Coreceptor Use by Primate Lentiviruses

Robert W. Doms,[1] **Aimee L. Edinger,**[2] **and John P. Moore**[3]

[1] *Corresponding author: University of Pennsylvania, Department of Pathology and Laboratory Medicine, 807 Abramson, 34th and Civic Center Blvd., Philadelphia, PA 19104*
phone: 215-898-0890, fax: 215-573-2883 email: doms@mail.med.upenn.edu

[2] *University of Pennsylvania, Department of Pathology and Laboratory Medicine, Philadelphia, PA 19104*

[3] *The Aaron Diamond AIDS Research Center, The Rockefeller University, 455 First Avenue, New York, NY 10016*

Since the original compilation of the coreceptors used by HIV-1 strains in 1998, considerable progress has been made in identifying coreceptors for SIV and HIV-2 strains. Hence, in addition to updating the record of coreceptor usage by HIV-1 strains, tables describing the coreceptors used by SIV and HIV-2 strains are now provided.

HIV-1

CCR5 and CXCR4 are the major coreceptors used by HIV-1 strains. All HIV-1 strains reported on to date use one or both of these receptors. For the vast majority of strains, CCR5 and CXCR4 support virus entry more efficiently than any of the growing number of alternative coreceptors, including CCR2, CCR3, CCR8, CX3CR1 (formerly V28), STRL33 (Bonzo), GPR1, GPR15 (BOB), APJ, and ChemR23. Each of these alternative coreceptors can function for virus entry or Env-mediated cell-cell fusion, to a greater or lesser extent, when they are transfected into CD4+ cell lines *in vitro*. However, none of them appears to be efficiently utilized by large numbers of virus strains. The question arises as to whether use of alternative coreceptors *in vivo* impacts viral tropism and pathogenesis. Potentially, use of receptors other than CCR5 or CXCR4 could enable virus strains to infect new types of cells, for example in the brain, thymus or mucosa. However, to the best of our knowledge infection of primary cells by HIV-1 is always mediated by CCR5 or CXCR4. It is particularly striking that infection of primary cells (CD4+ T-cells and macrophages) obtained from CCR5-negative individuals is always mediated by CXCR4. Use of receptors other than CXCR4 to infect these CD4-negative cells has not yet been demonstrated. Development of antibodies to the alternative coreceptors is needed, however, to determine the cell types in which they are expressed. Specific antibodies, or other inhibitors, targeted at the alternative coreceptors would also be helpful to gauge their importance in primary cells. Our experience is, however, that inhibitors targeted at CCR5 and CXCR4 are sufficient to inhibit the replication of all tested HIV-1 strains in primary cells.

The HIV-1 coreceptor use Table is updated from last year. The major coreceptor(s) used by each virus strain is listed, as are alternative coreceptors that support virus infection *in vitro* to an extent that is >10% of the efficiency of the major coreceptor used by each virus strain.

Strain	Proposed Accession[a]	Primary Clade	Other Tropism[b]	Designation[c]	Main Receptor[d]	Alternate Receptors[e]	References
DJ258	L22939	A	NSI	R5	CCR5		[Trkola (1998)]
92RW026	NA	A	NSI	R5	CCR5		[Trkola (1998)]
93KE101	NA	A	NSI	R5	CCR5		[Zhang (1996)]
93IN103	NA	A	NSI	R5	CCR5		[Zhang (1996)]
92UG037-8	U51190	A	NSI	R5	CCR5	CCR8*	[Bjorndal (1997), Rucker (1997)]
92RW020-5	U08794	A	NSI	R5	CCR5		[Rucker (1997)]
92UG31	L34667	A	NSI	R5	CCR5		[Dittmar (1997)]
92RW20	U08794	A	NSI	R5	CCR5		[Dittmar (1997)]
92UG029	NA	A	SI	X4	CXCR4		[Trkola (1998)]
92RW009	U88823	A	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
JR-FL	U63632	B	NSI	R5	CCR5	CCR3	[Deng (1997), Farzan (1997), Rucker (1997)]
JR-CSF	M38429	B	NSI	R5	CCR5		[Simmons (1996), Trkola (1998), Zhang (1996)]
SF162	M65024	B	NSI	R5	CCR5	STRL33*	[Liao (1997), Rucker (1997)]
YU2	M93258	B	NSI	R5	CCR5	CCR3, GPR15	[Choe (1996), Farzan (1997)]
ADA	AF004394	B	NSI	R5	CCR5	CCR3, GPR15, STRL33*, CCR8	[Choe (1996), Farzan (1997), Rucker (1997)]
Ba-L	M68893	B	NSI	R5	CCR5	CCR3, STRL33*	[Deng (1997), Dragic (1996), Liao (1997), Rucker (1997)]
92US657	U04908	B	NSI	R5	CCR5		[Trkola (1998)]
92US715.6	U08451	B	NSI	R5	CCR5		[Bjorndal (1997)]
92Br20-4	U08797	B	NSI	R5	CCR5		[Choe (1996), Rucker (1997)]
91US005.11	U27434	B	NSI	R5	CCR5		[Bjorndal (1997), Rucker (1997)]
SL-2	NA	B	NSI	R5	CCR5		[Simmons (1996)]
92TH014.12	U08801	B	NSI	R5	CCR5		[Bjorndal (1997)]
CM243	NA	B	NSI	R5	CCR5	GPR15, STRL33	[Rucker (1997)]
M23	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
E80	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
BR92	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
BR49	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
BR53	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
BR90	NA	B	NSI	R5	CCR5		[Dittmar (1997)]
92HA593[g]	U08444	B	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
92HT593.1[g]	U08444	B	NSI	R5X4	CXCR4, CCR5		[Bjorndal (1997)]
2028	NA	B	SI	R5X4	CXCR4, CCR5	CCR3	[Dittmar (1997), Simmons (1996)]

Primate Lentivirus Coreceptor Use

Strain	Proposed Accession[a]	Primary Clade	Other Tropism[b]	Designation[c]	Main Receptor[d]	Alternate Receptors[e]	References
2076	NA	B	SI	R5X4	CXCR4, CCR5		[Dittmar (1997), Simmons (1996), Trkola (1998)]
89.6	U39362	B	SI	R5X4	CXCR4, CCR5	CCR3, CCR2b, CCR8, V28	[Farzan (1997), Rucker (1997)]
DH123	NA	B	SI	R5X4	CXCR4, CCR5		[Trkola (1998)]
Isolate C 7/86	NA	B	SI	R5X4	CXCR4, CCR5		[Trkola (1998)]
92HA594	U08445	B	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
92HA596	U08446	B	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
M13	NA	B	SI	R5X4	CXCR4, CCR5		[Simmons (1996)]
2006	NA	B	SI	R5X4	CXCR4, CCR5		[Simmons (1996)]
2044	NA	B	SI	R5X4	CXCR4, CCR5		[Simmons (1996)]
2036	NA	B	SI	R5X4	CXCR4, CCR5		[Simmons (1996)]
2005	NA	B	SI	R5X4	CXCR4, CCR5		[Simmons (1996)]
92HT599.24	U08447	B	SI	X4	CXCR4		[Bjorndal (1997)]
BK132	L03697	B	SI	X4	CXCR4	CCR3*, CCR8*	[Rucker (1997)]
BR65	NA	B	SI	X4	CXCR4		[Dittmar (1997)]
HC4	NA	B	SI	X4	CXCR4		[Trkola (1998)]
SF2	K02007	B	SI/TCLA	R5X4	CXCR4, CCR5		[Trkola (1998)]
RF	M17451	B	SI/TCLA	R5X4	CXCR4, CCR5		[Alkhatib (1996), Deng (1997), Rucker (1997)]
NL 4-3	M19921	B	SI/TCLA	X4	CXCR4		[Trkola (1998), Zhang (1996)]
LAI	X01762	B	SI/TCLA	X4	CXCR4		[Trkola (1998)]
HXBc2	K03455	B	SI/TCLA	X4	CXCR4		[Choe (1996)]
GUN-1	D34590	B	SI/TCLA	R5X4	CXCR4, CCR5		[Simmons (1996)]
BH8	K02011	B	SI/TCLA	X4	CXCR4	CCR3*, STRL33*	[Rucker (1997)]
P1 22-211-V4		B	NSI	R5	CCR5		[Zhang (1998)]
P2 22-204-V2		B	NSI	R5	CCR5		[Zhang (1998)]
P3 19-245-V6		B	NSI	R5	CCR5		[Zhang (1998)]
P4 03-212-V8		B	NSI	R5	CCR5		[Zhang (1998)]
P5 11-213-V4		B	NSI	R5	CCR5		[Zhang (1998)]
P6 02-217-V3		B	NSI	R5	CCR5	BONZO	[Zhang (1998)]
P7 22-216-V5		B	NSI	R5	CCR5		[Zhang (1998)]
P8 02-236-V6		B	NSI	R5	CCR5		[Zhang (1998)]
P9 22-236-V6		B	NSI	R5	CCR5		[Zhang (1998)]

Strain	Proposed Accession[a]	Primary Clade	Other Tropism[b]	Designation[c]	Main Receptor[d]	Alternate Receptors[e]	References
P10 03-237-V6		B	NSI	R5	CCR5		[Zhang (1998)]
P11 22-202-V3		B	NSI	R5	CCR5		[Zhang (1998)]
P13 19-242-V3		B	NSI	R5	CCR5		[Zhang (1998)]
P14 22-207-V6		B	NSI	R5	CCR5		[Zhang (1998)]
P15 22-237-V4		B	NSI	R5	CCR5		[Zhang (1998)]
301657		B	NSI	R5	CCR5		[Zhang (1998)]
301714		B	NSI	R5	CCR5		[Zhang (1998)]
301073		B	NSI	R5	CCR5		[Zhang (1998)]
301056		B	NSI	R5	CCR5		[Zhang (1998)]
301660		B	NSI	R5	CCR5		[Zhang (1998)]
301727		B	NSI	R5	CCR5		[Zhang (1998)]
MWB		B	NSI	R5	CCR5		[Zhang (1998)]
301593		B	SI	R5X4	CXCR4, CCR5	V28	[Zhang (1998)]
AD73		B	SI	R5X4	CXCR4, CCR5	V28	[Zhang (1998)]
DH123		B	SI	R5X4	CXCR4, CCR5	CCR8	[Zhang (1998)]
NL4-3		B	SI	R4	CXCR4		[Zhang (1998)]
P6 02-217-V3-m1		B	NSI	R5	CCR5	BONZO	[Zhang (1998)]
P6 02-217-V4 m2		B	NSI	R5	CCR5	BONZO	[Zhang (1998)]
P6-02-217-V6-m6		B	NSI	R5	CCR5	BONZO	[Zhang (1998)]
P6 02-217-V8-m12		B	NSI	R5	CCR5	BONZO	[Zhang (1998)]
P6 02-217-V9-m18		B	NSI	R5	CCR5		[Zhang (1998)]
M6-V2-m4b		B	SI	R5X4	CXCR4, CCR5	BONZO, V28, APJ	[Zhang (1998)]
M6-V3-m1b		B	SI	R5X4	CXCR4, CCR5	BONZO, V28, APJ	[Zhang (1998)]
M6-V6-m6a		B	SI	R5X4	CXCR4, CCR5	BONZO, V28, APJ	[Zhang (1998)]
EL1		B	SI	X4	CXCR4	APJ, CCR3	[Choe (1998)]
2005		B	SI	X4	CXCR4		[Simmons (1998)]
2044		B	SI	X4	CXCR4		[Simmons (1998)]
2028		B	SI	R5X4	CXCR4, CCR5		[Simmons (1998)]
2076		B	SI	R5X4	CXCR4, CCR5	CCR3, CCR8, STRL33	[Simmons (1998)]
SL-2		B	NSI	R5	CCR5	GPR15	[Simmons (1998)]
92ZW101	NA	C	NSI	R5	CCR5		[Zhang (1996)]
92BR025.9	U52953	C	NSI	R5	CCR5		[Bjorndal (1997), Dittmar (1997)]
BR28	U16217	C	NSI	R5	CCR5		[Dittmar (1997)]
93MW965.26	U08455	C	NSI	R5	CCR5		[Bjorndal (1997)]
BR70	NA	C	NSI	R5	CCR5		[Dittmar (1997)]
JW1	NA	C	NSI	R5	CCR5		[Dittmar (1997)]

Primate Lentivirus Coreceptor Use

Strain	Proposed Accession[a]	Primary Clade	Other Tropism[b]	Designation[c]	Main Receptor[d]	Alternate Receptors[e]	References
JW4	NA	C	NSI	R5	CCR5		[Dittmar (1997)]
92ZW102	NA	C	NSI	R5	CCR5		[Zhang (1996)]
DJ259	L22940	C	NSI	R5	CCR5		[Trkola (1998)]
94ZW103	NA	C	NSI	R5	CCR5		[Trkola (1998)]
94ZW109	NA	C	NSI	R5	CCR5		[Trkola (1998)]
92ZW106	NA	C	SI	X4	CXCR4		[Zhang (1996)]
ZAM20	L22956	C	SI	X4	CXCR4		[Trkola (1998)]
94ZW106	NA	C	SI	X4	CXCR4		[Trkola (1998)]
94KE102	NA	D	NSI	R5	CCR5		[Trkola (1998), Zhang (1996)]
94KE103	NA	D	NSI	R5	CCR5		[Trkola (1998), Zhang (1996)]
92UG046	U08737	D	SI	X4	CXCR4		[Trkola (1998)]
UG270	NA	D	SI	X4	CXCR4		[Trkola (1998)]
92UG024.2	U08726	D	SI	X4	CXCR4	CCR8*, V28*, CCR3[f]	[Bjorndal (1997), Rucker (1997), Trkola (1998)]
92UG021.16	U27399	D	SI	X4	CXCR4		[Bjorndal (1997)]
JW5	NA	D	SI	X4	CXCR4		[Dittmar (1997)]
NDK	M27323	D	SI	X4	CXCR4	GPR15	[Deng (1997), Pleskoff (1997)]
93ZR001.3	U27419	D	NA	X4	CXCR4	V28*	[Rucker (1997)]
91ZR001.3		D	SI	R5X4	CXCR4, CCR5		[Bazan (1998)]
SE7076		D	SI	X4	CXCR4		[Vallejo (1998)]
SE8384		D	SI	X4	CXCR4		[Vallejo (1998)]
SE8646		D	SI	R5X4	CCR5, CXCR4		[Vallejo (1998)]
CM235	NA	E	NSI	R5	CCR5		[Trkola (1998)]
92TH001	NA	E	NSI	R5	CCR5		[Trkola (1998)]
M53	NA	E	NSI	R5	CCR5		[Dittmar (1997)]
92TH22	U09131	E	NSI	R5	CCR5		[Dittmar (1997)]
92TH23	NA	E	NSI	R5	CCR5		[Dittmar (1997)]
C2	NA	E	NSI	R5	CCR5		[Dittmar (1997)]
93TH305	NA	E	NSI	R5	CCR5		[Zhang (1996)]
93TH307	NA	E	NSI	R5	CCR5		[Zhang (1996)]
93TH966.8	U08456	E	NSI	R5	CCR5		[Bjorndal (1997)]
93TH976.17	U08458	E	NA	R5	CCR5		[Bjorndal (1997)]
93TH304	NA	E	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
SL6	NA	E	SI	X4	CXCR4		[Dittmar (1997)]
SL7	NA	E	SI	X4	CXCR4		[Dittmar (1997)]
SL8	NA	E	SI	X4	CXCR4		[Dittmar (1997)]
94TH304	NA	E	SI	X4	CXCR4		[Trkola (1998)]
BR58	NA	F	SI	R5X4	CXCR4, CCR5	CCR3	[Dittmar (1997)]

Strain	Proposed Accession[a]	Primary Clade	Other Tropism[b]	Designation[c]	Main Receptor[d]	Alternate Receptors[e]	References
BZ162	L22084	F	NSI	R5	CCR5		[Trkola (1998)]
R1	NA	F	NSI	R5	CCR5		[Trkola (1998)]
93BR029.2	U27413	F	NA	R5	CCR5		[Rucker (1997)]
RU23		F	NSI	R5	CCR5		[Vallejo (1998)]
RU29		F	NSI	R5	CCR5		[Vallejo (1998)]
RU30		F	NSI	R5	CCR5		[Vallejo (1998)]
92UG975.10	U27426	G	NSI	R5	CCR5		[Bjorndal (1997)]
CA9	NA	O	NSI	R5	CCR5		[Zhang (1996)]
MVP5180	L20571	O	SI	R5X4	CXCR4, CCR5		[Zhang (1996)]
ES1158.1		O	NSI	R5	CCR5		[Vallejo (1998)]
ES1159.1		O	NSI	R5	CCR5		[Vallejo (1998)]
MD.1		O	NSI	R5	CCR5		[Vallejo (1998)]
MVP-5180		O	SI	R5X4	CXCR4, CCR5		[Vallejo (1998)]

Footnotes:

[a] Accession numbers refer to sequences from the described isolate that contain the longest available sequence including Env (full length genome when avaiable, down to a minimum of the V3 region), but may not pertain directly to the sample used to determine the isolate's phenotype. Accession numbers have been deemed "NA" if there are no related locus names in the HIV Database, or if there is insufficient information to conclude that a similarly named locus in the database is referring to the same isolate.

[b] The tropism for each virus strain is indicated. SI = syncytium inducing; NSI = non syncytium inducing; SI/TCLA = syncytium inducing T-cell line adapted; NA = not available.

[c] As described in the text, we have proposed that viruses which use CCR5 be termed R5 viruses, viruses that use CXCR4 be termed X4 viruses, and viruses that use both be termed R5X4 viruses. For a virus to be termed an R5X4 virus, CXCR4 must be used at $>$ 10% of the efficiency of CCR5 for viruses that use CCR5 as their primary receptor, or CCR5 must be used at $>$ 10% of the efficiency of CXCR4 for viruses that use CXCR4 as their primary receptor.

[d] All virus strains in the Table have been tested for the ability to use CCR5 and CXCR4. The receptors used by each strain are indicated. For both receptors to be listed, the least efficiently used receptor must support virus entry by $>$10% of the levels supported by the most efficiently used receptor. For viruses that use both receptors, CXCR4 is listed first; this does not mean that CXCR4 is used more efficiently than CCR5.

[e] Receptors other than CCR5 or CXCR4 that are used by the indicated strains are listed. Since most viruses have not yet been tested for the ability to use receptors other than CCR5 and CXCR4, the absence of other receptors used in the Table should not be taken to mean that a virus uses only CCR5 or CXCR4. For example, if CCR3 is not listed as being used by a given virus strain, it may be because it has not yet been tested. Receptors that have been shown by experiments not to be used by a given virus strain are not indicated. Occasionally there are discrepancies in the literature concerning the use of one or more receptors. In these cases, we opted for 'majority rules'. If two papers report a positive result and one a negative result, the receptor is shown as being used.

[f] The virus isolate used CCR3 whereas the cloned env from this isolate did not [Bjorndal (1997)].

*Indicates that coreceptor use was determined only by fusion assays rather than by virus infection.

[g] 92HT593.1 (cloned env gene) and 92HA593 (whole virus) come from the same isolate and gave slightly different results in references [Dittmar (1997)] and [Zhang (1996)].

HIV-2

HIV-2 strains appear to be remarkably promiscuous in their use of coreceptors, with receptors other than CCR5 or CXCR4 often supporting very efficient virus infection in transfected cells. This is obvious from the table, where coreceptors that are used efficiently are listed separately from those that support infection inefficiently. In addition, whenever possible, information is provided about the virus (whether it is a molecular clone, biological clone, or virus swarm, and whether it can infect PBMCs from CCR5-negative individuals) and the clinical stage of the patient from which each virus was isolated. See the key at the end of the table for an explanation of abbreviations.

Isolate	Status	Primary Isolate	Δ32 PBMCs Replication	Patient Status	Coreceptors	Weak Coreceptors	References
ST	MC	NO	+	ASYMP	CCR5/GPR15/-STRL33(GPR1/APJ)	CCR1/-CCR2b/-CCR3/-CXCR4	[Edinger (1997b), Edinger (1998a), Edinger (1998b), Rucker (1997), Hill (1997), McKnight (1998), Deng (1997)]
ST/24.1C#2	MC				CCR5/GPR15/-STRL33		[Rucker (1997), Hill (1997), Hill (1998), Deng (1997)]
SBL6669	MC			SYMP	(CCR5/CXCR4/-CCR8/V28)		[Rucker (1997), Chakrabarti (1990), Albert (1987)]
ROD/A	MC			AIDS	CCR5/CXCR4/-CCR3/US28/V28		[Hill (1997), Sol (1998), Sol (1997), Clavel (1986), Bron (1997), Reeves (1997)]
ROD/B	MC	NO			CXCR4	CCR3/V28	[Clapham (1992), Reeves (1997)]
prCBL-20	MC	YES	+	AIDS	CXCR4	CCR1/-CCR2b/-CCR3/CCR5	[McKnight (1998), Schulz (1990)]
CBL-20	MC	NO	+		CXCR4		[McKnight (1998)]
prCBL-23	MC	YES		SYMP	CXCR4	CCR1/-CCR2b/-CCR3/CCR5	[McKnight (1998), Schulz (1990)]
UC1	MC			SYMP	CCR5		[Hill (1997), Evans (1988), Deng (1997)]
UC2	MC	NO		AIDS	CCR5/CXCR4/-STRL33/GPR15	CCR2b/CCR3	[Hill (1997), Evans (1988), Barnett (1996), Deng (1997)]
MIR	MC		+	AIDS	CXCR4	CCR1/-CCR2b/-CCR3/CCR5	[Sol (1997), McKnight (1998), Clavel (1986)]
V9				AIDS	CCR1/CCR2b/-CCR3/CCR5/CXCR4		[McKnight (1998)]
A-ND			+	SYMP	CXCR4	CCR1/-CCR2b/CCR3	[McKnight (1998)]
VCP	MC	NO			CXCR4		[Endres (1996)]

Isolate	Status	Primary Isolate	Δ32 PBMCs Replication	Patient Status	Coreceptors	Weak Coreceptors	References
F0784	MC				CCR5/GPR15		[Deng (1997), Gao (1992)]
A195811		YES	-	AIDS	CCR5/GPR15/-STRL33		[Chen (1998a), Owen (1998)]
A227011		YES	-	ASYMP	CCR5/GPR15/-STRL33		[Chen (1998a)]
G0415k		YES			CCR5/GPR15/-STRL33		[Chen (1998a)]
7924A		YES	+	AIDS	CXCR4/CCR2b/-CCR3/CCR5/-STRL33/GPR15		[Chen (1998a)]
JK7312A	MC		+	SYMP	CCR5/GPR15/-CCR4/CXCR4		[Hill (1997), Owen (1998), Gao (1992), Deng (1997)]
310342	S	YES			CCR5/CXCR4/-STRL33/CCR1		[Owen (1998)]
GB87	S	YES	+	SYMP	CCR5/GPR15/-CXCR4/STRL33/-CCR4/CCR2b/CCR1		[Owen (1998)]
310248	S	YES	+		CCR1/CCR4/CCR5/-CXCR4		[Owen (1998)]
310319	S	YES	+		CCR2b/CCR3/-CCR4/CXCR4/-STRL33/GPR15/-CCR5		[Owen (1998)]
77618	S	YES	+	AIDS	CCR2b/CCR3/-CXCR4/GPR15/-STRL33/CCR5		[Owen (1998)]
GB122	S	YES	+		CCR2b/CCR3/-GPR15	CCR5/-CXCR4	[Owen (1998)]
A2267	S	YES	-	ASYMP	CCR5		[Owen (1998)]
SLRHC	S	YES	-	ASYMP	CCR5		[Owen (1998)]
310072	S	YES	-	DONOR	CCR5		[Owen (1998)]
310340	S	YES	-	DONOR	CCR5		[Owen (1998)]
60415k	S	YES	-	ASYMP	CCR5		[Owen (1998)]
BAJE (B)	S	YES	-	ASYMP	CCR5/CCR3		[Sol (1998)]
BATI (A)	S	YES	-	ASYMP	CCR5	CCR3	[Sol (1997)]
BAPA (C)	S	YES	+	ASYMP	CCR5	CCR3	[Sol (1997)]
DESY (E)	S	YES		ASYMP	CCR5	CCR3	[Sol (1997)]
BAYO (G)	S	YES	+	AIDS	CXCR4		[Sol (1997)]
B3	S	YES			CCR5		[Heredia (1997)]
B4	S	YES			CCR5		[Heredia (1997)]
B7	S	YES			CCR5		[Heredia (1997)]
B8	S	YES			CCR5		[Heredia (1997)]
B9	S	YES			CCR5		[Heredia (1997)]

Isolate	Status	Primary Isolate	Δ32 PBMCs Replication	Patient Status	Coreceptors	Weak Coreceptors	References
B2	S	YES			CCR1/CCR2b/-CCR5/CXCR4		[Heredia (1997)]
B5	S	YES			CCR1/CCR2b/-CCR5/CXCR4		[Heredia (1997)]
B10	S	YES			CCR1/CCR2b/-CCR5/CXCR4		[Heredia (1997)]
RH-2-1	S	YES		EARLY	CCR5		[Guillon (1998)]
PH-2-1 C1	BC	YES		INTERMED	CCR5		[Guillon (1998)]
PH-2-1 C12	BC	YES		INTERMED	CCR5/CCR1/CCR3		[Guillon (1998)]
PH-2-1 E6	BC	YES		INTERMED	CCR5/CXCR4/-CCR3/CCR1		[Guillon (1998)]
PH-2-1 H8	BC	YES		INTERMED	CCR5/CCR3/CCR1		[Guillon (1998)]
PH-2-1 D5	BC	YES		INTERMED	CCR5	CCR3/-CXCR4/-CCR1	[Guillon (1998)]
PH-2-1 H12	BC	YES		INTERMED	CCR5/CCR3/CCR1	CXCR4	[Guillon (1998)]
RH-2-5 A10	BC	YES		INTERMED	CCR5	CCR3	[Guillon (1998)]
RH-2-5 E4	BC	YES		INTERMED	CCR5/CCR3/CCR1	CXCR4	[Guillon (1998)]
RH-2-5 E11	BC	YES		INTERMED	CCR5/CCR3/CCR1	CXCR4	[Guillon (1998)]
RH-2-5 F7	BC	YES		INTERMED	CCR5/CCR3/CCR1/-CXCR4		[Guillon (1998)]
RH-2-5 G7	BC	YES		INTERMED	CCR5	CXCR4/-CCR1/CCR3	[Guillon (1998)]
RH-2-7 A5	BC	YES		INTERMED	CCR5/CCR3	CCR1/-CXCR4	[Guillon (1998)]
RH-2-7 C9	BC	YES		INTERMED	CCR5/CCR1/CCR3/-CCR2b/CXCR4		[Guillon (1998)]
RH-2-7 C12	BC	YES		INTERMED	CCR5	CCR3/-CXCR4/-CCR1	[Guillon (1998)]
RH-2-7 D7	BC	YES		INTERMED	CCR5/CCR3/CCR1	CXCR4/-CCR2b	[Guillon (1998)]
RH-2-7 G12	BC	YES		INTERMED	CCR5/CCR3/CCR1	CXCR4/-CCR2b	[Guillon (1998)]
RH-2-2	S	YES		LATE	CCR3/CCR1/-CXCR4/CCR5	CCR2b	[Guillon (1998)]
RH-2-6	S	YES		LATE	CXCR4		[Guillon (1998)]

KEY FOR HIV-2 CORECEPTOR USE TABLE

MC = molecular clone
BC = biologic clone
S = virus swarm
ASYMP = asymptomatic
SYMP = symptomatic
DONOR = blood donor
EARLY = isolated at early timepoints
INTERMED = isolated at an intermediate point in disease progression
LATE = isolated late in disease
V28 has been redesignated CX3CR1
( ) indicates results are from cell-cell fusion assays, all other data are from infection assays

SIV

SIV strains are also rather promiscuous in their use of coreceptors. SIV strains use CCR5 with few exceptions, while CXCR4 is only rarely used, even by laboratory-adapted viruses, a feature that distinguishes them from HIV-1 strains. The Table indicates the tropism of the virus (when known) as well as whether the data were derived from a molecular clone or virus swarm.

Strain	Status	Tropism	Coreceptors	References
SIVmac251	S	M	CCR5/GPR15/STRL33	[Chen (1997), Chen (1998a), Kuhmann (1997), Luciw (1992)]
SIVmac251 (BK28 clone)	MC		CCR5/GPR15/STRL33/-GPR1	[Edinger (1997b), Edinger (1999)]
SIVmac251 (v194 clone)	MC		(CCR5/STRL33/GPR1/-GPR15)	[Rucker (1997), Edinger (1997a), Edinger (1997b), Koenig (1989)]
SIVmac 239	MC	T	CCR5/STRL33/GPR15/-GPR1/(ChemR23)	[Edinger (1997a), Edinger (1997b), Edinger (1999), Choe (1998), Rucker (1997), Chen (1997), Chen (1998a), Hill (1997), Hill (1998), Kirchhoff (1997), Marcon (1997), Samson (1998), Farzan (1997), Deng (1997)]
SIVmac316	MC	M	CCR5/STRL33/GPR15/-APJ/CCR8/GPR1/-(ChemR23)	[Edinger (1997a), Edinger (1997b), Choe (1998), Rucker (1997), Kirchhoff (1997), Samson (1998), Farzan (1997)]
SIVmac316mut	MC	Md	CCR5/(STRL33/GPR1/-GPR15/ChemR23/APJ)	[Edinger (1997a), Edinger (1997b), Edinger (1998b), Rucker (1997), Kirchhoff (1997), Kirchhoff (1994), Samson (1998)]
SIVmac316EM	MC	M	CCR5/GPR15/STRL33	[Chen (1997), Chen (1998a)]
SIVmac1A11	MC	M	CCR5/STRL33/GPR15	[Edinger (1997b), Edinger (1999), Chen (1997), Chen (1998a), Hill (1997), Banapour (1991a), Banapour (1991b), Deng (1997), Chen (1998a), Chen (1998b)]
SIVmac/17E-Fr	MC	M	CCR5/STRL33/GPR15/-APJ/(ChemR23/CCR8)	[Edinger (1997a), Edinger (1997b), Edinger (1998b), Edinger (1999), Rucker (1997), Flaherty (1997)]
SIVmac/17E-Cl	MC	M	(CCR5/GPR1/STRL33/-GPR15)	[Edinger (1998a), Flaherty (1997)]
SIVmacCP-MAC	S		CXCR4	[Endres (1996)]
SIVmacCP-MAC	MC		CCR5/STRL33/GPR15/APJ	[Edinger (1997b), Edinger (1998b), Edinger (1999)]
SIVmac(mne)			CCR5/GPR15	[Chen (1998a)]

Strain	Status	Tropism	Coreceptors	References
SIVsmΔB670 clone 3	MC		CCR5/GPR15/STRL33	[Edinger (1997a), Edinger (1997b), Rucker (1997)]
SIVsmΔB670 clone 12	MC	(M)	CCR5/GPR15	[Edinger (1997b), Edinger (1999), Amedee (1995)]
SIVsm62A	MC	T	(CCR5/GPR1/GPR15/STRL33/ChemR23)	[Edinger (1997b), Hirsch (1994)]
SIVsm62B	MC		(CCR5)	[Edinger (1997b), Hirsch (1994)]
SIVsm62D	MC	M	CCR5	[Edinger (1997b), Hirsch (1994)]
SIVsmE543-3	MC	M	CCR5/GPR15	[Edinger (1997b), Hirsch (1997)]
SIVsmE543/B10	MC		(CCR5/GPR15/GPR1/STRL33)	[Edinger (1997b), Hirsch (1997)]
SIVsmPBj6.6	MC		(STRL33/CCR5/GPR1/GPR15)	[Edinger (1998a), Novembre (1993)]
SIVsmSL92a	S		CCR5/GPR15/STRL33	[Chen (1997), Chen (1998a)]
SIVsmSL92b	S		CCR5/GPR15/STRL33	[Chen (1998a)]
SIVsmLib-1	S		CCR5/GPR15/STRL33	[Chen (1997), Chen (1998a)]
SIVsmFNS	S		CCR5/GPR15/STRL33	[Chen (1998a)]
SIVagmSab1.4	MC		(CCR5/GPR15/GPR1/STRL33)	[Edinger (1997b)]
SIVagm9063-2	MC	M	(CCR5)	[Edinger (1997b), Hirsch (1995)]
SIVagmTYO	MC		CCR5/GPR15/STRL33	[Deng (1997), Chen (1998a), Chen (1998b)]
SIVmneCl8	MC		CCR5	[Chackerian (1997)]
SIVrcm			CCR2b/STRL33	[Marx & Chen(1998)]
SIVcpzGAB	S		CCR5	[Chen (1997), Marx & Chen(1998)]
SIVmnd(GB-1)	S		CXCR4	[Schols & De Clercq(1998)]

KEY FOR SIV CORECEPTOR TABLE

S = uncloned virus swarm
MC = molecular clone
M = macrophage tropic, Md = delayed infection kinetics in macrophages, (M) = probably M-tropic, T = T-tropic
( ) indicate fusion results, all other data from infection assays

REFERENCES

[Albert (1987)] J. Albert, U. Bredberg, F. Chiodi, B. Bottiger, E. M. Fenyo, E. Norrby, & G. Biberfeld. A new human retrovirus isolate of West African origin (SBL-6669) and its relationship to HTLV-IV, LAV-II, and HTLV-IIIB. *AIDS Res Hum Retroviruses* **3**:3–10, 1987.

NOTE: (Medline: 87299193).

[Alkhatib (1996)] G. Alkhatib, C. Combadiere, C. C. Broder, Y. Feng, P. E. Kennedy, P. M. Murphy, & E. A. Berger. CC CKR5: a RANTES, MIP-1alpha, MIP-1beta receptor as a fusion cofactor for macrophage-tropic HIV-1. *Science* **272**:1955–8, 1996.

NOTE: (Medline: 96275693).

[Amedee (1995)] A. M. Amedee, N. Lacour, J. L. Gierman, L. N. Martin, J. E. Clements, R. Bohm, R. M. Harrison, & M. Murphey-Corb. Genotypic selection of simian immunodeficiency virus in macaque infants infected transplacentally. *J Virol* **69**:7982–90, 1995.

NOTE: (Medline: 96079048).

[Banapour (1991a)] B. Banapour, M. L. Marthas, R. J. Munn, & P. A. Luciw. In vitro macrophage tropism of pathogenic and nonpathogenic molecular clones of simian immunodeficiency virus (SIV-mac). *Virology* **183**:12–9, 1991a.

NOTE: (Medline: 91272471).

[Banapour (1991b)] B. Banapour, M. L. Marthas, R. A. Ramos, B. L. Lohman, R. E. Unger, M. B. Gardner, N. C. Pedersen, & P. A. Luciw. Identification of viral determinants of macrophage tropism for simian immunodeficiency virus SIVmac. *J Virol* **65**:5798–805, 1991b.

NOTE: (Medline: 92015471).

[Barnett (1996)] S. W. Barnett, H. S. Legg, Y. Sun, J. Klinger, D. J. Blackbourn, C. P. Locher, & J. A. Levy. Molecular cloning of the human immunodeficiency virus subtype 2 strain HIV-2UC2. *Virology* **222**:257–61, 1996.

NOTE: (Medline: 96400130).

[Bazan (1998)] H. A. Bazan, G. Alkhatib, C. C. Broder, & E. A. Berger. Patterns of CCR5, CXCR4, and CCR3 usage by envelope glycoproteins from human immunodeficiency virus type 1 primary isolates. *J Virol* **72**:4485–91, 1998.

NOTE: (Medline: 98216824).

[Bjorndal (1997)] A. Bjorndal, H. Deng, M. Jansson, J. R. Fiore, C. Colognesi, A. Karlsson, J. Albert, G. Scarlatti, D. R. Littman, & E. M. Fenyo. Coreceptor usage of primary human immunodeficiency virus type 1 isolates varies according to biological phenotype. *J Virol* **71**:7478–87, 1997.

NOTE: (Medline: 97456513).

[Bron (1997)] R. Bron, P. J. Klasse, D. Wilkinson, P. R. Clapham, A. Pelchen-Matthews, C. Power, T. N. Wells, J. Kim, S. C. Peiper, J. A. Hoxie, & M. Marsh. Promiscuous use of CC and CXC chemokine receptors in cell-to-cell fusion mediated by a human immunodeficiency virus type 2 envelope protein. *J Virol* **71**:8405–15, 1997.

NOTE: (Medline: 98001362).

[Chackerian (1997)] B. Chackerian, E. M. Long, P. A. Luciw, & J. Overbaugh. Human immunodeficiency virus type 1 coreceptors participate in postentry stages in the virus replication cycle and function in simian immunodeficiency virus infection. *J Virol* **71**:3932–9, 1997.

NOTE: (Medline: 97248442).

[Chakrabarti (1990)] S. Chakrabarti, T. Mizukami, G. Franchini, & B. Moss. Synthesis, oligomerization, and biological activity of the human immunodeficiency virus type 2 envelope glycoprotein expressed by a recombinant vaccinia virus. *Virology* **178**:134–42, 1990.

NOTE: (Medline: 90357756).

[Chen (1998a)] Z. Chen, A. Gettie, D. D. Ho, & P. A. Marx. Primary SIVsm isolates use the CCR5 coreceptor from sooty mangabeys naturally infected in west Africa: a comparison of coreceptor usage of primary SIVsm, HIV-2, and SIVmac. *Virology* **246**:113–24, 1998a.

NOTE: (Medline: 98321155).

[Chen (1998b)] Z. Chen, D. Kwon, Z. Jin, S. Monard, P. Telfer, M. S. Jones, C. Y. Lu, R. F. Aguilar, D. D. Ho, & P. A. Marx. Natural infection of a homozygous delta24 CCR5 red-capped mangabey with an R2b-tropic simian immunodeficiency virus. *J Exp Med* **188**:2057–65, 1998b.

NOTE: (Medline: 99059829).

[Chen (1997)] Z. Chen, P. Zhou, D. D. Ho, N. R. Landau, & P. A. Marx. Genetically divergent strains of simian immunodeficiency virus use CCR5 as a coreceptor for entry. *J Virol* **71**:2705–14, 1997.

NOTE: (Medline: 97213934).

[Choe (1998)] H. Choe, M. Farzan, M. Konkel, K. Martin, Y. Sun, L. Marcon, M. Cayabyab, M. Berman, M. E. Dorf, N. Gerard, C. Gerard, & J. Sodroski. The orphan seven-transmembrane receptor apj supports the entry of primary T-cell-line-tropic and dualtropic human immunodeficiency virus type 1. *J Virol* **72**:6113–8, 1998.

NOTE: (Medline: 98285773).

[Choe (1996)] H. Choe, M. Farzan, Y. Sun, N. Sullivan, B. Rollins, P. D. Ponath, L. Wu, C. R. Mackay, G. LaRosa, W. Newman, N. Gerard, C. Gerard, & J. Sodroski. The beta-chemokine receptors CCR3 and CCR5 facilitate infection by primary HIV-1 isolates. *Cell* **85**:1135–48, 1996.

NOTE: (Medline: 96270515).

[Clapham (1992)] P. R. Clapham, A. McKnight, & R. A. Weiss. Human immunodeficiency virus type 2 infection and fusion of CD4- negative human cell lines: induction and enhancement by soluble CD4. *J Virol* **66**:3531–7, 1992.

NOTE: (Medline: 92260623).

[Clavel (1986)] F. Clavel, D. Guetard, F. Brun-Vezinet, S. Chamaret, M. A. Rey, M. O. Santos-Ferreira, A. G. Laurent, C. Dauguet, C. Katlama, & C. Rouzioux. Isolation of a new human retrovirus from West African patients with AIDS. *Science* **233**:343–6, 1986.

NOTE: (Medline: 86261773).

[Deng (1997)] H. K. Deng, D. Unutmaz, V. N. KewalRamani, & D. R. Littman. Expression cloning of new receptors used by simian and human immunodeficiency viruses (see comments). *Nature* **388**:296–300, 1997.

NOTE: (Medline: 97373958).

[Dittmar (1997)] M. T. Dittmar, G. Simmons, S. Hibbitts, M. O'Hare, S. Louisirirotchanakul, S. Beddows, J. Weber, P. R. Clapham, & R. A. Weiss. Langerhans cell tropism of human immunodeficiency virus type 1 subtype A through F isolates derived from different transmission groups. *J Virol* **71**:8008–13, 1997.

NOTE: (Medline: 97456582).

[Dragic (1996)] T. Dragic, V. Litwin, G. P. Allaway, S. R. Martin, Y. Huang, K. A. Nagashima, C. Cayanan, P. J. Maddon, R. A. Koup, J. P. Moore, & W. A. Paxton. HIV-1 entry into CD4+ cells is mediated by the chemokine receptor CC- CKR-5 (see comments). *Nature* **381**:667–73, 1996.

NOTE: (Medline: 96260018).

[Edinger (1997a)] A. L. Edinger, A. Amedee, K. Miller, B. J. Doranz, M. Endres, M. Sharron, M. Samson, Z. H. Lu, J. E. Clements, M. Murphey-Corb, S. C. Peiper, M. Parmentier, C. C. Broder, & R. W. Doms. Differential utilization of CCR5 by macrophage and T cell tropic simian immunodeficiency virus strains. *Proc Natl Acad Sci U S A* **94**:4005–10, 1997a.

NOTE: (Medline: 97268687).

[Edinger (1999)] A. L. Edinger, C. Blanpain, K. Kunstman, S. M. Wolinsky, M. Endres, M. Parmentier, & R. W. Doms. Functional dissection of CCR5 coreceptor function through the use of CD4-independent SIV strains. 1999.

NOTE: Submitted.

[Edinger (1998a)] A. L. Edinger, T. L. Hoffman, M. Sharron, B. Lee, B. O'Dowd, & R. W. Doms. Use of GPR1, GPR15, and STRL33 as coreceptors by diverse human immunodeficiency virus type 1 and simian immunodeficiency virus envelope proteins. *Virology* **249**:367–78, 1998a.

NOTE: (Medline: 99009390).

[Edinger (1998b)] A. L. Edinger, T. L. Hoffman, M. Sharron, B. Lee, Y. Yi, W. Choe, D. L. Kolson, B. Mitrovic, Y. Zhou, D. Faulds, R. G. Collman, J. Hesselgesser, R. Horuk, & R. W. Doms. An orphan seven-transmembrane domain receptor expressed widely in the brain functions as a coreceptor for human immunodeficiency virus type 1 and simian immunodeficiency virus. *J Virol* **72**:7934–40, 1998b.

NOTE: (Medline: 98406195).

[Edinger (1997b)] A. L. Edinger, J. L. Mankowski, B. J. Doranz, B. J. Margulies, B. Lee, J. Rucker, M. Sharron, T. L. Hoffman, J. F. Berson, M. C. Zink, V. M. Hirsch, J. E. Clements, & R. W. Doms. CD4-independent, CCR5-dependent infection of brain capillary endothelial cells by a neurovirulent simian immunodeficiency virus strain. *Proc Natl Acad Sci U S A* **94**:14742–7, 1997b.

NOTE: (Medline: 98070822).

[Endres (1996)] M. J. Endres, P. R. Clapham, M. Marsh, M. Ahuja, J. D. Turner, A. McKnight, J. F. Thomas, B. Stoebenau-Haggarty, S. Choe, P. J. Vance, T. N. Wells, C. A. Power, S. S. Sutterwala, R. W. Doms, N. R. Landau, & J. A. Hoxie. CD4-independent infection by HIV-2 is mediated by fusin/CXCR4. *Cell* **87**:745–56, 1996.

NOTE: (Medline: 97083584).

[Evans (1988)] L. A. Evans, J. Moreau, K. Odehouri, D. Seto, G. Thomson-Honnebier, H. Legg, A. Barboza, C. Cheng-Mayer, & J. A. Levy. Simultaneous isolation of HIV-1 and HIV-2 from an AIDS patient. *Lancet* **2**:1389–91, 1988.

NOTE: (Medline: 89069975).

[Farzan (1997)] M. Farzan, H. Choe, K. Martin, L. Marcon, W. Hofmann, G. Karlsson, Y. Sun, P. Barrett, N. Marchand, N. Sullivan, N. Gerard, C. Gerard, & J. Sodroski. Two orphan seven-transmembrane segment receptors which are expressed in CD4-positive cells support simian immunodeficiency virus infection. *J Exp Med.* **186**:405–11, 1997.

NOTE: (Medline: 98105758).

[Flaherty (1997)] M. T. Flaherty, D. A. Hauer, J. L. Mankowski, M. C. Zink, & J. E. Clements. Molecular and biological characterization of a neurovirulent molecular clone of simian immunodeficiency virus. *J Virol* **71**:5790–8, 1997.

NOTE: (Medline: 97366637).

[Gao (1992)] F. Gao, L. Yue, A. T. White, P. G. Pappas, J. Barchue, A. P. Hanson, B. M. Greene, P. M. Sharp, G. M. Shaw, & B. H. Hahn. Human infection by genetically diverse SIVSM-related HIV-2 in west Africa. *Nature* **358**:495–9, 1992.

NOTE: (Medline: 92350299).

[Guillon (1998)] C. Guillon, M. E. van der Ende, P. H. Boers, R. A. Gruters, M. Schutten, & A. D. Osterhaus. Coreceptor usage of human immunodeficiency virus type 2 primary isolates and biological clones is broad and does not correlate with their syncytium-inducing capacities. *J Virol* **72**:6260–3, 1998.

NOTE: (Medline: 98285800).

[Heredia (1997)] A. Heredia, A. Vallejo, V. Soriano, J. S. Epstein, & I. K. Hewlett. Chemokine receptors and HIV-2 [letter]. *AIDS* **11**:1198–9, 1997.

NOTE: (Medline: 97377877).

[Hill (1997)] C. M. Hill, H. Deng, D. Unutmaz, V. N. Kewalramani, L. Bastiani, M. K. Gorny, S. Zolla-Pazner, & D. R. Littman. Envelope glycoproteins from human immunodeficiency virus types 1 and 2 and simian immunodeficiency virus can use human CCR5 as a coreceptor for viral entry and make direct CD4-dependent interactions with this chemokine receptor. *J Virol* **71**:6296–304, 1997.

NOTE: (Medline: 97404634).

[Hill (1998)] C. M. Hill, D. Kwon, M. Jones, C. B. Davis, S. Marmon, B. L. Daugherty, J. A. DeMartino, M. S. Springer, D. Unutmaz, & D. R. Littman. The amino terminus of human CCR5 is required for its function as a receptor for diverse human and simian immunodeficiency virus envelope glycoproteins. *Virology* **248**:357–71, 1998.

NOTE: (Medline: 98389855).

[Hirsch (1997)] V. Hirsch, D. Adger-Johnson, B. Campbell, S. Goldstein, C. Brown, W. R. Elkins, & D. C. Montefiori. A molecularly cloned, pathogenic, neutralization-resistant simian immunodeficiency virus, SIVsmE543-3. *J Virol* **71**:1608–20, 1997.

NOTE: (Medline: 97151152).

[Hirsch (1995)] V. M. Hirsch, G. Dapolito, P. R. Johnson, W. R. Elkins, W. T. London, R. J. Montali, S. Goldstein, & C. Brown. Induction of AIDS by simian immunodeficiency virus from an African green monkey: species-specific variation in pathogenicity correlates with the extent of in vivo replication. *J Virol* **69**:955–67, 1995.

NOTE: (Medline: 95115151).

[Hirsch (1994)] V. M. Hirsch, J. E. Martin, G. Dapolito, W. R. Elkins, W. T. London, S. Goldstein, & P. R. Johnson. Spontaneous substitutions in the vicinity of the V3 analog affect cell tropism and pathogenicity of simian immunodeficiency virus. *J Virol* **68**:2649–61, 1994.

NOTE: (Medline: 94187106).

[Kirchhoff (1994)] F. Kirchhoff, K. Mori, & R. C. Desrosiers. The "V3" domain is a determinant of simian immunodeficiency virus cell tropism. *J Virol* **68**:3682–92, 1994.

NOTE: (Medline: 94246713).

[Kirchhoff (1997)] F. Kirchhoff, S. Pohlmann, M. Hamacher, R. E. Means, T. Kraus, K. Uberla, & P. Di Marzio. Simian immunodeficiency virus variants with differential T-cell and macrophage tropism use CCR5 and an unidentified cofactor expressed in CEMx174 cells for efficient entry. *J Virol* **71**:6509–16, 1997.

NOTE: (Medline: 97404658).

[Koenig (1989)] S. Koenig, V. M. Hirsch, R. A. Olmsted, D. Powell, W. Maury, A. Rabson, A. S. Fauci, R. H. Purcell, & P. R. Johnson. Selective infection of human CD4+ cells by simian immunodeficiency virus: productive infection associated with envelope glycoprotein- induced fusion. *Proc Natl Acad Sci U S A* **86**:2443–7, 1989.

NOTE: (Medline: 89184643).

[Kuhmann (1997)] S. E. Kuhmann, E. J. Platt, S. L. Kozak, & D. Kabat. Polymorphisms in the CCR5 genes of African green monkeys and mice implicate specific amino acids in infections by simian and human immunodeficiency viruses. *J Virol* **71**:8642–56, 1997.

NOTE: (Medline: 98001387).

[Liao (1997)] F. Liao, G. Alkhatib, K. W. Peden, G. Sharma, E. A. Berger, & J. M. Farber. STRL33, A novel chemokine receptor-like protein, functions as a fusion cofactor for both macrophage-tropic and T cell line-tropic HIV-1. *J Exp Med* **185**:2015–23, 1997.

NOTE: (Medline: 97311099).

[Luciw (1992)] P. A. Luciw, K. E. Shaw, R. E. Unger, V. Planelles, M. W. Stout, J. E. Lackner, E. Pratt-Lowe, N. J. Leung, B. Banapour, & M. L. Marthas. Genetic and biological comparisons of pathogenic and nonpathogenic molecular clones of simian immunodeficiency virus (SIVmac). *AIDS Res Hum Retroviruses* **8**:395–402, 1992.

NOTE: (Medline: 92239216).

[Marcon (1997)] L. Marcon, H. Choe, K. A. Martin, M. Farzan, P. D. Ponath, L. Wu, W. Newman, N. Gerard, C. Gerard, & J. Sodroski. Utilization of C-C chemokine receptor 5 by the envelope glycoproteins of a pathogenic simian immunodeficiency virus, SIVmac239. *J Virol* **71**:2522–7, 1997.

NOTE: (Medline: 97184592).

[Marx & Chen(1998)] P. A. Marx & Z. Chen. The function of simian chemokine receptors in the replication of SIV. *Semin Immunol* **10**:215–23, 1998.

NOTE: (Medline: 98317008).

[McKnight (1998)] A. McKnight, M. T. Dittmar, J. Moniz-Periera, K. Ariyoshi, J. D. Reeves, S. Hibbitts, D. Whitby, E. Aarons, A. E. Proudfoot, H. Whittle, & P. R. Clapham. A broad range of chemokine receptors are used by primary isolates of human immunodeficiency virus type 2 as coreceptors with CD4. *J Virol* **72**:4065–71, 1998.

NOTE: (Medline: 98216773).

[Novembre (1993)] F. J. Novembre, P. R. Johnson, M. G. Lewis, D. C. Anderson, S. Klumpp, H. M. McClure, & V. M. Hirsch. Multiple viral determinants contribute to pathogenicity of the acutely lethal simian immunodeficiency virus SIVsmmPBj variant. *J Virol* **67**:2466–74, 1993.

NOTE: (Medline: 93233209).

[Owen (1998)] S. M. Owen, D. Ellenberger, M. Rayfield, S. Wiktor, P. Michel, M. H. Grieco, F. Gao, B. H. Hahn, & R. B. Lal. Genetically divergent strains of human immunodeficiency virus type 2 use multiple coreceptors for viral entry. *J Virol* **72**:5425–32, 1998.

NOTE: (Medline: 98285695).

[Pleskoff (1997)] O. Pleskoff, N. Sol, B. Labrosse, & M. Alizon. Human immunodeficiency virus strains differ in their ability to infect CD4+ cells expressing the rat homolog of CXCR-4 (fusin). *J Virol* **71**:3259–62, 1997.

NOTE: (Medline: 97214002).

[Reeves (1997)] J. D. Reeves, A. McKnight, S. Potempa, G. Simmons, P. W. Gray, C. A. Power, T. Wells, R. A. Weiss, & S. J. Talbot. CD4-independent infection by HIV-2 (ROD/B): use of the 7-transmembrane receptors CXCR-4, CCR-3, and V28 for entry. *Virology* **231**:130–4, 1997.

NOTE: (Medline: 97288333).

[Rucker (1997)] J. Rucker, A. L. Edinger, M. Sharron, M. Samson, B. Lee, J. F. Berson, Y. Yi, B. Margulies, R. G. Collman, B. J. Doranz, M. Parmentier, & R. W. Doms. Utilization of chemokine receptors, orphan receptors, and herpesvirus encoded receptors by diverse human and simian immunodeficiency viruses. *J Virol* **71**:8999–9007, 1997.

NOTE: (Medline: 98037607).

[Samson (1998)] M. Samson, A. L. Edinger, P. Stordeur, J. Rucker, V. Verhasselt, M. Sharron, C. Govaerts, C. Mollereau, G. Vassart, R. W. Doms, & M. Parmentier. ChemR23, a putative chemoattractant receptor, is expressed in monocyte- derived dendritic cells and macrophages and is a coreceptor for SIV and some primary HIV-1 strains. *Eur J Immunol* **28**:1689–700, 1998.

NOTE: (Medline: 98264639).

[Schols & De Clercq(1998)] D. Schols & E. De Clercq. The simian immunodeficiency virus mnd(GB-1) strain uses CXCR4, not CCR5, as coreceptor for entry in human cells. *J Gen Virol* **79 (Pt 9)**:2203–5, 1998.

NOTE: (Medline: 98418501).

[Schulz (1990)] T. F. Schulz, D. Whitby, J. G. Hoad, T. Corrah, H. Whittle, & R. A. Weiss. Biological and molecular variability of human immunodeficiency virus type 2 isolates from The Gambia. *J Virol* **64**:5177–82, 1990.

NOTE: (Medline: 90376478).

[Simmons (1998)] G. Simmons, J. D. Reeves, A. McKnight, N. Dejucq, S. Hibbitts, C. A. Power, E. Aarons, D. Schols, E. De Clercq, A. E. Proudfoot, & P. R. Clapham. CXCR4 as a functional coreceptor for human immunodeficiency virus type 1 infection of primary macrophages. *J Virol* **72**:8453–7, 1998.

NOTE: (Medline: 98406265).

[Simmons (1996)] G. Simmons, D. Wilkinson, J. D. Reeves, M. T. Dittmar, S. Beddows, J. Weber, G. Carnegie, U. Desselberger, P. W. Gray, R. A. Weiss, & P. R. Clapham. Primary, syncytium-inducing human immunodeficiency virus type 1 isolates are dual-tropic and most can use either Lestr or CCR5 as coreceptors for virus entry. *J Virol* **70**:8355–60, 1996.

NOTE: (Medline: 97126031).

[Sol (1997)] N. Sol, F. Ferchal, J. Braun, O. Pleskoff, C. Treboute, I. Ansart, & M. Alizon. Usage of the coreceptors CCR-5, CCR-3, and CXCR-4 by primary and cell line-adapted human immunodeficiency virus type 2. *J Virol* **71**:8237–44, 1997.

NOTE: (Medline: 98001340).

[Sol (1998)] N. Sol, C. Treboute, E. Gomas, F. Ferchal, B. Shacklett, & M. Alizon. The rhesus macaque CCR3 chemokine receptor is a cell entry cofactor for HIV-2, but not for HIV-1. *Virology* **240**:213–20, 1998.

NOTE: (Medline: 98118446).

[Trkola (1998)] A. Trkola, W. A. Paxton, S. P. Monard, J. A. Hoxie, M. A. Siani, D. A. Thompson, L. Wu, C. R. Mackay, R. Horuk, & J. P. Moore. Genetic subtype-independent inhibition of human immunodeficiency virus type 1 replication by CC and CXC chemokines. *J Virol* **72**:396–404, 1998.

NOTE: (Medline: 98080427).

[Vallejo (1998)] A. Vallejo, A. Heredia, A. Mas, S. F. Lee, J. S. Epstein, V. Soriano, & I. K. Hewlett. Tropism, coreceptor use, and phylogenetic analysis of both the V3 loop and the protease gene of three novel HIV-1 group O isolates. *J Acquir Immune Defic Syndr Hum Retrovirol* **18**:417–25, 1998.

NOTE: (Medline: 98379694).

[Zhang (1996)] L. Zhang, Y. Huang, T. He, Y. Cao, & D. D. Ho. HIV-1 subtype and second-receptor use (letter). *Nature* **383**:768, 1996.

NOTE: (Medline: 97048157).

[Zhang (1998)] Y. J. Zhang, T. Dragic, Y. Cao, L. Kostrikis, D. S. Kwon, D. R. Littman, V. N. KewalRamani, & J. P. Moore. Use of coreceptors other than CCR5 by non-syncytium-inducing adult and pediatric isolates of human immunodeficiency virus type 1 is rare in vitro. *J Virol* **72**:9337–44, 1998.

NOTE: (Medline: 98440604).