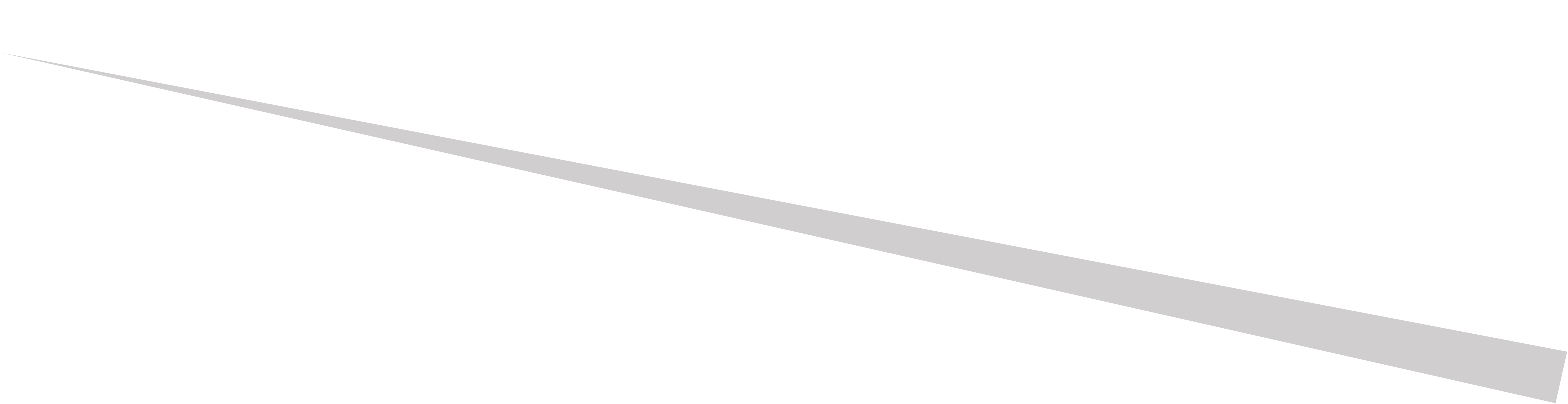


Nei and Kumar.2000.pp.33-50

1969

Evolution of model complexity









- Count the number of different bases
- p-distance



- All rates are equal
- One parameter

	A	T	C	G
A	-	α	α	α
T	α	-	α	α
C	α	α	-	α
G	α	α	α	-



kinura2-parameter

- Ts/Tv rate bias
- 2 parameters

1980



juke-s-antor

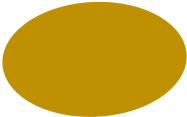






- Ts/Tv rate bias
- Base composition bias

Hasagawa-Kishino-Yano





T

a

n

n

u

r

a

-

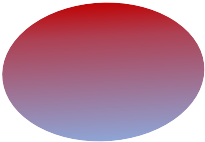
N

i

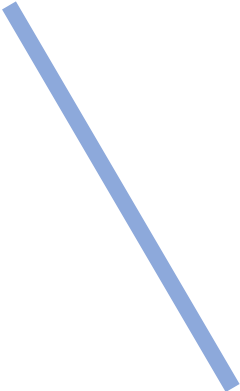
- Purine/Pyrimidine rates
- Ts/Tv rate bias
- 6 parameters



1993



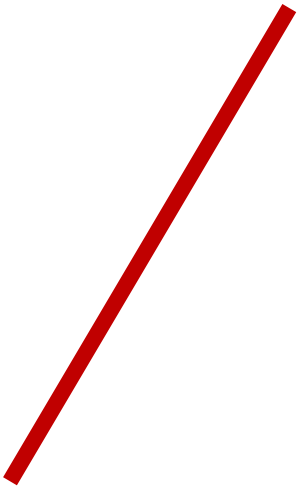
- Time reversible
- Different rates
- 9 parameters



General-
time-reversible

Unrestricted model

- All different rates
- Not time reversible



	A	T	C	G
A	-	a_{12}	a_{13}	a_{14}
T	a_{21}	-	a_{23}	a_{24}
C	a_{31}	a_{32}	-	a_{34}
G	a_{41}	a_{42}	a_{43}	-

	A	T	C	G
A	-	βg_T	βg_C	αg_G
T	βg_A	-	αg_C	βg_G
C	βg_A	αg_T	-	βg_G
G	αg_A	βg_T	βg_C	-

	A	T	C	G
A	-	β	β	α
T	β	-	α	β
C	β	α	-	β
G	α	β	β	-

	A	T	C	G
A	-	ag_T	bg_C	dg_G
T	ag_A	-	cg_C	eg_G
C	bg_A	dg_T	-	fg_G
G	cg_A	eg_T	fg_C	-

	A	T	C	G
A	-	βg_T	βg_C	$\alpha_1 g_G$
T	βg_A	-	$\alpha_2 g_C$	βg_G
C	βg_A	$\alpha_2 g_T$	-	βg_G
G	$\alpha_1 g_A$	βg_T	βg_C	-

1986

slide courtesy of Dr. Qiqing Tao

Evolution of model complexity

Observations

- Count the number of different bases
- p-distance



1969

Jukes-Cantor

- All rates are equal
- One parameter

	A	T	C	G
A	-	α	α	α
T	α	-	α	α
C	α	α	-	α
G	α	α	α	-

Kimura 2-parameter

- Ts/Tv rate bias
- 2 parameters

	A	T	C	G
A	-	β	β	α
T	β	-	α	β
C	β	α	-	β
G	α	β	β	-

1980

1985

Hasegawa-Kishino-Yano

- Ts/Tv rate bias
- Base composition bias

	A	T	C	G
A	-	βg_T	βg_C	αg_G
T	βg_A	-	αg_C	βg_G
C	βg_A	αg_T	-	βg_G
G	αg_A	βg_T	βg_C	-

1986

Tamura-Nei

- Purine/Pyrimidine rates
- Ts/Tv rate bias
- 6 parameters

	A	T	C	G
A	-	βg_T	βg_C	$\alpha_1 g_G$
T	βg_A	-	$\alpha_2 g_C$	βg_G
C	βg_A	$\alpha_2 g_T$	-	βg_G
G	$\alpha_1 g_A$	βg_T	βg_C	-

1993

1994

Unrestricted model

- All different rates
- Not time reversible

	A	T	C	G
A	-	a_{12}	a_{13}	a_{14}
T	a_{21}	-	a_{23}	a_{24}
C	a_{31}	a_{32}	-	a_{34}
G	a_{41}	a_{42}	a_{43}	-

General-time-reversible

- Time reversible
- Different rates
- 9 parameters

	A	T	C	G
A	-	ag_T	bg_C	dg_G
T	ag_A	-	cg_C	eg_G
C	bg_A	dg_T	-	fg_G
G	cg_A	eg_T	fg_C	-

Quantifying selection on coding sequences

1.) selectively constrained:

$$d_N / d_S < 1$$

2.) strictly neutral:

$$d_N / d_S = 1$$

3.) adaptive evolution:

$$d_N / d_S > 1$$

