (Almeida et al, 1996). Airways hyporeactive to acetylcholine (c.f. 3/7) (Zhang et al, 1995). High voluntary comsumption of morphine in two-bottle choice situation (1/15) (Belknap et al, 1993). Estrogen induces an increase in VLDL and LDL-cholesterol (like C57L, contrast BALB/c and C3H) (Srivastava, 1995). Nine-fold higher ED50 for haloperidol-induced catalepsy than DBA/2, but this is not associated with numbers of cholinergic neurons (Dains et al, 1996). Accumulates three to five-fold lower levels of mercury in liver and blood than DBA/2 or A.SW after 4 weeks exposure to mercuric chloride, but higher levels in spleen following 8-12 weeks of exposure (Griem et al, 1997).

C57BL/10

Nicotine decreases shock-avoidance learning (8/9) (Bovet *et al*., 1966). Low ED50 to behavioural effects of nicotine (1/19) (Marks et al 1989). Congenic line B10.BR susceptible to induction of subcutaneous tumours by 3-methylcholanthrene (Kouri *et al*., 1973).

C57BR/cd

Inbr (J) 178. Brown: *a*,*b*. Origin: Little in 1921 from the same cross that gave rise to C57BL, C57BR/a and C57L. Black and brown substrains were separated in the first generation. Substrain cd was established at F13 from a cross between two brown substrains, one of which had previously given rise to C57BR/a. To Heston 1938, to J 1947 at F66. Maint. by J.

Life-span and spontaneous disease
Primary lung tumours 3% in males, 1%,, in breeding females and zero in virgin females, lymphatic leukaemia less than 1% (Hoag, 1963). Pituitary tumours 33% in old breeding females (Murphy, 1966).

Long life-span in conventional conditions (20/22 = 703 days in males and 19/22 = 694 days in females), hepatomas 25% in males (Storer, 1966). Life-span intermediate in both sexes in SPF fostered conditions (10/17 = 577 days in males, 9/17 = 660 days in females) (Festing and Blackmore, 1971).

Drugs
Nicotine decreases shock-avoidance learning (9/9) (Bovet *et al*., 1966). Susceptible to tumour induction by 3-methylcholanthrene (4/12) (Whitmire *et al*., 1971). Sensitive to insulin (1/9) and histamine (1/9) (Brown, 1965). Resistant to hyperbaric oxygen (18/18) with few central nervous system manifestations (Hill *et al.*, 1968). Resistant to X-irradiation as judged by the LD_{50} (2/9) (Yuhas and Storer, 1969), (2/9) (Storer, 1966).
Resistant to chloroform toxicity (cf. 5/9) (Deringer *et al*., 1953). Sensitive (eosinophil response) to cortisone acetate (cf. 3/6) (Wragg and Speirs, 1952). Highly susceptible to the induction of liver tumours by N,N-diethylnitrosamine. At 50 weeks of age mean tumour multiplicity following a single dose of DEN given at 12 days of age was 28±13 tumours compared with only 1.4 and 0.5 in C3H and C57BL/6, respectively. Ovariectomy increased tumour multiplicity (Poole and Drinkwater, 1996).

C57L
Inbr: F 130 +. Grey (colour very similar to DBA). Genet: *a, b, ln*. Origin: Murray 1933 from a mutation in F22 of a C57BR substrain which is now extinct. Maintained by Cloudman, to Heston 1938, then to Jackson Laboratory 1947 at F45. Differs from C57BR/cd at the *H2, Igh1, Pgk2, Qa2* and *Qa3* loci. Maint. by J, N.

Life-span and spontaneous disease
Low incidence of RNA tumour virus group-specific antigen expression (5/5) (Diwan *et al*., 1973). Primary lung tumours less than 1%; lymphatic leukaemia less than 1% in males and breeding females, but about 4% in virgin females; mammary adenocarcinomas 3% in breeding females, zero in males and virgin females (Hoag, 1963). 25% incidence of Hodgkin's-like lesions, reticulum cell neoplasm type B at 18 months (Heston, 1963) (55% according to Dunn and Deringer, 1968). Pituitary tumours 33% in old breeding females (Murphy, 1966).

Life-span short in males (3/17 = 473 days), intermediate in females (6/17 = 604 days) in SPF fostered conditions (Festing and Blackmore, 1971). Congenital cystic ovaries frequent (Staats, 1976).

Drugs
Low susceptibility to transplacental induction of tumours by 1-ethyl-1-nitrosourea (5/5) (Diwan *et al*., 1973). Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Low susceptibility to tumour induction by 3-methylcholanthrene (8/8) (Whitmire

and Salerno, 1972). Resistant to the induction of tumours by N-Methyl-N-Nitrosourea (MNU) due to a gene on chromosome 7 (Angel et al, 1993).
Susceptible to teratogenic effects of 1-ethyl-1-nitrosourea (1/5) (Diwan, 1974). Sensitive to Warfarin (4/12) (Lush and Arnold, 1975). Long sleeping time under hexobarbital anaesthetic (14/15) (Lovell, 1976), long sleeping time under pentobarbitone anaesthetic (21/23), Lovell (1986). Resistant to chloroform toxicity (cf. 5/9) (Deringer *et al*., 1953). Susceptible to the development of lung fibrosis following a single dose of thoracic irradiation (Franko and Sharplin, 1994). Estrogen induces an increase in VLDL and LDL-cholesterol (like C57BL/6, contrast BALB/c and C3H) (Srivastava, 1995). A diet containing 15% dairy fat, 1% cholesterol and 0.5% cholic acid caused a high incidence of cholesterol gallstones (like SWR, A, contrast SM, AKR, DBA/2) (Faulkner et al, 1995). Inbr. F?+33 (1989). Mus musculus castaneous wild mice trapped in Thailand by J.T. Marshall, to Chapman, then Roderick and Eicher in 1971.Resistant to flavivirus, unlike most laboratory mice except C3H.RV (Sangster et al 1993). Low retinal ganglion cell number (3/24) (Williams et al, 1996)

CAST

Inbr ?+34 (1989). Origin: same as CASA. Resistant to flavivirus, unlike most laboratory mice except C3H.RV (Sangster et al 1993). Low retinal ganglion cell number (2/24) (Williams et al, 1996). Used as a tester strain in a novel strategy for mapping new mutations in laboratory mice using simple sequence repeats (SSR) with DNA pools from mutant and wild-type F2 progeny. A set of 39 SSRs is expected to screen 94% of the autosomal genome in crosses with laboratory strains (Taylor et al, 1994).

CBA

Inbr: F90-170 depending on substrain. Agouti. Genet. + . Developed by Strong in 1920 from a cross of a Bagg albino female and a DBA male. Strain CBA was selected for a low mammary tumour incidence and C3H for a high incidence. Now widely distributed, and used as a general-purpose strain. Differences between substrains are probably too large to be accounted for by mutation, and some degree of genetic contamination in the past is probable. The following major substrains are recognised:

CBA/Ca or CBA/H

Strong, to Jackson Laboratory, to Haldane and Gruneberg in 1932. To Carter 1947 and Harwell 1954. This substrain used in most British research.

CBA/Br

Jackson Laboratory, to Haldane 1932, to Bonser (Leeds) approx. 1933.

CBA/CaN

Harwell, to National Institutes of Health in 1966. Carries sex-linked immunological deficit which prevents it from responding to type III pneumococcal polysaccharide. Deficit is expressed on B cells (Gershon and Kondo, 1976; Scher *et al*., 1976). Do not carry naturally occurring tumour-reactive antibodies commonly found in other strains (Martin and Martin, 1975).

CBA/J

Strong, to Andervont 1947, to Jackson Laboratory 1948. Carries gene for retinal degeneration *(rd).* Skin grafts between CBA/J and CBA/Ca are rejected (Green and Kaufer, 1965).

CBA/St

Original strain maintained by Strong.

CBA/H-T6

T6 translocation backcrossed to CBA/H by Dr M. F. Lyon. Now homozygous for the marker translocation T(14;15) 6Ca, but otherwise congenic with CBA/H.

Life-span and spontaneous disease

Life-span intermediate both sexes (J substrain) in conventional conditions (11/22 = 527 days males, 10/22 = 527 days females) (Storer, 1966). Life-span (Ca substrain) short in males (4/17 = 486 days) and long in females (17/17 = 825 days) in SPF fostered conditions. Short life-span of males associated with a high incidence of haemothorax, suggesting a high sensitivity to vitamin K deficiency in SPF conditions (Festing and Blackmore, 1971).

High gross tumour incidence (J) (3/22) (Storer, 1966). Overall tumour incidence 29% in males, 55% in females, including lymphoma 6% in males, 15% in females, hepatoma 24% in males, zero in females and mammary tumours 33% in females and zero in males (Smith *et al*., 1973). Lung adenomas 2-11% in BrA substrain, leukaemia 4-10% (Muhlbock and Tengbergen, 1971). Resistant to the induction of atherosclerosis by a high-fat and high-cholesterol diet (1/13) (Roberts and Thompson, 1976).
Develop a mild hearing loss with onset late in life (contrast C57BL/6J) (Li, 1992, Willott et al, 1993, Li et al, 1993, Li and Borg, 1993). Do not carry any of the single recessive genes found in BALB/cBy, C57BL/6 and WB/ReJ, causing age-related hearing loss. All three genes are present in DBA/2 (Willott et al, 1995).

Drugs

Resistant to urethane-induced lung tumours (Falconer and Bloom, 1962). Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Susceptible to induction of leukaemia (2/6) and liver tumours (2/6) by neonatally administered DMBA (Flaks, 1968). Susceptible to X-irradiation (27/27) (Roderick, 1963), but resistant to `CNS syndrome' with high doses of X-irradiation (1/5) (Yuhas, 1968). Susceptible to hyperbaric oxygen, showing central nervous system manifestations (11/18) (Hill *et al*., 1968). Sensitive to lethal effect of ozone (2/21) (Goldstein *et al*., 1973), but resistant (cf 3/8) to ozone-induced decreases of tracheal potential (Takahashi et al, 1995). Sensitive to teratogenic effect of acetazolamide (1/6) (Green *et al*., 1973, Hackman and Hurley 1983), but resistant to induction of cleft palate in embryos by cortisone (5/5) (Kalter, 1965). Insensitive to insulin (7/9) (Brown, 1965). Long survival on Warfarin (11/12) (Lush and Arnold, 1975). High ED50 to behavioural effects of nicotine (16/19) (Marks et al 1989). Susceptible to weight loss induced by cocaine, but this is attenuated by anisomycin (cf C3H, SJL) (Shimosato et al, 1994). More resistant to acute toxic effects of aflatoxin B-1 than strain C57BL/6 (Almeida et al, 1996).

CE

Inbr: F? + 68. Black-eyed grey. Genet: A^w, c^e. Originating in 1920 from wild mice trapped by J. E. Knight. The coat colour genetics later studied by Detlefsen. However, as the strain closely resembles `laboratory mice' (Taylor, 1972) and is not wild in behaviour, it seems possible that the original mutant mice were crossed with unidentified laboratory mice before being inbred. The strain is not widely used, and has a poor reproductive performance. However, its unique coat colour ensures authenticity, and it has an interesting range of tumour types, including a high incidence of ovarian tumours. F_1 hybrids with DBA/ 1, DBA/2 and C3H have a high incidence of hepatomas (Hancock and Dickie, 1969).

Characteristics

Sporadic high incidence of ear chewing of young by mother in Lac substrain (Festing 1976, original observation). Low preference for sweet tasting substances (saccharin, sucrose, dulcin and acesulfame, averaged) (22/26) (Lush 1988).

Life-span intermediate in males (6/17 = 498 days) and long in females (14/17 = 703 days) in SPF fostered stock (Festing and Blackmore, 1971). High incidence of adrenal cortical tumours following castration (Heston, 1963). Progressively severe endocrine imbalance involving the ovaries, adrenal cortex and pituitary in CE x DBA F1 hybrids (Dickie and Atkinson, 1957; Dickie *et al*., 1957). Liver tumours 11-57% (Festing and Blackmore, 1971). Develops granulosa cell tumours of ovaries (Chai and Dickie, 1966). Ovarian tumours 34% in virgin females (Murphy, 1966).

Low serum ceruloplasmin levels in females (26/27) but intermediate in males (Meier and MacPike, 1968). Low systolic blood pressure (15/19) (Schlager and Weibust, 1967). Low brain choline acetyltransferase activity (7/7) (Tunnicliff *et al*., 1973).

Accessory spleens uncommon (8/9) (Hummel *et al*., 1966). Sensitive to Warfarin (1/12) (Lush and Arnold, 1975). Short sleeping time under hexobarbital anaesthetic (1/15 males, 2/15 females) (Lovell, 1976). High lymphocyte phytohaemagglutinin response (3/43) (Heiniger *et al*., 1975). Non-discriminator between `H' and `L' sheep RBC (cf. 6/18) (McCarthy and Dutton, 1975).

Resistant to induction of diabetes mellitus by encephalomyocarditis virus (cf. 7/14) (Boucher *et al*., 1975). Carries no detectable endogenous ecotropic MuLV DNA sequences (Jenkins et al 1982). Low voluntary comsumption of morphine in two-bottle choice situation (14/15) (Belknap et al, 1993).

Short sleeping time under pentobarbitone anaesthetic (1/23), Lovell (1986). Highly resistant to azocasein-induced amyloidosis (contrast 5 strains). This is associated with a single novel isoform of the serum amyloid A gene (Sipe et al, 1993, De Beer et al, 1993). This is inherited as an autosomal dominant gene (Gonnerman et al, 1995). Mice produce amyloid enhancing factor (Gonnerman et al, 1996).

Poor reproductive performance (23/25), colony output 0.53 young/female/wk, although litter size is large (6/22) at 6.1 (Festing, 1976a). High ratio of males at birth (1/11) (Cook and Vlcek, 1961).
Recommended host for transplantable rhabdomyosarcoma BW10139 (Kaliss, 1972).

DBA

rey: *a,b,d.* Origin: Little 1909 from stock segregating for coat colour. Oldest of all inbred strains of mice. In 1929-30 crosses were made between substrains, and several new substrains established, including the widely used substrains /1 and /2. Differences between the substrains are probably too large to be accounted for by mutation, and are probably due to substantial residual heterozygosity following the crosses between substrains. Thus DBA/1 and DBA/2 differ at least at the following loci: *Car2, Ce2, Hc, H2, If1, Lsh, Tla,* and *Qa3.* With such large differences, they should probably be regarded as different strains rather than substrains of the same strain. In this listing the two are listed separately. DBA/LiA differs from /1 and /2 at the *Gpd1* locus, and is similar to DBA/2 at the *Tla* locus. Note that unfostered substrains carry the mammary tumour virus and have a high indicence of mammary tumours.

Main substrains are:

DBA/LiA
Inbr(A) ?+126. Origin: Little to Amsterdam circa 1932. Maint. by A.

DBA/1
Inbr (J) ?+117. Origin: Substrain maintained by Little at the Jackson Laboratory. Maint. by J,N,Ola.

DBA/2
Inbr (J) 150. Origin: Substrain maintained at the Jackson Laboratory. Maint. by J,N, Ola.

Characteristics of substrains other than DBA/1 and DBA/2:
Ehling (1964) reported sensitivity to X-irradiation (1/5). Lung adenomas 1-11% in DBAf/A, and leukaemia 0-% in DBA/LiA and 5-8% in DBAf/A (Muhlbock and Tengbergen, 1971). DBA/Li is resistant to colon carcinogenesis by 1,2-dimethylhydrazine (cf. 4/7) (Evans *et al*., 1977).

DBA/1

For origins see DBA

Life-span and spontaneous disease
Primary lung tumours 3% in males, 1% in breeding females and zero in virgin females; lymphatic leukaemia less than 1%. Mammary adenocarcinomas zero in males, 90% in breeding females and 61% in virgin females in unfostered substrain (Hoag, 1963). A high proportion of the mammary tumours are of the acinar type (1/7) (Tengbergen, 1970). Lung tumours 2-27% (Festing and Blackmore, 1971). Low gross tumour incidence in males (19/22) (Storer, 1966).

Life-span of males short in conventional conditions (6/22 = 433 days) but long in females (21/22 = 750 days) (Storer, 1966). Life-span in SPF fostered conditions also short in males (5/17 = 487 days) and long in females (13/17 = 686 days) (Festing and Blackmore, 1971).

Drugs
Resistant to skin ulceration by DMBA (cf. 9/22) (Thomas *et al*., 1973). Resistant to induction of subcutaneous tumours by 3-methylcholanthrene (14/14) (Kouri *et al*., 1973), (12/12) (Whitmire *et al*., 1971).
Sensitive to X-irradiation (21/27) (Roderick, 1963). Males have a long sleeping time under hexobarbital (15/15) (Lovell, 1976), long sleeping time under pentobarbitone anaesthetic (23/23), Lovell (1986). Insensitive (eosinophil response) to cortisone acetate (cf. 3/6) (Wragg and Speirs, 1952). Sensitive to teratogenic effect (cleft palate) by cortisone acetate (2/6) (Kalter 1981). Sensitive to seizures induced by nicotine (19/19) (Marks et al 1989). Clonidene induces a strong aggressive behavioural response (2/9) (Nikulina and Klimek, 1993).

DBA/2
For origins see DBA

Life-span and spontaneous disease
Primary lung tumours l% in males, 2% in females. Lymphatic leukaemia zero in males, 2% in females and 3% in virgin females. Mammary adenocarcinomas in unfostered substrains l% in males, 72% in breeding females and 48% in virgin females (Hoag, 1963). A high proportion of mammary tumours are of the acinar type (1/7) (Tengbergen, 1970). Overall tumour incidence 15% in males, 49% in females, including lymphomas 10% in males and 12% in females; mammary tumours zero in males and 31% in virgin females (Smith *et al*., 1973). Leukaemia 3% (Myers *et al*., 1970).

Long life-span in SPF fostered conditions (12/17 = 629 days in males, 15/17 = 719 days in females) with 6-35% liver and 1-23% lung tumours (Festing and Blackmore, 1971). Long life-span in conventional conditions (21/22 = 707 days in males, 20/22 = 714 days in females) (Storer, 1966). Life-span 722±30 days in males and 683±26 days in females (Goodrick, 1975).

High incidence of expression of RNA tumour virus group-specific antigen (2/5) (Diwan *et al*., 1973). Type B reticulum cell neoplasms 18% at about 20 weeks (Dunn and Deringer, 1968).

Spontaneous calcified heart lesions progress with age. 90% of individuals affected by 1 year (Rings and Wagner, 1971). Incidence of calcareous heart lesions high (1/5) among some related strains (Di Paola *et al*., 1964). Dystrophic cardiac calcification may be related to disturbed myocyte calcium metabolism (Brunnert, 1997). Chronic hypertropic gastritis, duodenal polyps and calcareous pericarditis frequently observed. Other lesions include malignant lymphoma and degenerative processes in the myocardium, skeletal

muscle, subcutaneous adipose tissue, cornea and blood vessels. Lesions partly depend on diet (Hare and Stewart, 1956).
Carry three separate recessive genes similar to those found separately in C57BL/6J, BALB/cBy and WB/ReJ, causing age-related hearing loss (Willott et al, 1995).

Drugs
Resistant to skin ulceration by DMBA (cf. 9/22) (Thomas *et al*., 1973). Resistant to induction of subcutaneous tumours by 3-methylcholanthrene (12/14) (Kouri *et al*., 1973), (11/12) (Whitmire *et al*., 1971). Resistant to induction of adenocarcinomas of the colon by 1,2-dimethylhydrazine (cf. 2/4) (Evans *et al*., 1974).
Resistant to teratogenic effect of 1-ethyl-1-nitrosourea (4/5) (Diwan, 1974).
Phenobarbital i.p. does not induce hepatic epoxide hydrase (cf. 3/7) (Oesch *et al*., 1973).
Resistant to lethal effects of ozone (21/22) (Goldstein *et al*., 1973). Susceptible to induction of cleft palate by cortisone (2/5) (Kalter, 1965). Good ovulatory response to 3 I.U. of PMS but zero response to 7 I.v. (Zarrow *et al*., 1971). Low incidence of convulsions induced by flurothyl (5/5) (Davis and King, 1967). Long hexobarbital sleeping time (8/9) and low liver hexobarbital oxidase level (2/9) (Vesell, 1968).
Sensitive to chloroform toxicity (cf. 4/9) (Hill *et al*., 1975; Deringer *et al*., 1953).
Sensitive to seizures induced by nicotine (1/19) (Marks et al 1989). Sensitivity may be related to brain alpha-bungarotoxin binding, which is significantly higher in ST/b than in sensitive DBA/2 mice (Marks et al, 1996). High self-selection of nicotine (2/6) which is inversely correlated with sensitivity to nicotine-induced seizures (Robinson et al, 1996).
High bronchial reactivity (2/6) to methacholine and serotonin (Konno et al 1993).
Resistant (7/8) to daunomycin-induced nephorsis (Kimura et al 1993). High (1/10) neural sensitivity to pentylenetetrazol convulsions (Kosobud et al 1992). Sensitive (1/3) to neurotoxic effects of monocrotophos (Rao et al 1991). Low histamine release from peritoneal mast cells induced by compound 48/80, a calcium dependent histamine releaser (c.f. 5/8) (Toda et al 1989). High histamine release from peritoneal mast cells induced by Ca2+ ionophore A23187 (c.f. 7/8, contrast C57BL/6) (Toda et al 1989).
Carries gene (*Tpmt*) for high levels of thiopurine methyltransferase activity, catalyzing the *S*-methylation of 6-mercaptopurine and other heterocyclic and aromaticthiol compounds (unlike C57BL/6 and AKR) (Otterness and Weinshilboum 1987a,b).
Resistant (contrast 5 strains) to the induction of micronuclei by polycyclic aromatic hydrocarbons, presumably due to uninducible Ah locus (Sato et al, 1987). Iron overload does not cause inhibition of hepatic uroporphyrinogen decarboxylase and uroporphyria in contrast with C57BL/10ScSn . This was not correlated with the *Ah* locus in a study involving 12 mouse strains (Smith and Francis, 1993). Resistant to hepatotoxic effects of cadmium (Shaikh et al, 1993). Low voluntary comsumption of morphine in two-bottle choice situation (13/15) (Belknap et al, 1993). Less susceptible to the development of micronuclei than BALB/c following treatment with clastogenic base analogues and nucleosides (Sato et al, 1993). Unique poor responsiveness to the antinociceptive effects of nitrous oxide, a polygenic trait (Quock et al, 1996). Nine-fold lower ED50 for haloperidol-induced catalepsy than C57BL/6, but this is not associated with numbers of cholinergic neurons (Dains et al, 1996).
Airways hyperreactive to acetylcholine (c.f. 3/7) (Zhang et al, 1995). Resistant (1/4) to rate-depressant effects of ethanol on schedule-controlled behaviour (Elmer and George, 1995). A diet containing 15% dairy fat, 1% cholesterol and 0.5% cholic acid did not

cause a high incidence of cholesterol gallstones (like AKR, SM contrast C57L, SWR, A) (Faulkner et al, 1995)

FVB

Inbr. F38. Albino,*A,B,c,D,P*. Origin: Outbred N:GP (NIH General Purpose) Swiss mice established at the National Institutes of Health in 1935. In 1966 two strains (HSFS/N and HSFR/N) were selected for sensitivity and resistance, respectively, to challenge with histamine following pertussis vaccination. In the early 1970s a group of mice at the eighth inbred generation of HSFS/N were found to carry the $Fv1^b$ allele for sensitivity to the B strain of Friend leukaemia virus. Homozygous mice were then inbred as strain FVB, without further selection for histamine sensitivity (Taketo et al 1991). Rowe (NIH) to Amsterdam, 1978.

Characteristics

Strain is useful for the production of transgenic mice on a fully inbred genetic background. They have a vigorous reproductive performance with large litters. Fertilized eggs contain large and prominant pronuclei which facilitate the microinjection of DNA, and following injection survive as well as C57BL/6 x SJL F1 hybrids, and much better than pure-line C57BL/6 (Taketo et al 1991). The strain has been typed at at least 44 marker loci on 15 chromosomes. Relatively insensitive to the initiation of papillomas following initiation by 7,12-dimethylbenz(a)anthracene and promotion with 12-o-tetradecanoylphorbol-13-acetate (TPA), but a high proportion progress to carcinomas (Hennings et al, 1993). A new strain 129-derived embryonic stem cell line, H3. gives good levels of germ-line transmission in chimeras involving FVB (Kim et al, 1996). 60% survival to 24 months of age in both sexes with 55% and 66% gross tumour incidence in males and females, respectively at that time. Most common tumour types were lung alveolar-bronchiolar, hepatocellular, subcutis neural crest and Harderian gland adenomas in males and lung, pituitary, ovarian, lymphomas, histiocytic sarcomas, Harderian gland adenomas and pheochromocytomas in females (Mahler et al, 1996). Maint. by N, A, J.

LP

Inbr (J) 125. Colour: white-bellied agouti with white patches A^w,*s.* Origin: Dunn 1928 from a chinchilla stock from Castle and some coat colour stocks from English fanciers. To Scott, to Dickie 1947, to J 1949. Maint. by J.

Characteristics

High emotionality (4/15) (Thompson, 1953). Susceptible to audiogenic seizures (1/11) (Fuller and Sjursen, 1967). Long life-span in conventional conditions (22/22 = 748 days in males, 22/22 = 799 days in females) (Storer, 1966). Overall tumour incidence 26% in males and 30% in females, with a wide range of tumour types, including mammary tumours (14% in females, 3% in males), lymphoma (1% in males, 8% in females), lung tumours (5% in males, 4% in females) and soft-tissue sarcomas (7% in males, 6% in females) (Smith et al. 1973). High plasma cholesterol at 12 and 24 weeks (1/8) (Weibust, 1973). High serum ceruloplasmin levels in females (5/27) and males (8/26) (Meier and MacPike, 1968). Low plasma cholinesterase activity in males (19/22) (Angel *et al.*, 1967). Low hypoxanthene-guanine phosphoribosyl transferase in thalamus (7/7) (Suran,

1973). Low brain monoamine oxidase (6/7) and catechol-*O*-methyltransferase activity (7/7) (Tunnicliff *et al*., 1973). High mean heart rate adaptation (1/7) (Blizard and Welty, 1971). Large spinal cord (4/25) (Roderick *et al*., 1973). Small kidney/body weight ratio (17/21) (Schlager, 1968). Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Highly resistant to the induction of catalepsy by haloperidol (8/8) associated with midbrain dopamine D2 receptor density levels (Kanes et al, 1993)
Low retinal ganglion cell number (5/24) (Williams et al, 1996).
High lymphocyte phytohaemagglutinin response (9/43) (Heiniger *et al*., 1975). Poor immune response to ovomucoid, but good response to ovalbumin (cf. 6/12) (Vaz *et al*., 1971). Discriminator between `H' and `L' sheep erythrocytes (cf. 12/18) (McCarthy and Dutton, 1975).

Resistant to induction of diabetes mellitus by encephalomyocarditis virus (cf. 7/14) (Boucher *et al*., 1975).

MOLG/Dn

Inbr. F17+14. White-bellied agouti , A^{W} . Derived by Davisson from an incipient inbred strain MOLC/Rk (now extinct) at F14, itsself derived from *Mus musculus molussinus* imported from Dr. Michael Potter to the Jackson Laboratory in 1969. These mice were said to be "within one to three generations of [mice] captured in the wild." Has a very large probable duplication of heterochromatin C-band near the centromere of chr. 2. which provides a cytological marker for gene mapping of proximal end of this chromosome.

NZW

Inbr: F 70. Albino. Genet: *b, c, p.* Origin: see NZB.

Characteristics

High within-strain aggression. Litter mate males housed together often fight severely by 6-8 weeks (original observation). High balsa-wood gnawing activity (15/16) (Fawdington and Festing 1980). Long life-span in both sexes (17/17 = 802 days in males, 16/17 = 733 days in females) in SPF fostered conditions. Lung tumours 2-24%, lymphatic leukaemia 3-29% and heart defects 2-24% (Festing and Blackmore, 1971). Short sleeping time under hexobarbital anaesthetic (3/15 in males, 1/15 in females) (Lovell, 1976), short sleeping time under pentobarbitone anaesthetic (3/23), Lovell (1986). Phenobarbital i.p. induces hepatic epoxide hydrase (cf. 4/7) (Oesch *et al*., 1973). High incidence of exencephaly reported by Vogelwide et al (1993). High retinal ganglion cell number (20/24) (Williams et al, 1996).
Serum antinuclear factor found in 12% of animals (6/17) (Barnes and Tuffrey, 1967). The TCR beta-chain locus of NZW mice carries an 8.8-kb deletion which encompasses the C beta 1, D beta 2, and all six J beta 2 gene segments Studies suggest that D beta 2 and J beta 2 gene segments are required to maintain a diverse T cell repertoire and that their deletion from the genome may confer a significant selective disadvantage in the wild.(Woodland et al 1990). Resistant to immunosuppression of contact hypersensitivity by ultraviolet B light (cf 4/18) (Noonan and Hoffman, 1994). Deficient in eosinophil

peroxidase, one of the enzymes in the eosinophil-specific granules, resembling the similar condition in humans (Ohmori et al, 1996).
Intermediate breeding performance (13/25), colony output 1.00 young/female/ week, litter size at weaning low (23/25) at 4.1 (Festing 1976a). Poor breeding performance (19/24) (Hansen *et al*., 1973).
Strain widely used as the NZB x NZW F1 hybrid (also known as the B x W hybrid), giving a model of systemic lupus erythematosus (see also NZB). Syndrome includes typical lupus erythematosus cells, antinuclear antibody, haemolytic anaemia, proteinuria with casts and terminal nephrosis with renal failure before 8 months (see Milich and Gershwin 1981). Incidence and severity of the disease is greater in females than males (Dubois *et al*., 1966).
NZW x BXSB F1 male mice develop systemic autoimmunity involving autoantibodies, thrombocytopenia, lupus nephritis and coronary vascular disease with myocardial infarction. These effects can be modulated by diet, and may be mediated by anti-cardiolipin autoantibodies (Mizutani et al, 1994), and can be treated effectively by ACE inhibitors such as imidapril and captopril (Ogiku et al, 1994).

RF

Inbr: F113 (J). Albino. Genet: *a, c*. Origin: Furth 1928 from Rockefeller Institute general-purpose stock. Transferred to Oak Ridge. History somewhat questionable.

Life-span and spontaneous disease

Intermediate life-span in males (15/22 = 651 days) but short in females (5/22 = 452 days) in conventional conditions. High gross tumour incidence in males (4/22) (Storer, 1966). Necrotising arteritis involving the aorta, its major branches and other arteries and arterioles seen in 10-20% of aged mice. Disease may involve an autoimmune mechanism (Upton *et al*., 1967). Mean life- span 619±7 days. Leukaemia 66%, glomerulosclerosis 63% and reticulum cell sarcoma 52% (Yuhas and Clapp, 1972). Spontaneous glomerular hyalinisation and glomerrnlosclerosis develops at 8-20 months (Russell and Meier, 1966). Leukaemia 46% (Myers *et al*., 1970)

Drugs

Resistant to skin ulceration by DMBA (cf. 9/22) (Thomas *et al*., 1973). Sensitive to lethal effects of ozone (5/21) (Goldstein *et al*., 1973). Sensitive to hyperbaric oxygen (5/18) (Hill *et al*., 1968). Resistant to X-irradiation as judged by the LD50 (3/8) (Yuhas and Storer, 1969).

RIII

Inbr 80+. Albino: *A,c*. Origin: Dobrovolskaia-Zavadskaia, Inst. du Radium, Paris 1928, then see below. High mammary tumour incidence in unfostered substrains.
The following substrains are recognised:

RIII.

Origin as above.

RIII/An.

Dobrovolskaia-Zavadskaia to Andervont.

RIII/SeA.

From Severi (Perugia) to Muhlbock (Amsterdam) 1964. Differs from the other substrains at the *Hbb* and *Mup* loci

Life-span and spontaneous disease

Long life-span in conventional conditions (19/22 = 685 days in males, 16/22 = 655 days in females) (Storer, 1966). High incidence (88%) of mammary tumours in breeding females (Heston, 1963), but a low proportion are of the acinar type (7/7) (Tengbergen, 1970). Ovarian tumours 60% in breeding females, 50% in virgin females (Murphy, 1966). Mammary tumours 96% at 9 months (Schlom *et al*., 1973), 70% at 12 months (Seman and Dmochowski, 1973). Has been known to loose the mammary tumour virus spontaneously (Andervont and Dunn, 1962).

Drugs

Sensitive to X-irradiation (24/27) (Roderick, 1963). Low susceptibility to endotoxin lipopolysaccharide (5/5) (Heppner and Weiss, 1965).

RIIIS

In 1967 both RIII and RIII/An maintained at The Jackson Laboratory failed to produce viable young. RIII/2J was developed from a cross between the two substrains. Name later changed to RIIIS. High serum complement activity (c.f. 8/26) (Ong et al 1989)

Characteristics

RIIIS carries no detectable endogenous ecotropic MuLV DNA sequences (Jenkins et al 1982). High ED50 to behavioural effects of nicotine (16/19) (Marks et al 1989). Has the largest known deletion of the T cell receptor (TCR) V beta genes, having lost approximately 130 kb of V beta chromosome and with it 13 V beta genes out of the known 21 V beta genes of the TCR. The deletion is marked by the presence of V beta 10 gene upstream and V beta 3 gene downstream. (Haqqi et al 1989).

Develops a condition resembling human type I von Willebrand's disease characterised by a prolonged bleeding time, normal von Willebrand factor multimer (VWF) distribution, autosomal dominant inheritance and proportionally decreased plasma von Willebrand factor antigen and factor VIII activity. The disease is caused by a genetic defect at a locus distinct from the murine von Willebrand factor gene (Nichols et al, 1994). A single dominant modifier locus (*Mvwf*) on distil chromosome 11 accounted for 63% of variation in plasma VWF levels in a cross with CASA/Rk. This is distinct from the *Vwf* locus on chromosome 6 (Mohlke et al, 1996).

Resistant to the induction of arthritis by type II collagen (Ortman et al, 1994). Carries two mutations causing defects in cortosteroid-binding globulin (Orava et al, 1994).

SAMR1

Inbr. F?+49. Albino, *c*. *Origin*: Dr. Toshio Takeda, Dept. of Senescence Biology, Chest Disease Research Institute, Kyoto University, Sakyo-ku, Kyoto 606, Japan, from AKR/J mice imported from J in 1968 and crossed (?) with mice of an unknown strain, followed by sib mating since 1975 with selection for normal life-span.

Characteristics:
About 25% and 22% of the mice aged over 16 months which die naturally have lymphocytic and histiocytic neoplasia, respectively. About 68% of females which die after 20 months of age have ovarian cysts. Median survival is 568 days in conventional conditions. Good passive avoidance skills up to 22 months of age. Used as a normally-aging control strain for the SAMP (Senescence-Accelerated Mouse) strains (see Takeda et al 1981, Hosokawa et al 1984, Takeda et al 1991)

SM/J

Inbr (J) 112. White-bellied agouti or black A^w/a or *a/a.* Origin: MacArthur, 1939 by crossing seven stocks including DBA and selecting for small body size. To Runner 1948, who began b x s mating. Small body size at birth and weaning, but this relatively small size tends to disappear as the animals mature. Very low tumour incidence. Carries a number of relatively rare polymorphic alleles. Maint. by A,J.

Characteristics
Intermediate life-span in conventional conditions (13/22 = 572 days in males, 14/22 = 591 days in females). Low gross tumour incidence (20/22) (Storer, 1966). Life-span, sexes combined, 422 days (Chai, 1959). High incidence of amyloidosis (Russell and Meier, 1966). High porphyrin content of Harderian gland (4/16) (Margolis, 1971). High spermatazoal beta-glucuronidase activity (2/9) (Erickson, 1976). Low brain weight in males (15/18) (Storer, 1969). Large brain/body weight ratio (4/20) (Roderick *et al*., 1973). Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Long survival on Warfarin (10/12) (Lush and Arnold, 1975). Low lymphocyte phytohaemagglutinin response (39/43) (Heiniger *et al*., 1975). Susceptible to the development of atherosclerosis on a semi-synthetic high fat diet but in contrast with C57BL/6 and SWR they had the same level of high-density lipoprotein cholesterol levels as on chow and high fat diets (3/9) (Nishina et al, 1993). A diet containing 15% dairy fat, 1% cholesterol and 0.5% cholic acid did not cause a high incidence of cholesterol gallstones (like AKR, DBA/2 contrast C57L, SWR, A) (Faulkner et al, 1995). Small body weight which differs from that of the large strain LG/J as a result of about seven quantitative trait loci at one week and 17 loci at 10 weeks of age. Each locus has a small effect (Cheverud et al, 1996).

ST

Inbr.(J) 143. Albino *a,b,c.* Origin: Englebreth-Holm from outbred Danish white mice in about 1940. To Heston in 1947 at F23. Two major substrains are known which differ at the *H2* locus. These were separated after more than eight generations of sib-mating.

ST/a
See above. This is the $H2^b$ substrain which is not so widely used.

ST/b
See above. $H2^k$ substrain. Maint. by J,N.

Characteristics
Life-span in conventional conditions short (5/22 = 433 days in males, 9/22 = 511 days in females), but low gross tumour incidence (21/22 in females, 19/22 in males) (Storer, 1966).
High preference for sweet tasting substances (saccharin, sucrose,dulcin and acesulfame, averaged) (2/26) (Lush 1988). Low metabolic rate (17/18) (Storer, 1967). Low serum ceruloplasmin levels in females (27/27), but intermediate levels in males (Meier and MacPike, 1968). Large spinal cord (3/25) (Roderick *et al*., 1973). Low thyroid weight (5/5) (Mendoza *et al*., 1967). Low haemoglobin per ml blood (18/18) (Russell *et al*., 1951). Susceptible to skin ulceration by DMBA (cf. 13/22) (Thomas *et al*., 1973). Resistant to X-irradiation (4/27) (Roderick, 1963). Short survival in 90% oxygen (10/10), but high susceptibility to pulmonary hyaline-membrane formation (2/10) (Lieberman and Kellog, 1967). Resistant to chloroform toxicity (cf. 5/9) (Deringer *et al*., 1953). Resistant to experimental allergic encephalomyelitis (cf. 7/18) (Levine and Sowinski, 1973). Erythrocytes have low agglutinability (cf. 11/25) in b substrain (Rubinstein *et al*., 1974). Susceptible to *Plasmodium berghei* infection (2/8) (Most *et al*., 1966). Resistant to seizures induced by nicotine (1/19) (Marks et al 1989). Low self-selection of nicotine (6/6) which is inversely correlated with sensitivity to nicotine-induced seizures (Robinson et al, 1996). Resistance may be related to brain alpha-bungarotoxin binding, which is significantly higher in ST/b than in sensitive DBA/2 mice (Marks et al, 1996). Defect in the expression of the alloantigen, Ly6C, which is not detectable on spleen or lymph node cells (c.f. NOD and NZB but contrast most other strains) and may be due to an interruption in the flanking region of the Ly6C gene at a point 475 bp upstream of the transcription initiation site, as found in NOD (Philbrick et al 1990).

SWR

Inbr: F148 (J). Albino. Genet: *c, rd.* Origin: Swiss mice from A. de Coulon of Lausanne, inbred by Lynch from about 1926 (Lynch, 1969). Now widely used in research as a general-purpose strain. Develops extreme polydipsia and polyuria on ageing. Maint. by J, Ola.

Life-span and spontaneous disease
Life-span in conventional conditions intermediate in males (14/22 = 616 days) but short in females (7/22 = 496 days) (Storer, 1966). Pulmonary tumours 80% in mice living to 18 months (Heston, 1963). Mammary tumours 7-28% (Deringer, 1970). Develops extreme polydipsia and polyuria (nephrogenic diabetes insipidus) on ageing (Kutscher *et al*., 1975; Kutscher and Schmalback, 1975). Low gross tumour incidence in females (19/22) (Storer, 1967). One or more tumours found in 62% of mice. Lung tumours 36%, mammary tumours 30% (Rabstein *et al*., 1973). Arteriosclerosis common (Russell and Meier, 1966). About 10-25% of SWRxSWXJ-9 F1 hybrid mice spontaneously develop granulosa cell tumours. These secrete inhibin, which can be used as a marker for tumour-bearing animals (Gocze et al, 1997).

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