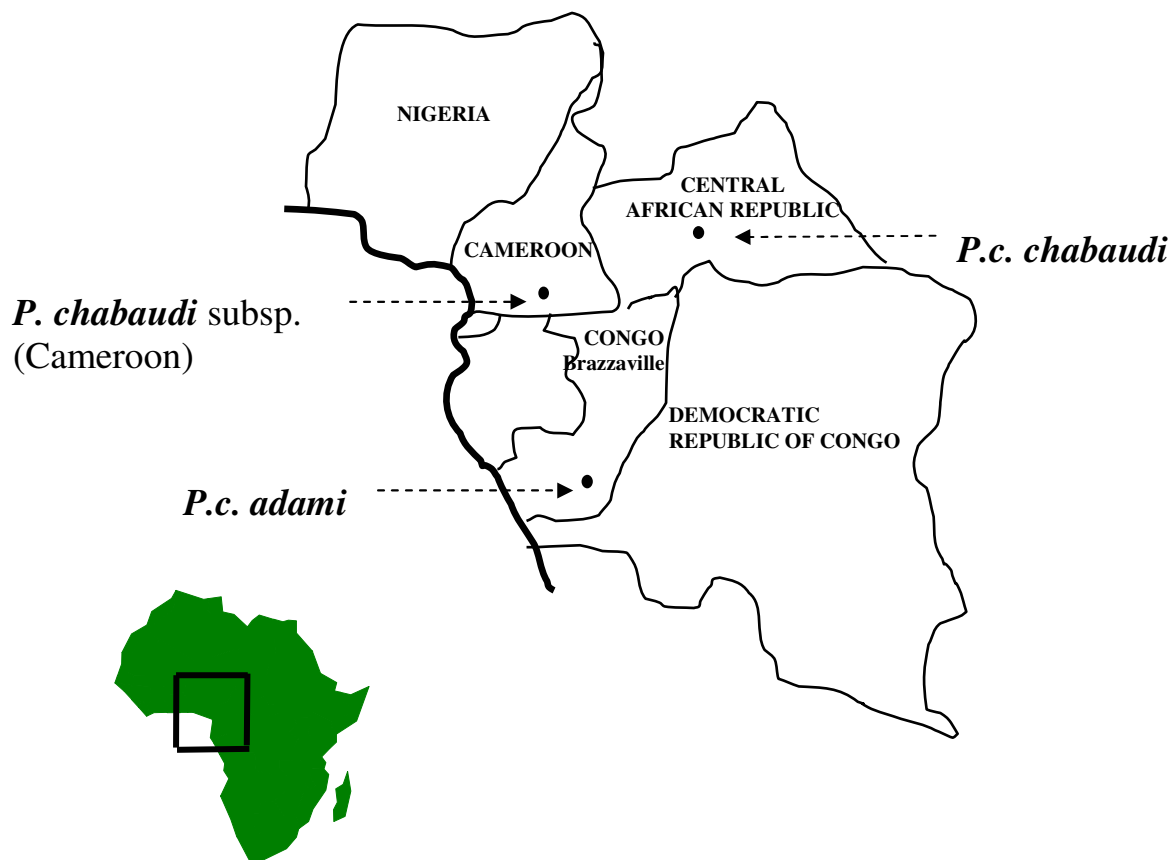


Plasmodium chabaudi

Life-histories and stabilates (deep-frozen samples) of isolates, lines and clones maintained at the University of Edinburgh

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Plasmodium chabaudi subspecies: countries of origin



General information

Isolates, lines and clones

An isolate is a sample of parasites collected from a wild-caught animal on a unique occasion. An isolate may contain more than species of parasite, and more than one genetically distinct clone of a given species.

A line refers to parasites which have undergone a particular passage or treatment. Parasites in a line usually have certain characteristics in common, but are not necessarily genetically identical.

A clone is an infection derived in the laboratory from a single haploid parasite, usually an asexual blood form, or sometimes a sporozoite.

Mixed species infections

Note that the majority of wild-caught rodents have been found to contain mixed infections of more than one species. It must be assumed, therefore, that uncloned isolates may contain such mixtures, even after prolonged passage through laboratory animals.

Numbering of stabilates

For historic reasons, different types of numbering system are used for denoting deep-frozen stabilate material. In general, recent samples are denoted according to their rodent passage number, while older stabilates have a simple number unrelated to passage.

Parasites sent to MR4

Parasites which have been supplied to the Malaria Reference and Research Reagent Resource Center (MR4) (American Type Culture collection) are indicated in the life-histories by red boxes, together with their MR4 accession numbers. Note that these accession numbers are uniquely allocated by MR4, and do not correspond with Edinburgh stabilate or passage numbers.

P. chabaudi isolates and clones - summary

P.c. chabaudi (Central African Republic)

<u>Isolates</u>	<u>Clones</u>
AC	
AD →	AD88/6
AF	
AJ →	AJ3030/12 (=AJ(MJM)), 17AJ17, 97AJ6, 96AJ15 and derived clones
AL →	AL34/12
AQ →	AQ31/4
AS →	AS8793/3 (=AS(MJM), 28AS20, AS(sens) and clones resistant to pyrimethamine, sulfadoxine-pyrimethamine, chloroquine and mefloquine
AT →	AT20/3
BC →	BC23/2
BE	
BK →	BK28/5, BK29/2, BK29/13
BS →	4BS20
CB →	CB821/5, 50CB2 and clones resistant to pyrimethamine
CE →	13CE11
CP	
CQ →	CQ23/10
CR →	CR508/14, 197CR6
CW →	CW37/7
DR (Red line)	
DT (864VD)	
DY (54X)	
EC (Landau original)	
ER (56L) →	8ER12

P. chabaudi isolates and clones**P.c. adami (Congo-Brazzaville)****Isolates****Clones**

DS (408XZ) —————> 15DS12

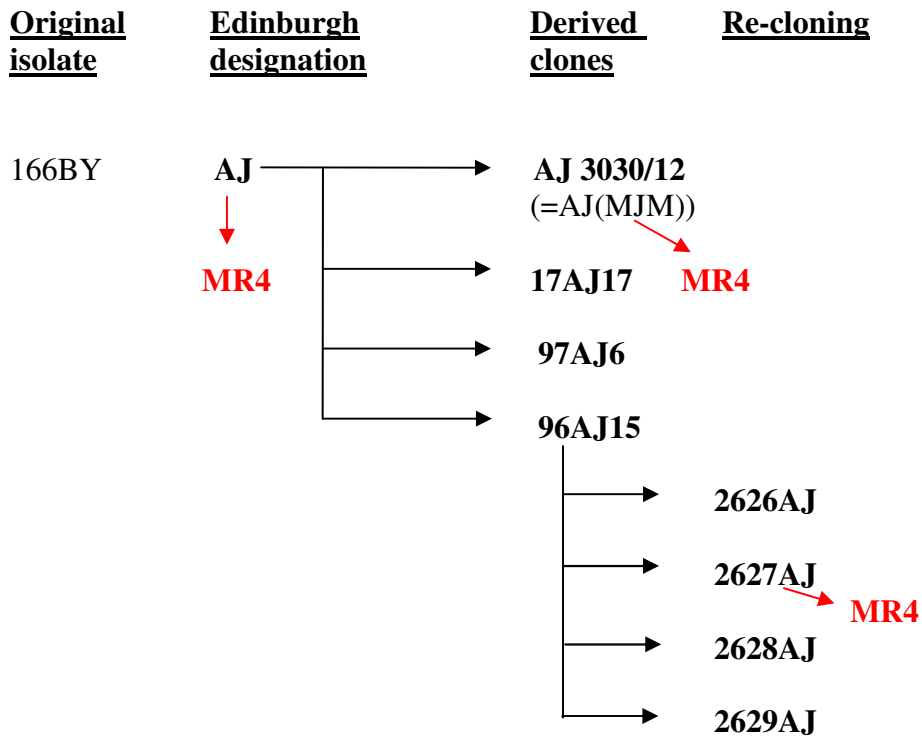
DK (556KA) —————> 19DK1, 19DK23

P. chabaudi subsp. (Cameroon)**Isolates****Clones**

EF (Biboto 37) —————> 6EF4, 7EF1

***P. chabaudi chabaudi* (Central African Republic)**

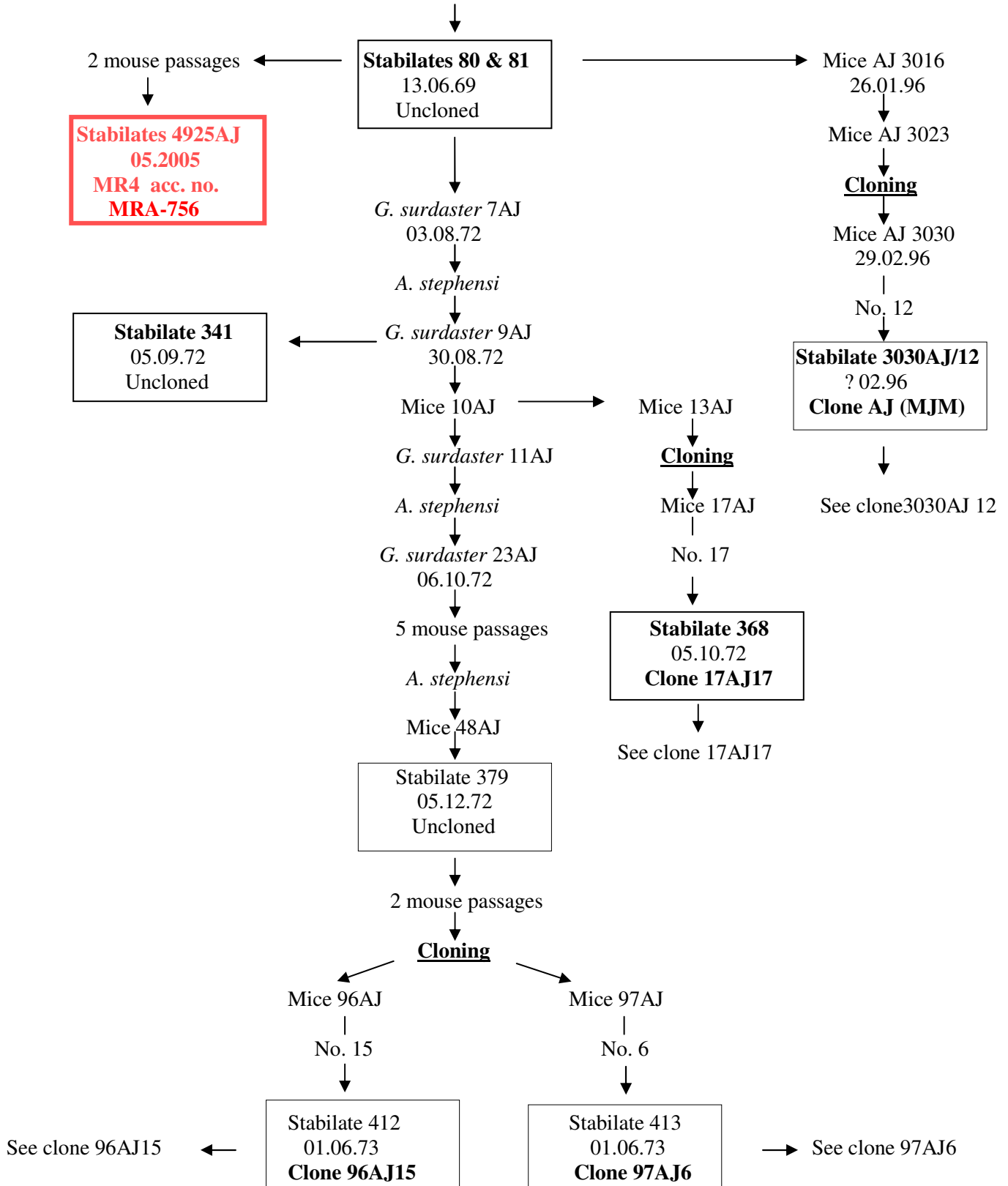
Clones derived from isolate AJ (166BY).



P. chabaudi chabaudi (Central African Republic)

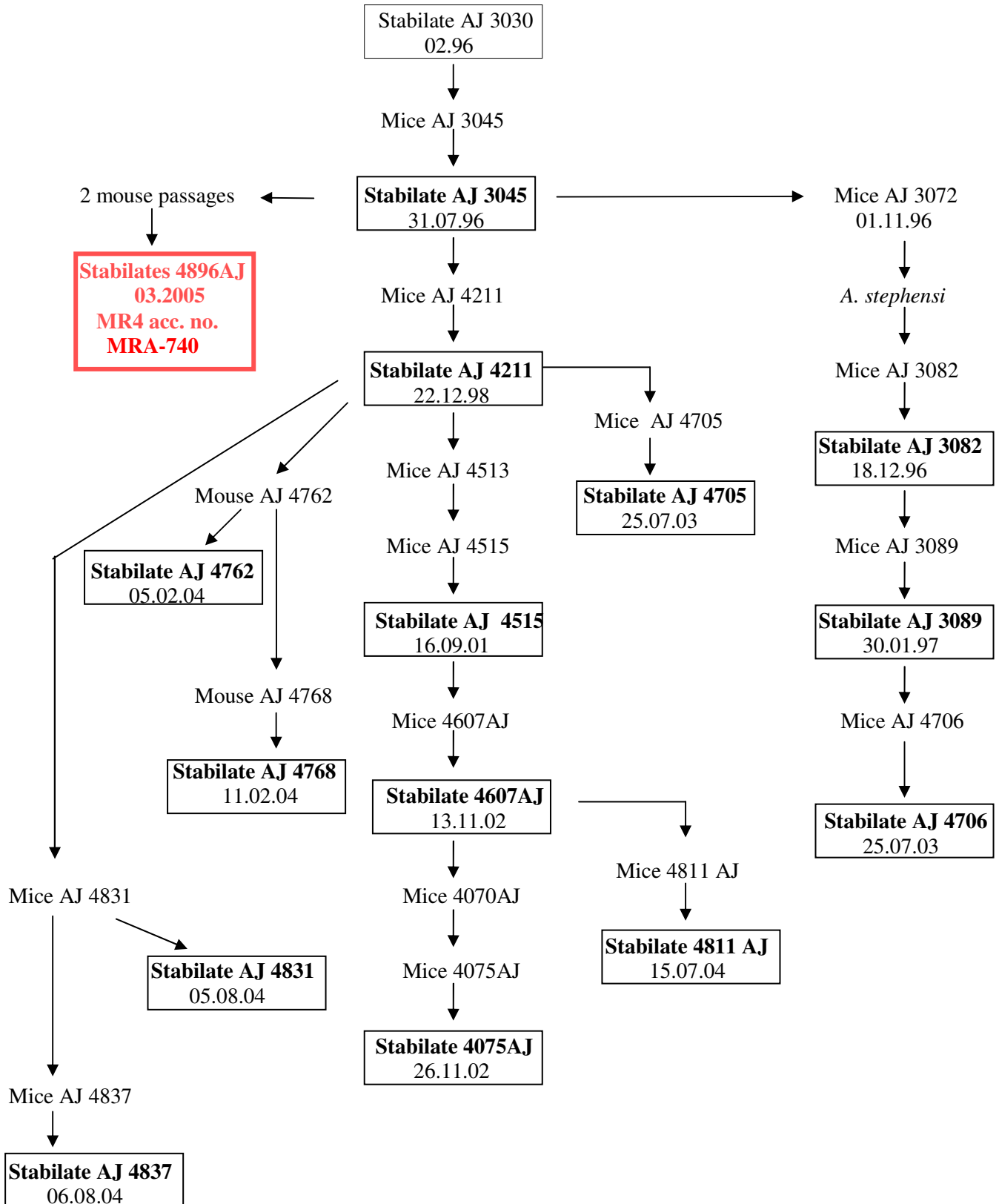
Isolate AJ (*P.c. chabaudi* and *P.v. petteri* visible)

T. rutilans no. 166BY, from Central African Republic
Sent by I. Landau (Paris) 19.03.69



P.c. chabaudi (Central African Republic)**Clone 3030AJ 12 (=AJ(MJM))**

See isolate AJ for previous history



P.c. chabaudi* (Central African Republic)*Clone 17AJ 17**

See isolate AJ for previous history

Stabilate 368 05.10.72 Clone 17AJ17

***P.c. chabaudi* (Central African Republic)**

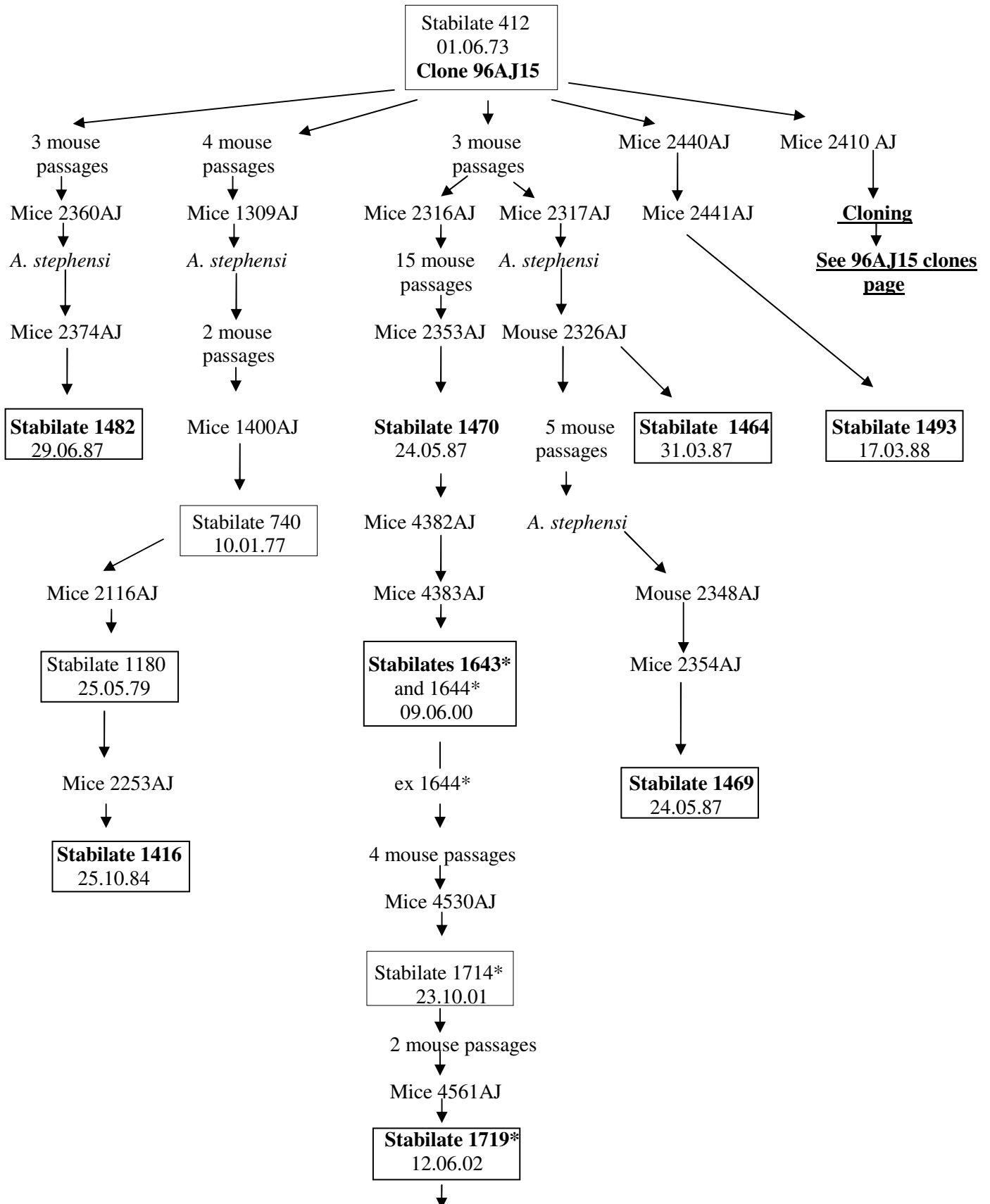
Clone 97AJ 6

See isolate AJ for previous history

Stabilate 413 01.06.73 Clone 97AJ6
--

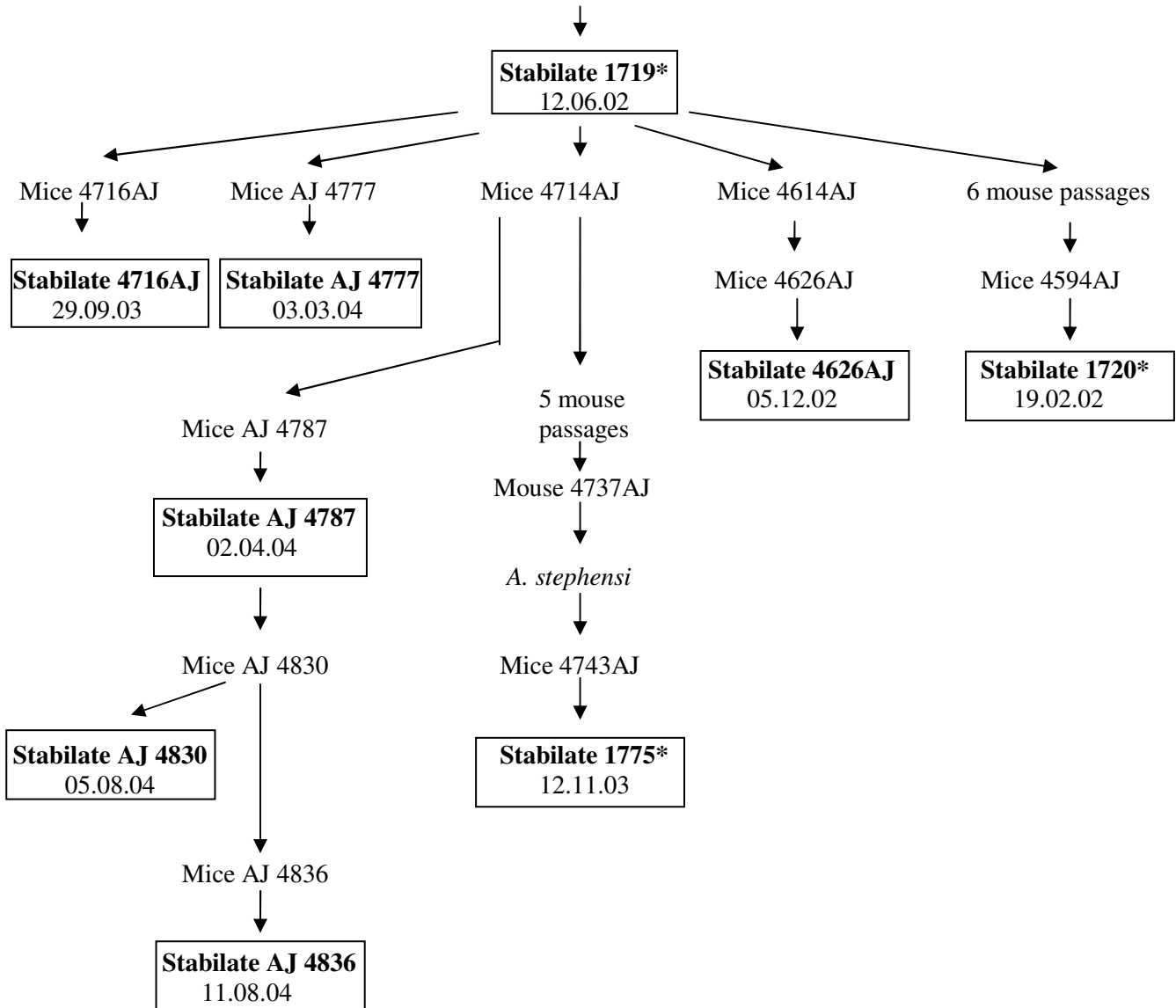
P.c. chabaudi (Central African Republic)**Clone 96AJ15**

See isolate AJ for previous history



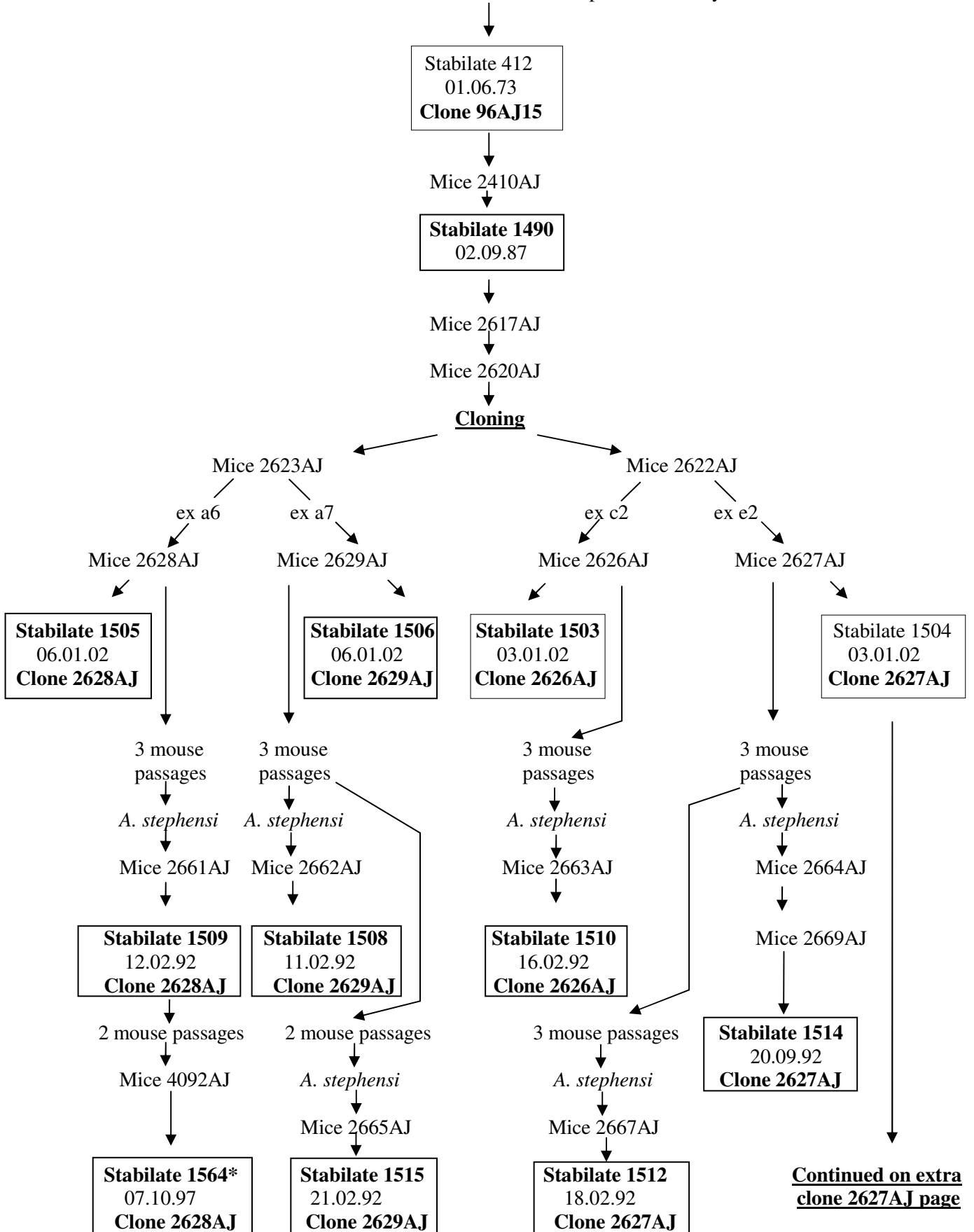
P.c. chabaudi : clone 96AJ 15 (continued)

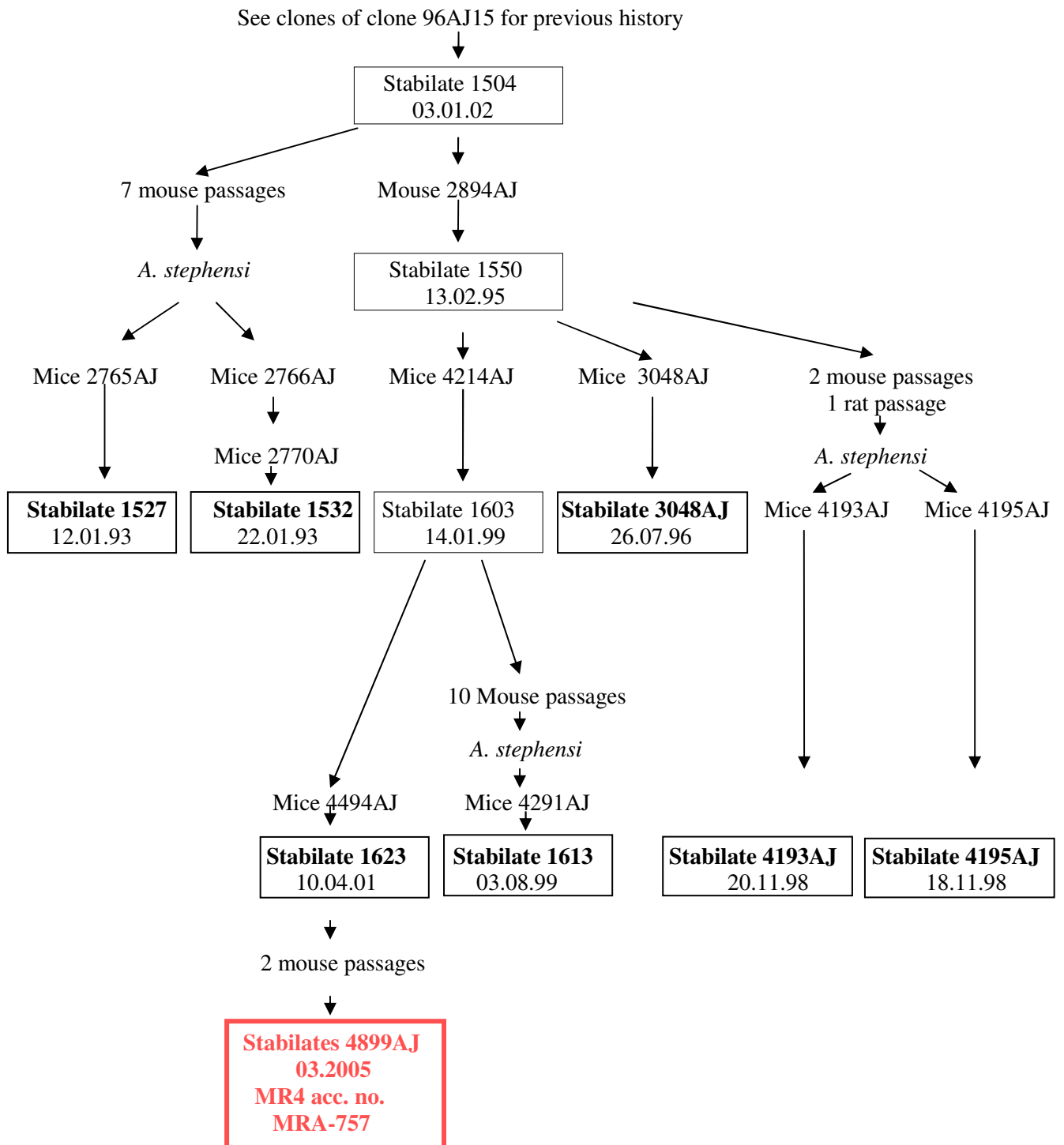
See previous page for history



P.c. chabaudi: clones of clone 96AJ15 - origins and passages of clones 2626AJ, 2627AJ, 2628AJ and 2629AJ

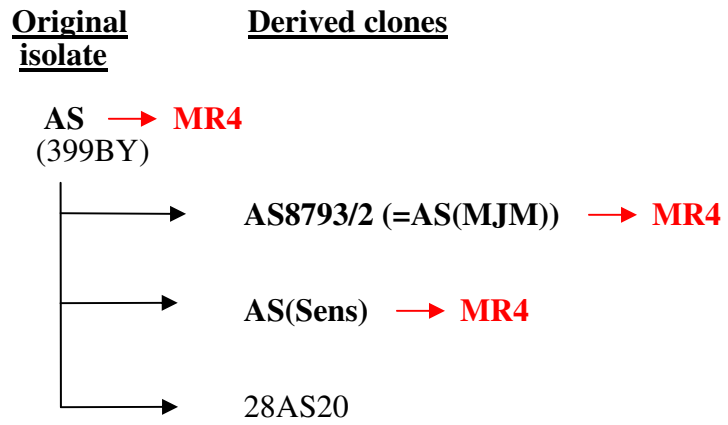
See isolate AJ and clone 96AJ15 for previous history



Clone 2627AJ (= clone of 96AJ15) continued

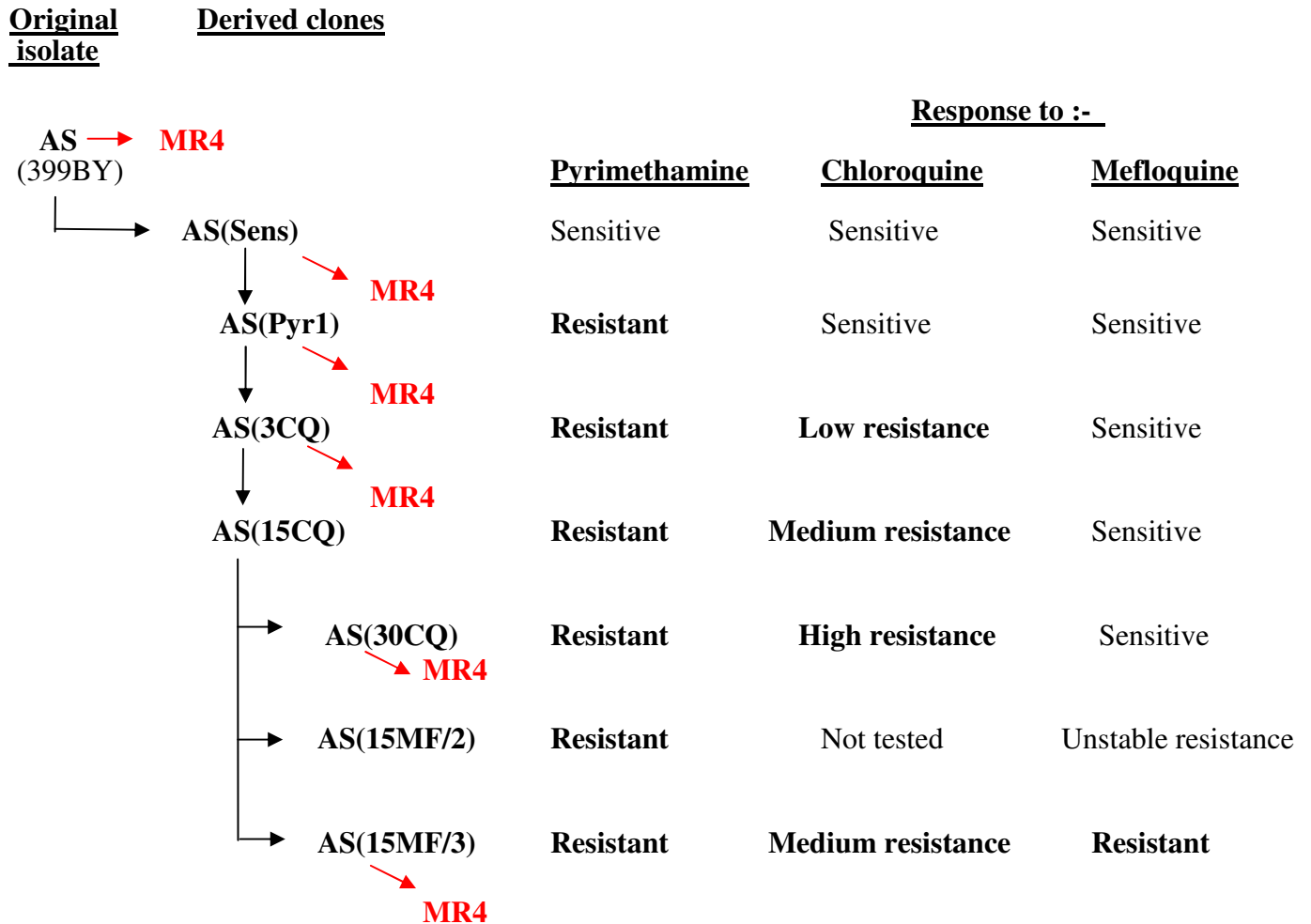
***P. chabaudi chabaudi* (Central African Republic)**

Clones (drug-sensitive) derived from isolate AS.



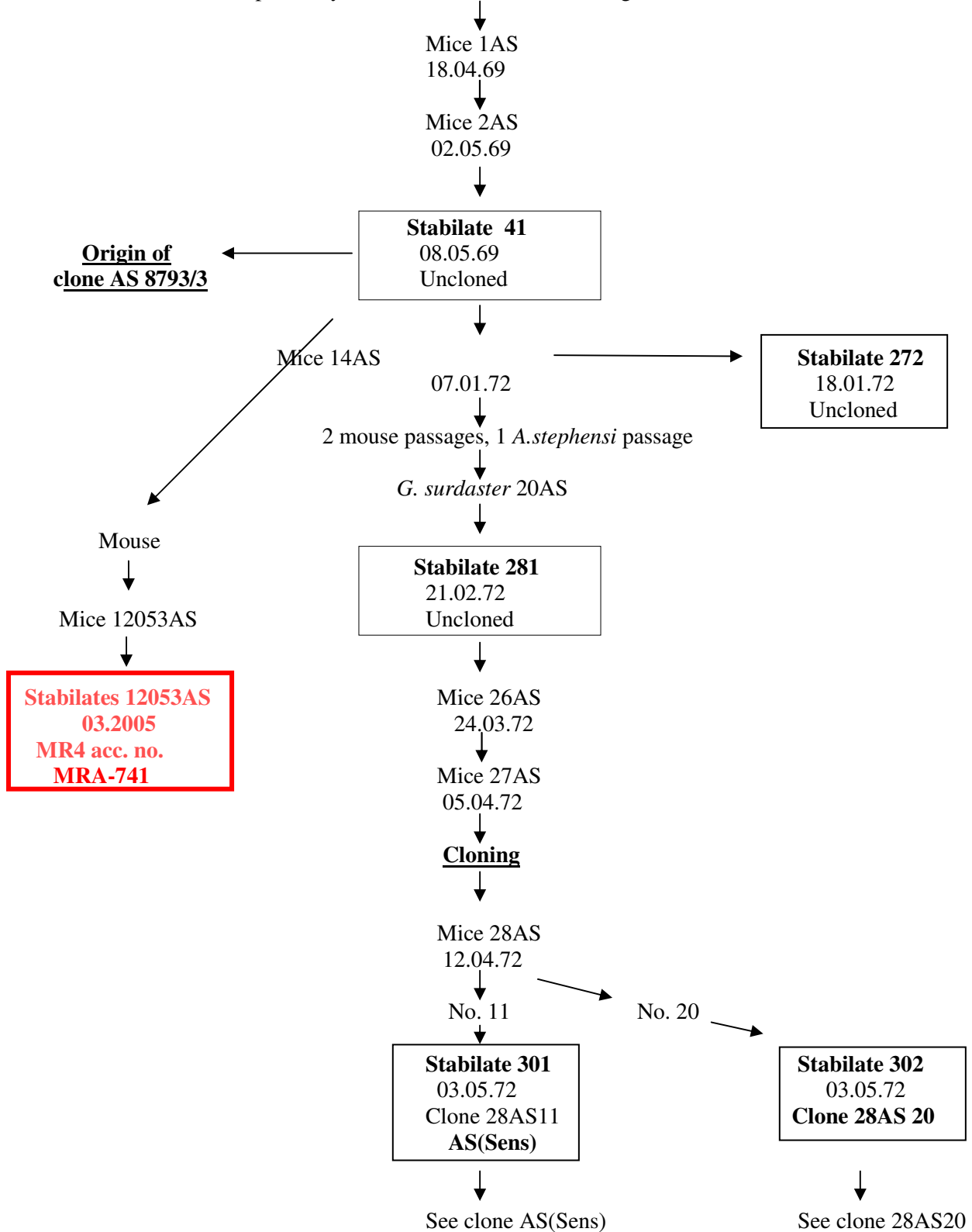
P. chabaudi chabaudi (Central African Republic)Clones resistant to pyrimethamine and to pyrimethamine/sulfadoxine (S/P), derived from clone AS (Sens)

<u>Original isolate</u>	<u>Derived clones</u>	<u>Response to :-</u>		
		<u>Pyrimethamine</u>	<u>Sulfadoxine</u>	<u>Sulfadoxine pyrimethamine (S/P)</u>
AS (399BY) → MR4	AS(Sens)	Sensitive	Resistant	Sensitive
	→ 42AS37	Resistant	Not tested	Not tested
	→ AS(Pyr1) → MR4	Resistant	Sensitive	Low resistance
	→ AS(50S/P) → MR4	Resistant	Low resistance	Resistant
	→ AS(75S/P)	Resistant	Low resistance	Resistant
	→ AS(Pyr2)	Resistant	Not tested	Not tested
	→ AS(Pyr3)	Resistant	Not tested	Not tested
	→ AS(Pyr4)	Resistant	Not tested	Not tested
	→ AS(Pyr5)	Resistant	Not tested	Not tested
	→ AS(Pyr6)	Resistant	Not tested	Not tested
	→ AS(Pyr7)	Resistant	Not tested	Not tested
	→ AS(Pyr8)	Resistant	Not tested	Not tested

P. chabaudi chabaudi* (Central African Republic)*Clones resistant to chloroquine and to mefloquine, derived from clone AS(Pyr1),**

P. chabaudi chabaudi (Central African Republic)**Isolate AS** (only *P.c. chabaudi* visible)

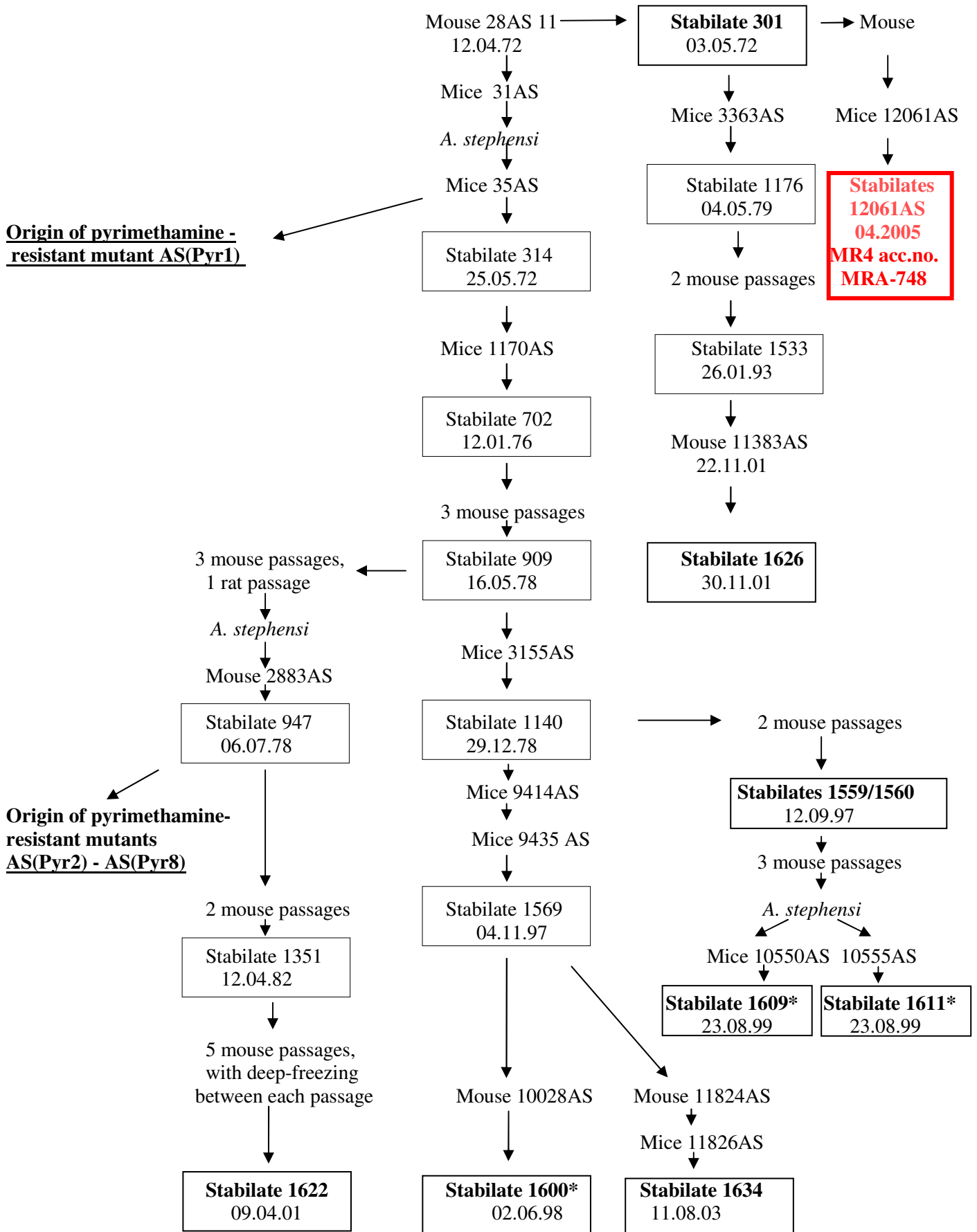
Thamnomys rutilans 399BY from La Maboké field station, CAR.
 Captured by Y. Boulard. Arrived Edinburgh 18.04.69



P. chabaudi chabaudi (Central African Republic)

Clone AS(Sens)

For previous history, see isolate AS

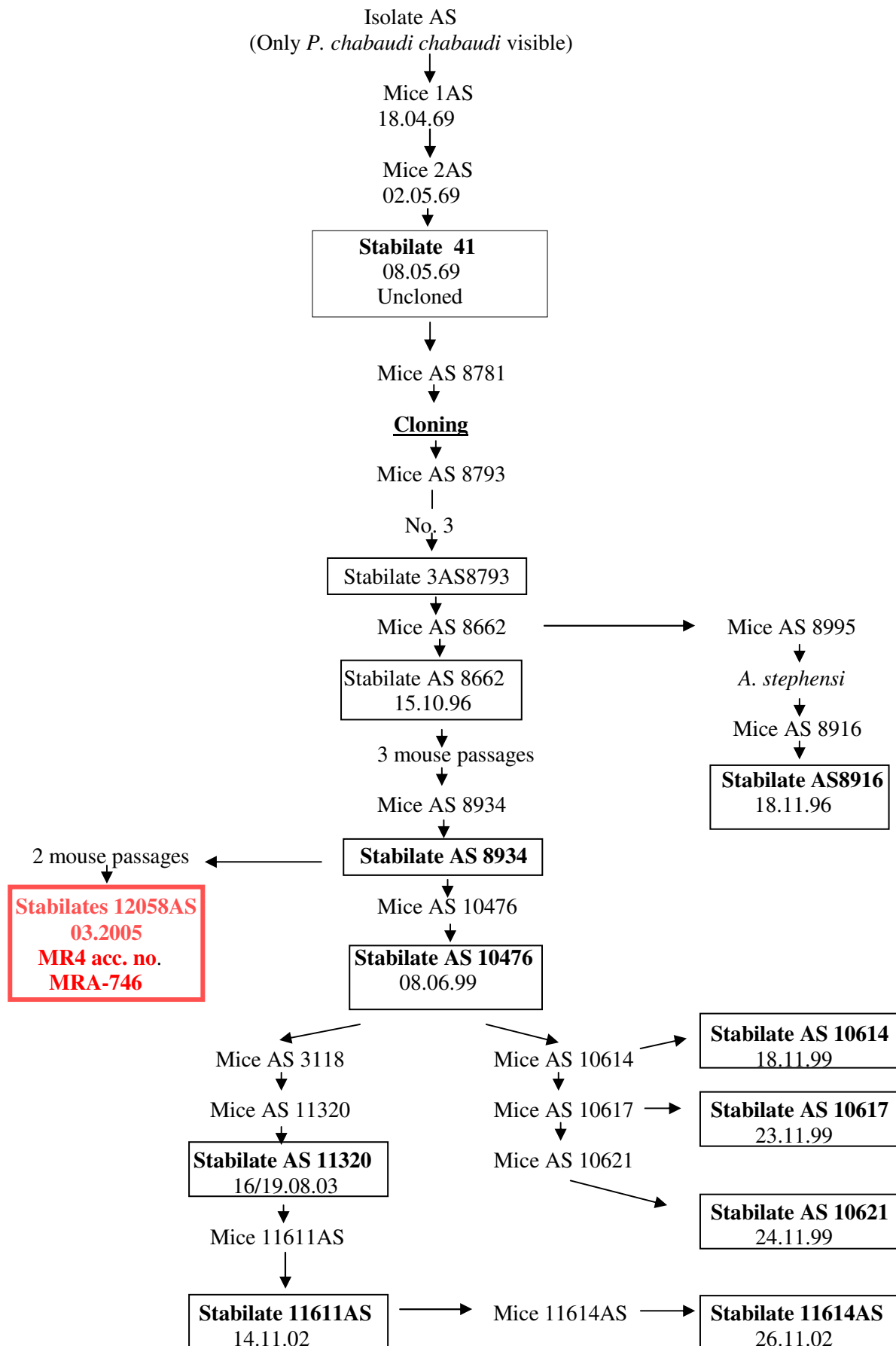


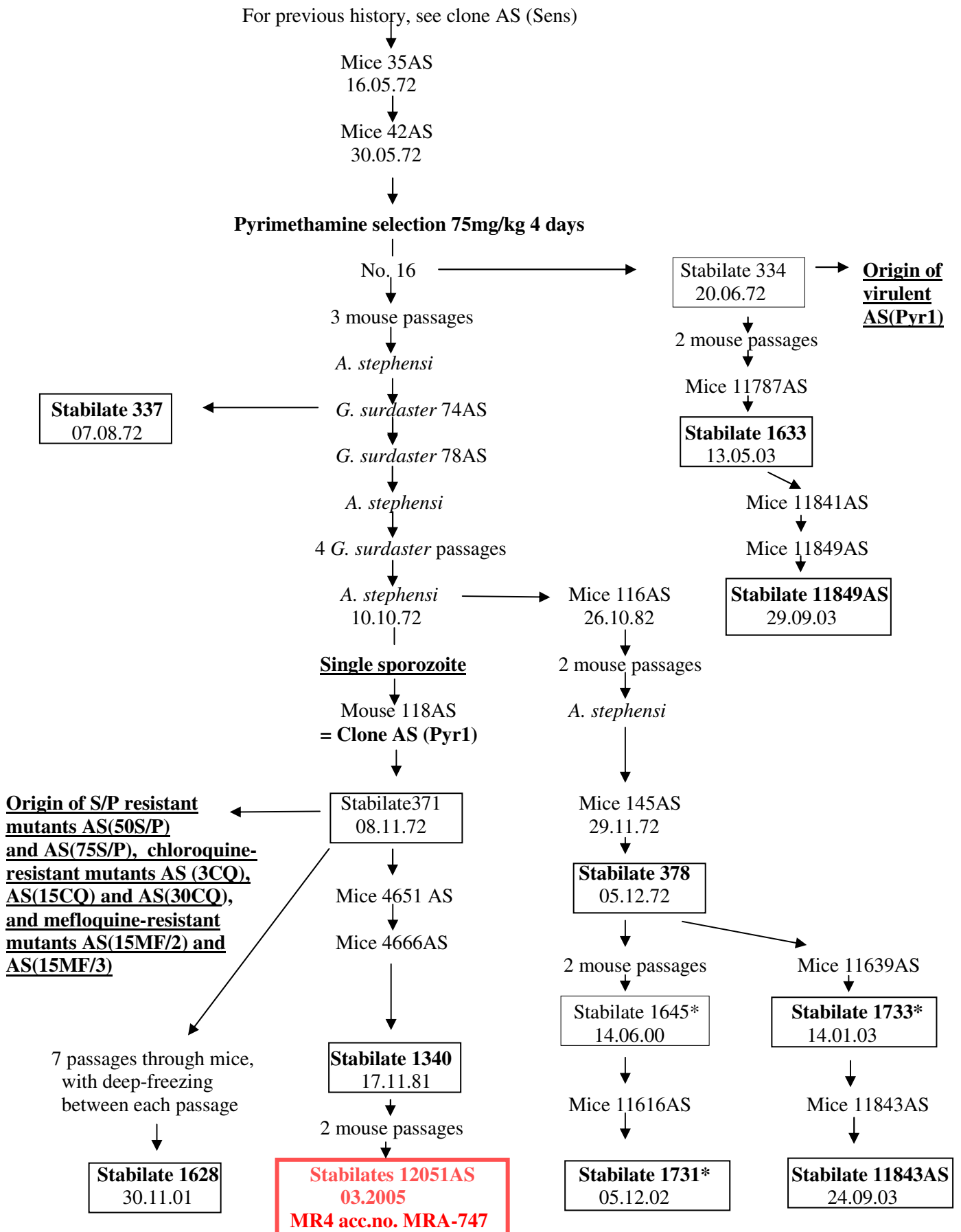
***P. c. chabaudi* (Central African Republic)**

Clone 28AS20

For previous history, see isolate AS (399BY)

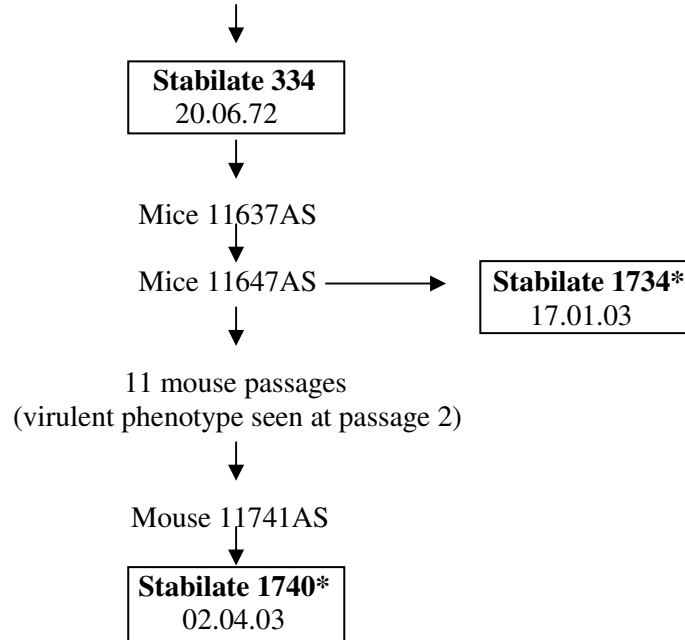
<p>Stabilate 302 03.05.72 Clone 28AS 20</p>

P. c. chabaudi (Central African Republic)**Clone AS 8793/3 (=AS(MJM))**

P. c. chabaudi (Central African Republic)**Clone AS(Pyr1)** (pyrimethamine-resistant)

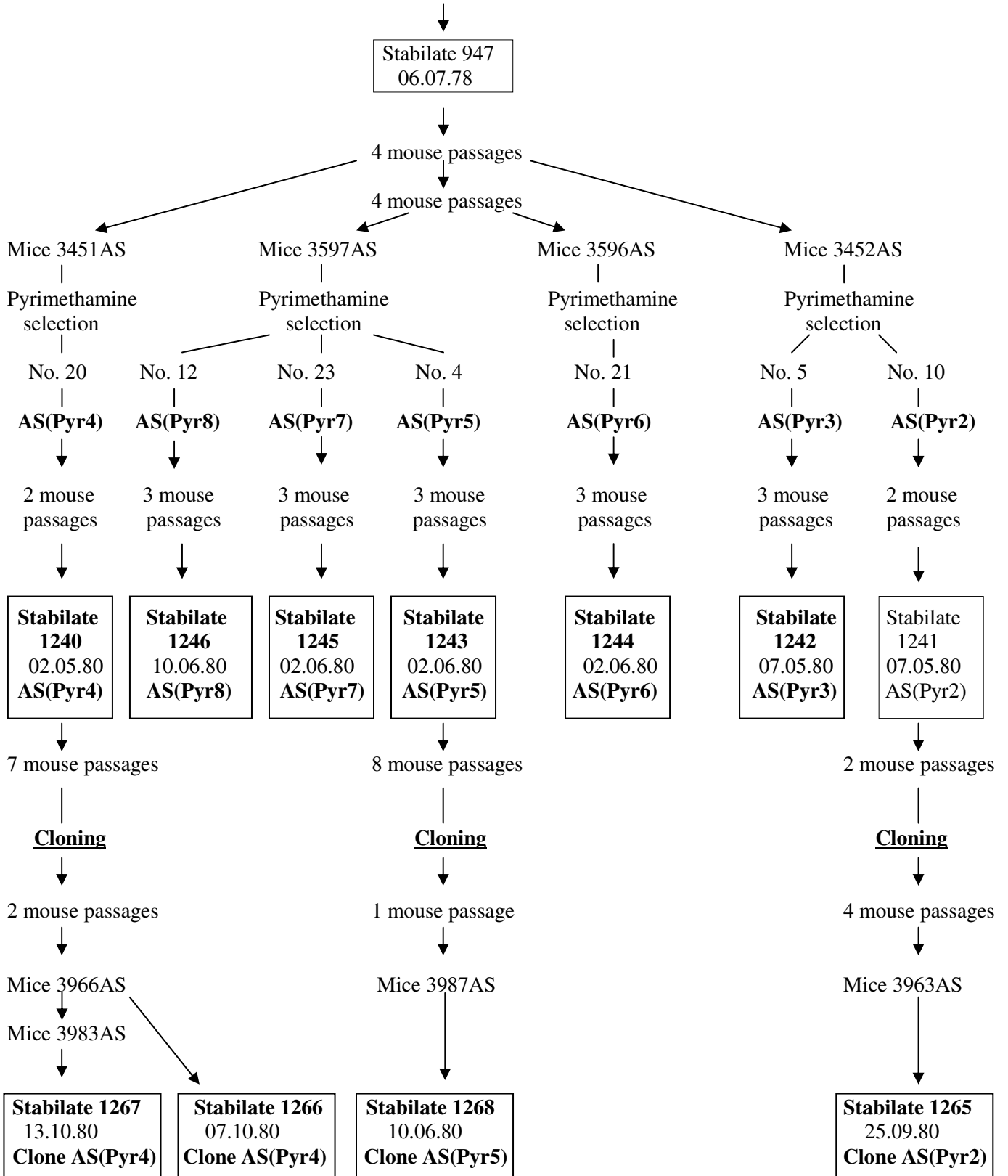
P. c. chabaudi* (Central African Republic)*Clone AS(Pyr1) - origin of virulent form**

For previous history, see clone AS (Pyr1)



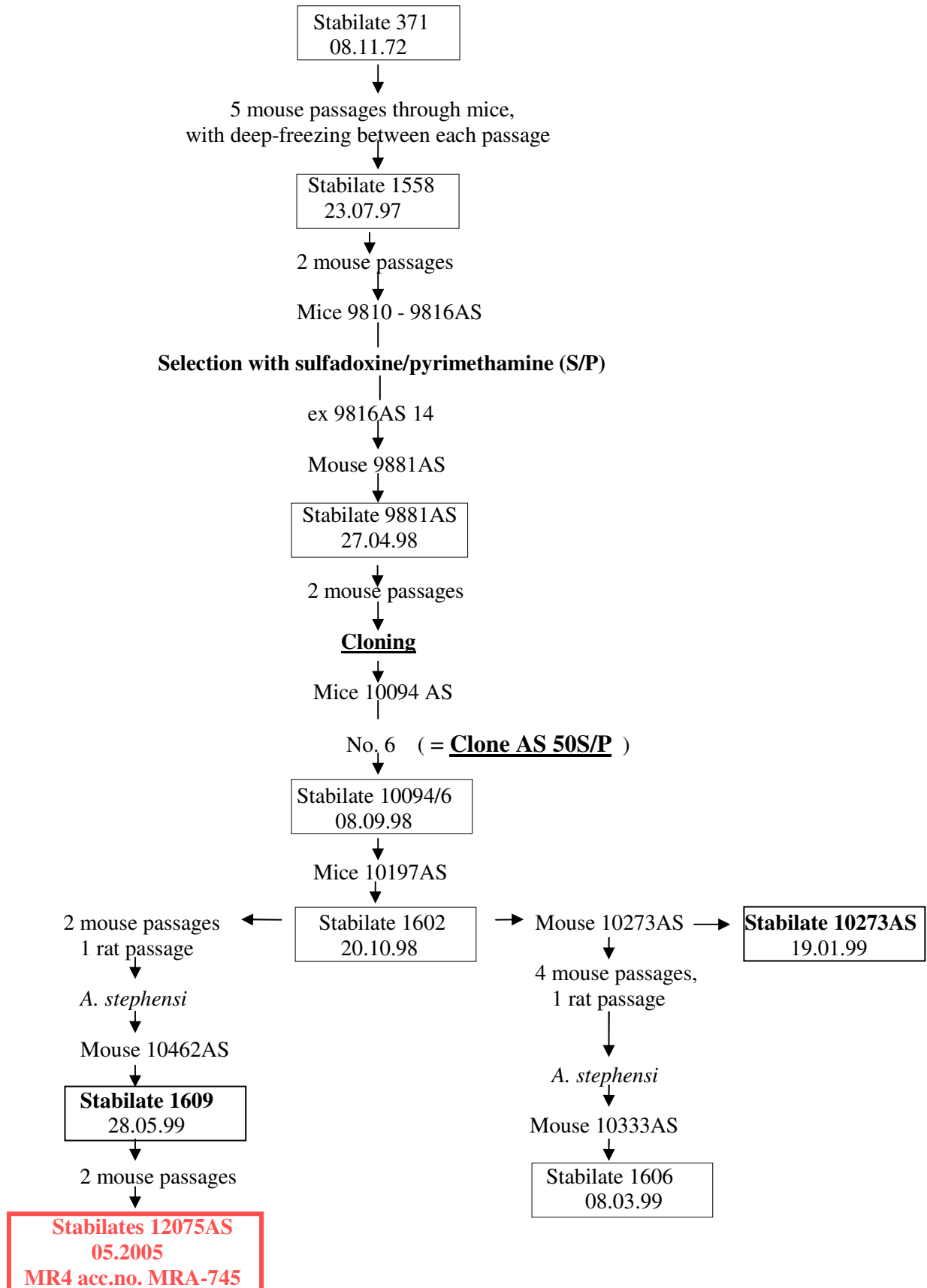
P. c. chabaudi (Central African Republic)**Clones AS(Pyr2) – AS(Pyr8) (pyrimethamine-resistant)**

For previous history, see clone AS (Sens)



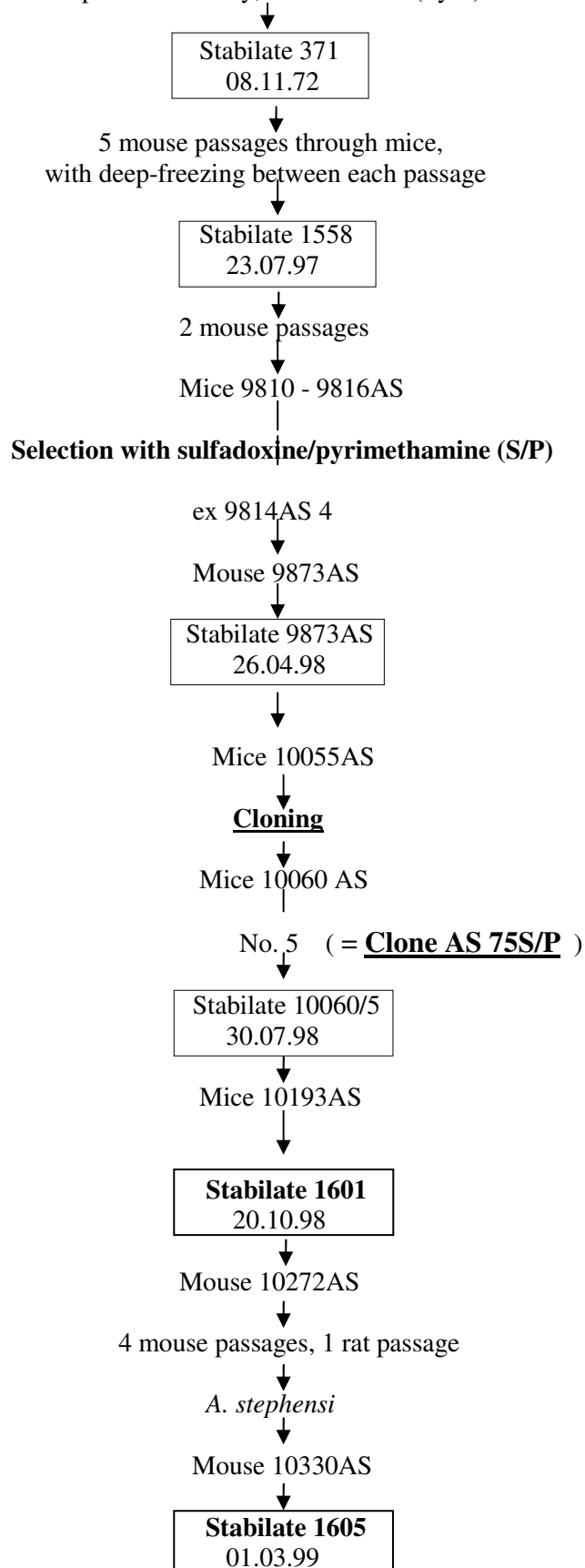
P. c. chabaudi (Central African Republic)**Clone AS(50S/P)** (sulfadoxine-pyrimethamine resistant)

For previous history, see clone AS (Pyr1)



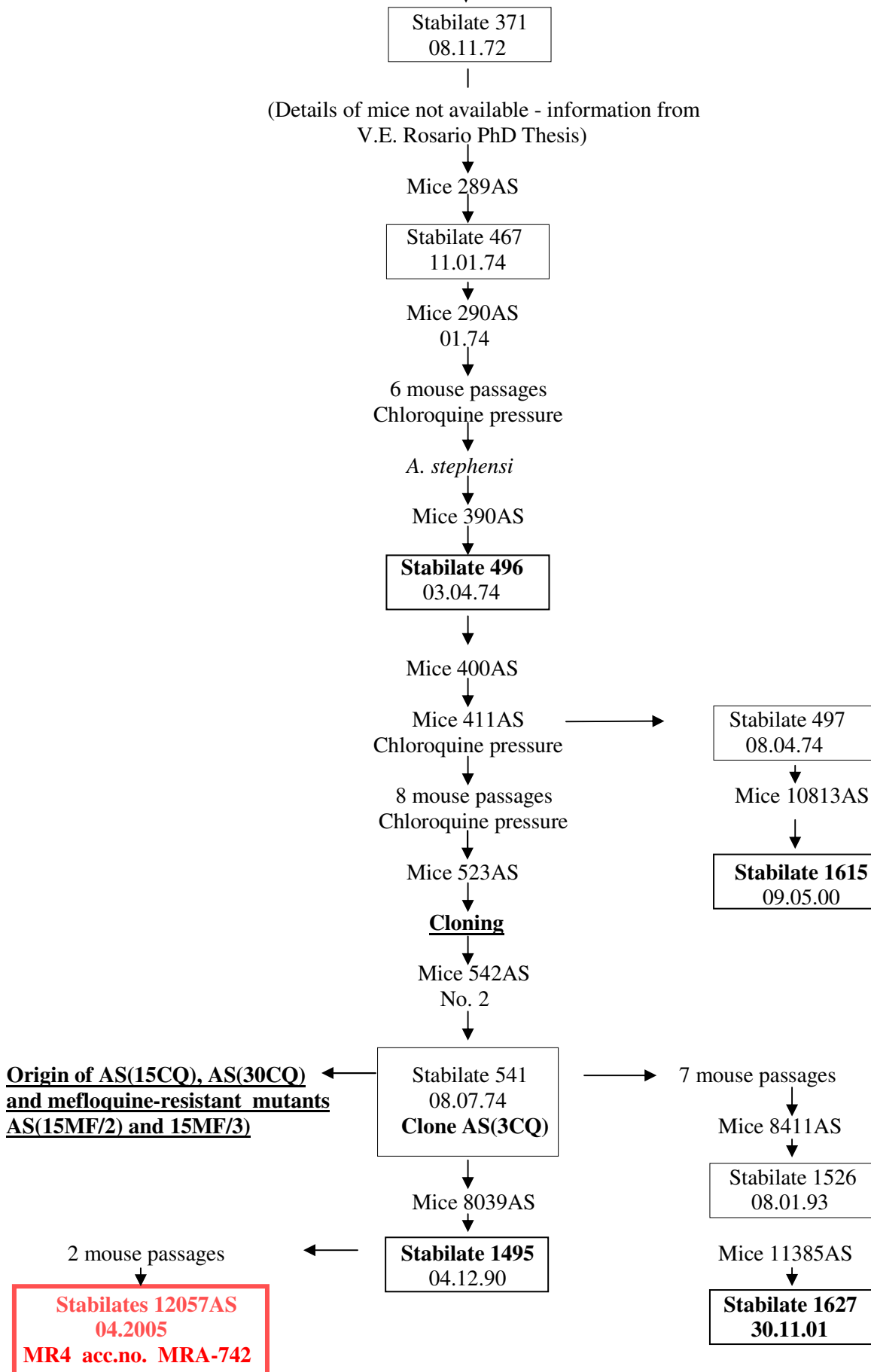
P. c. chabaudi (Central African Republic)**Clone AS(75S/P)** (sulfadoxine-pyrimethamine resistant)

For previous history, see clone AS (Pyr1)



Clone AS(3CQ) (chloroquine-resistant)

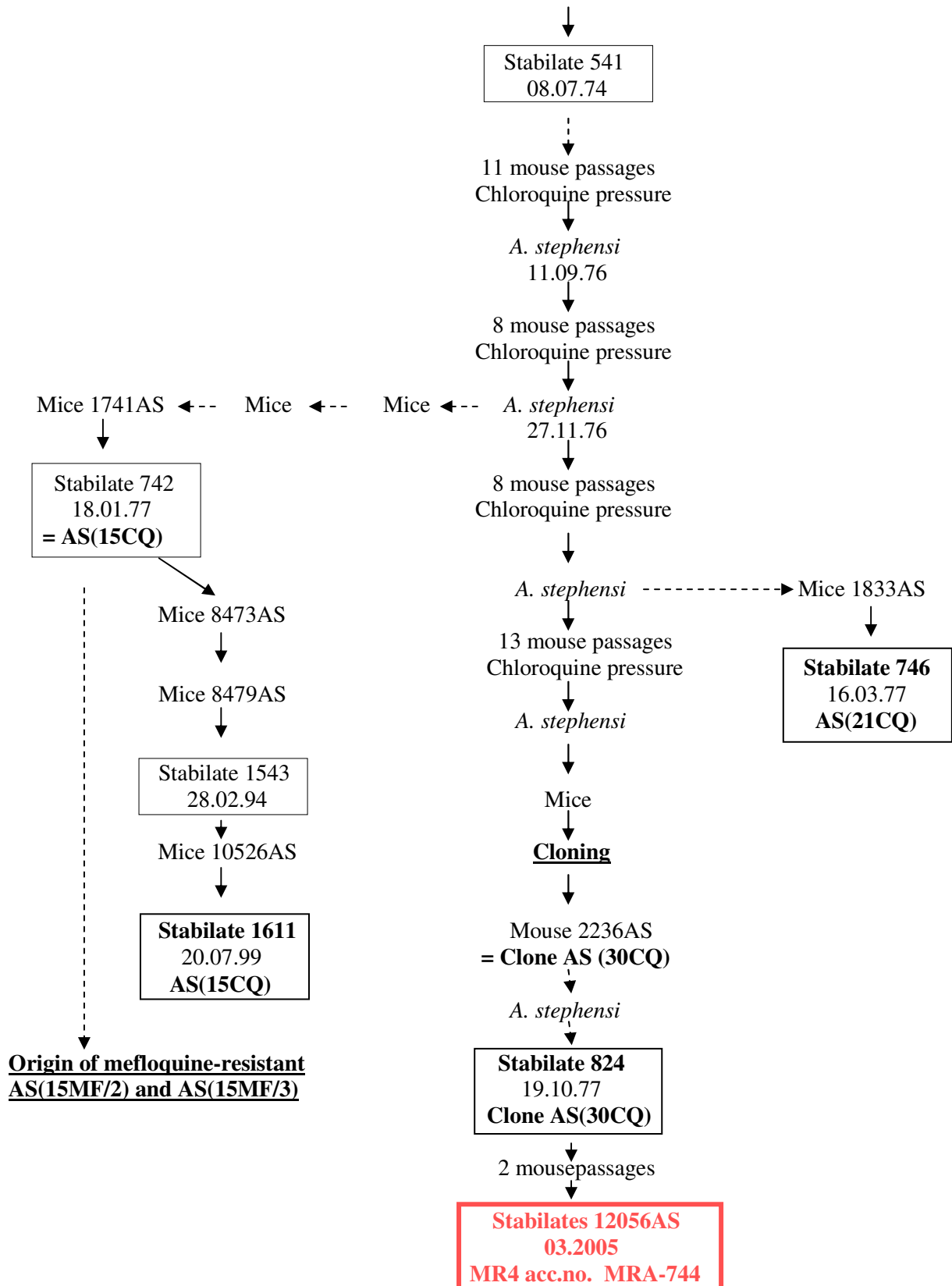
For previous history, see clone AS (Pyr1)



Clones AS(15CQ), AS(21CQ) and AS(30CQ) (chloroquine-resistant)

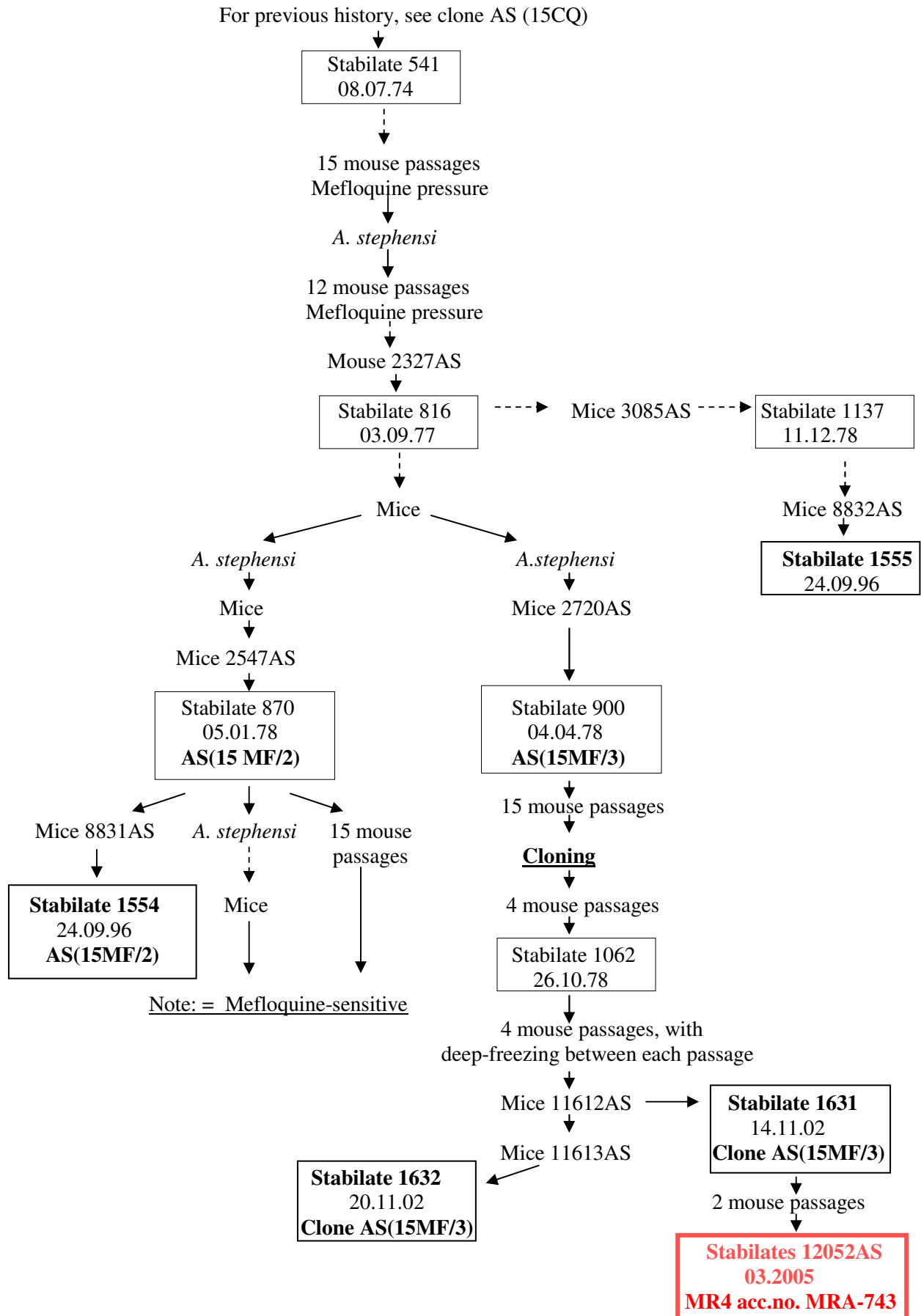
Information from R.A. Padua, PhD Thesis. Note: details of passages marked - - - - not available

For previous history, see clone AS (3CQ)



Clones AS(15MF/2) and clone AS(15MF/3) (mefloquine-resistant)

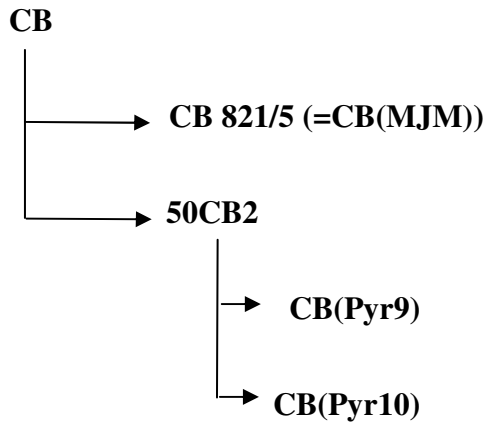
Information from R.A. Padua, PhD Thesis. Note: details of passages marked - - - - not available



***P. chabaudi chabaudi* (Central African Republic)**

Clones derived from isolate CB.

Original isolate **Derived clones**



P. chabaudi chabaudi (Central African Republic)

Isolate CB (only *P.c. chabaudi* visible)

Thamnomys rutilans from La Maboké field station, CAR.

Arrived Edinburgh 25.09.70. Denoted 1CB

↓
G. surdaster 2CB

↓

Stabilate 143 09.10.70

→ **Origin of clone CB821/5 (=CB(MJM))**

↓
 5 mouse, 1 *A. stephensi* passages

↓
 Mice 10CB

↓

Stabilates 387, 388 14.12.72
--

↓
 Mice 49CB

Cloning

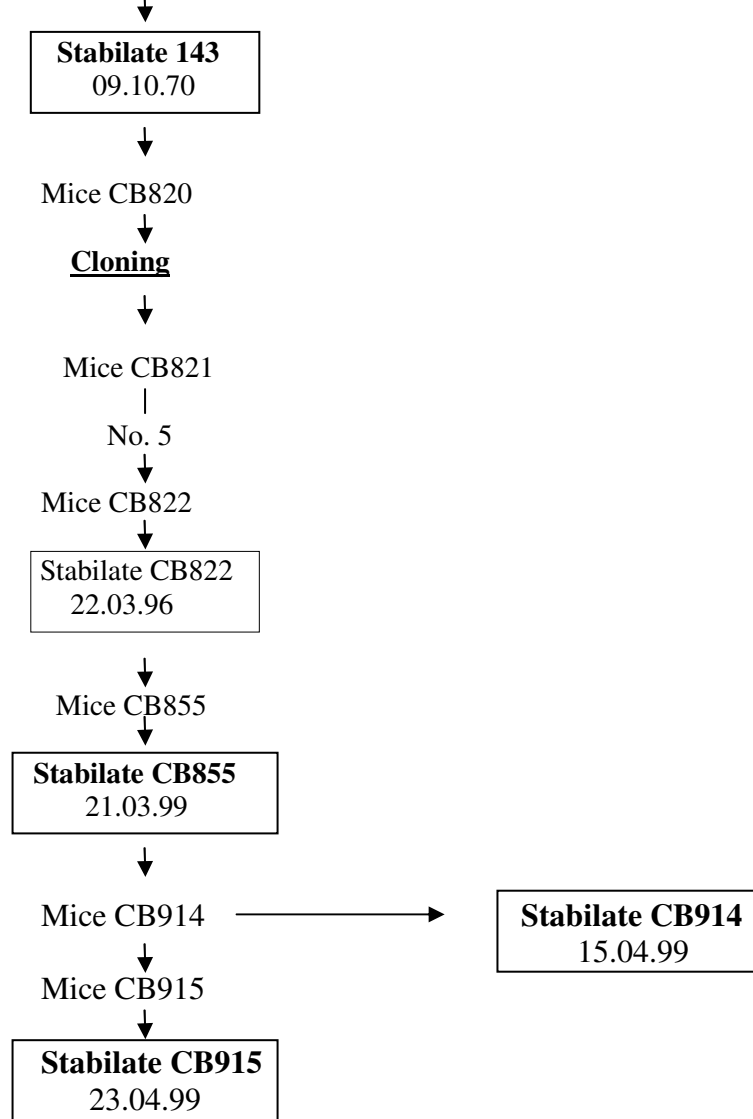
↓
 Mice 50CB

↓
Origin of clone 50CB2

P. chabaudi chabaudi (Central African Republic)

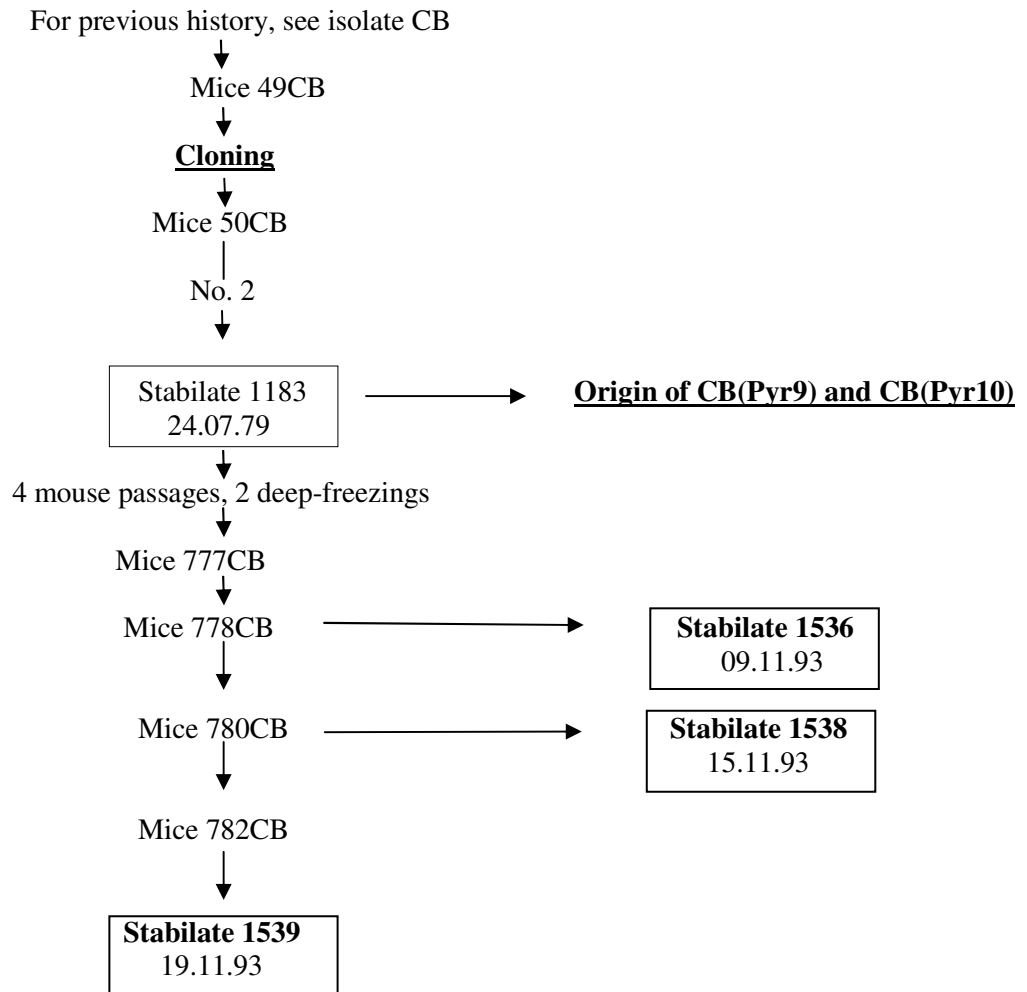
Clone CB 821/5 (=CB(MJM))

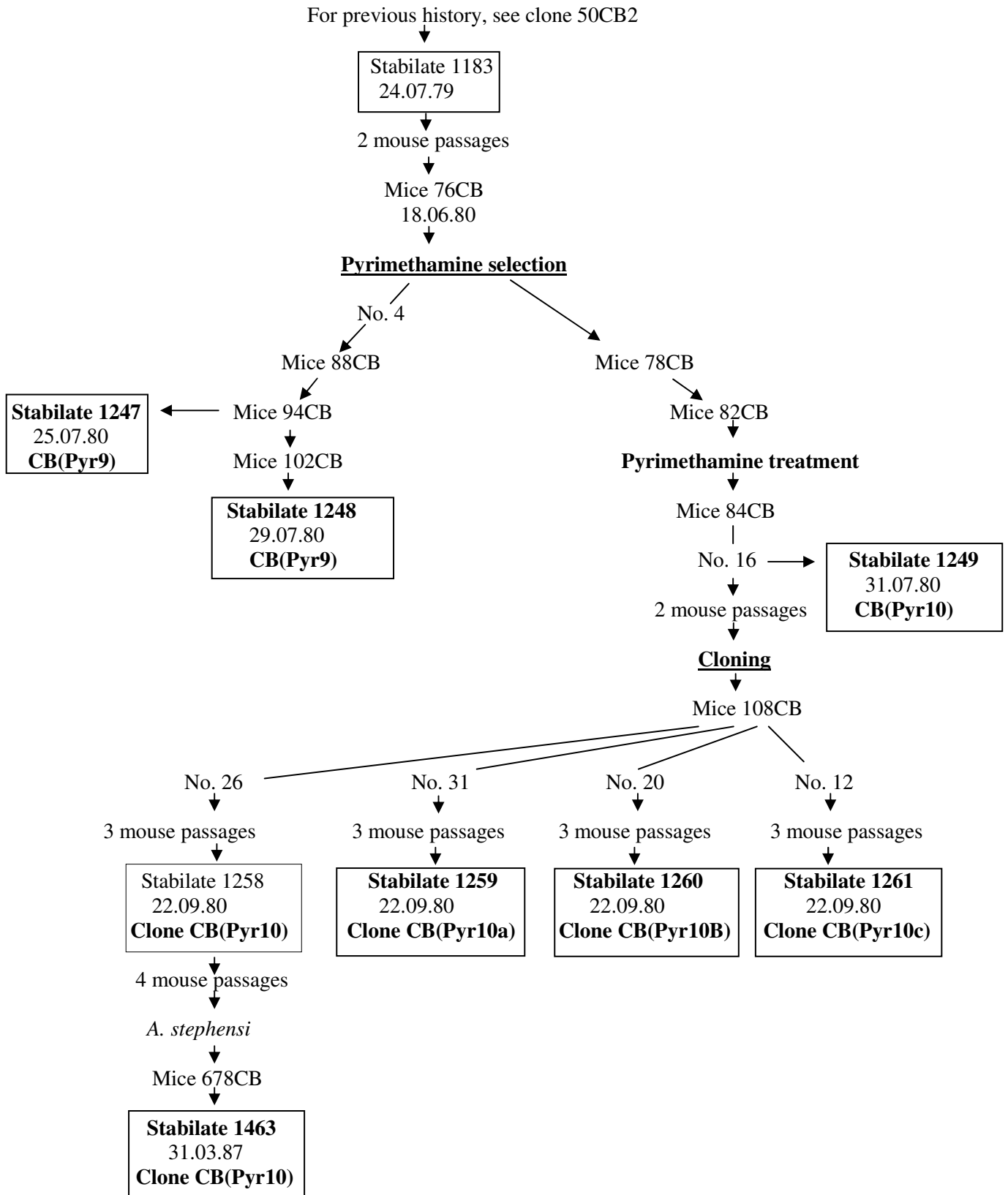
For previous history, see isolate CB



P. chabaudi chabaudi (Central African Republic)

Clone 50CB2

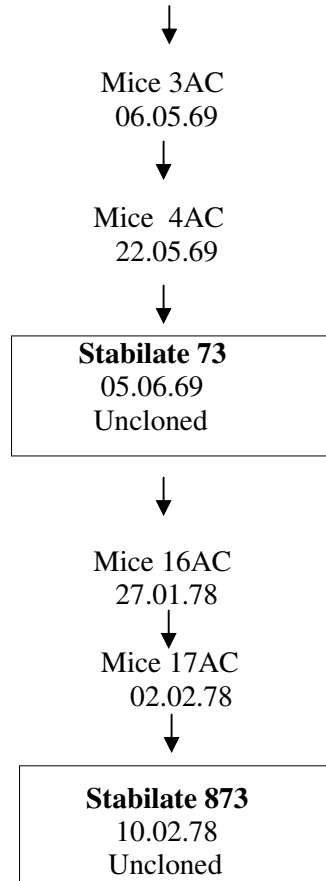


P. chabaudi chabaudi (Central African Republic)**Clones CB(Pyr9) and CB(Pyr10) - pyrimethamine-resistant**

P. chabaudi chabaudi (Central African Republic)

Isolate AC (only *P. c. chabaudi* visible)

T. rutilans no. 20BY, from Central African Republic
Sent by I. Landau (Paris) 19.03.69



P. chabaudi chabaudi (Central African Republic)

Isolate AD (*P.c. chabaudi* and *P.y. yoelii* visible)

T. rutilans no. 29BY, from Central African Republic
Sent by I. Landau (Paris) 19.03.69

↓
Mice 2AD
11.04.69

↓
Stabilate 38
23.04.69
Uncloned

↓
Mice AD87 → Cloning → Origin of clone AD88/6

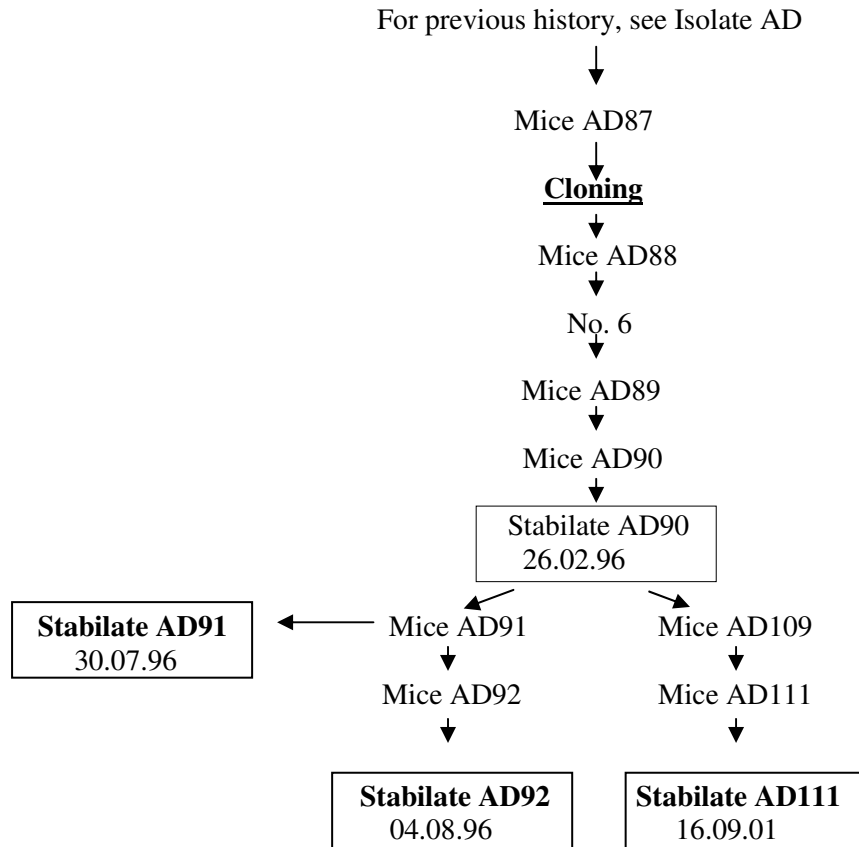
↓
Stabilate AD87
10.02.96

↓
Mice AD97

↓
Stabilate AD97
15.10.96

P. chabaudi chabaudi (Central African Republic)

Clone AD88/6



***P. chabaudi chabaudi* (Central African Republic)**

Isolate AF (*P.c. chabaudi* and *P.y. yoelii* visible)

T. rutilans no. 10BY, from Central African Republic
Sent by I. Landau (Paris) 19.03.69



G. surdaster 16AF
17.09.69

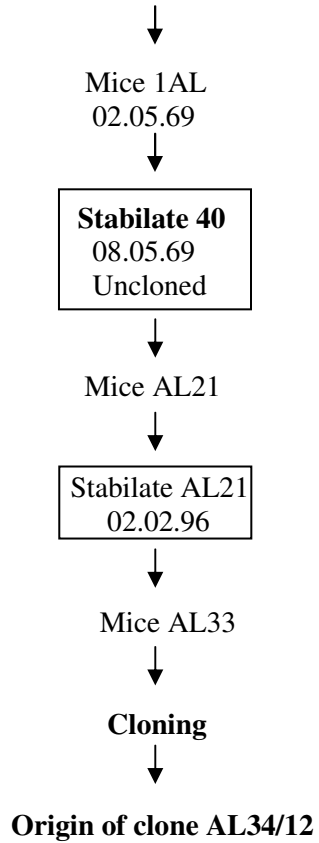


Stabilate 91 01.10.69 Uncloned

P. chabaudi chabaudi (Central African Republic)

Isolate AL (only *P.c. chabaudi* visible)

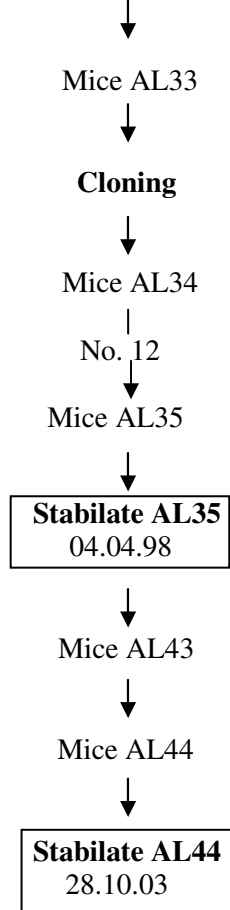
T. rutilans no. 326BY, Captured, Y. Boulard, CAR,
Sent by I. Landau (Paris) 18.04.69



***P. chabaudi chabaudi* (Central African Republic)**

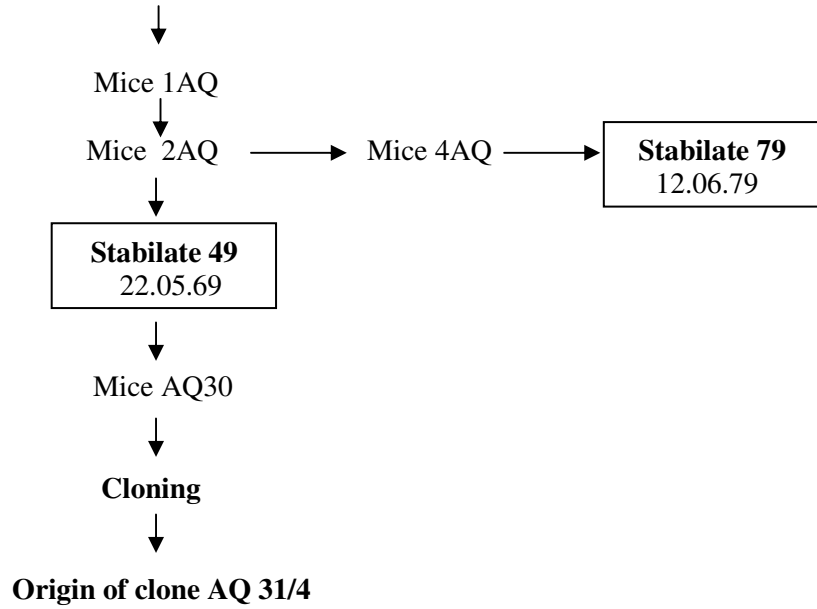
Clone AL34/12

For previous history, see Isolate AL



P. chabaudi chabaudi (Central African Republic)**Isolate AQ** (only *P.c. chabaudi* visible)

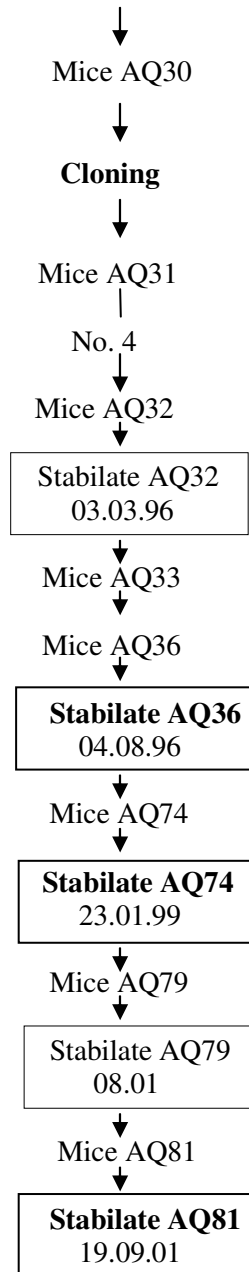
T. rutilans no. 288BY, from Central African Republic
Arrived Edinburgh 18.04.69



P. chabaudi chabaudi (Central African Republic)

Clone AQ31/4

For previous history, see Isolate AQ



P. chabaudi chabaudi (Central African Republic)

Isolate AT (only *P.c. chabaudi* visible)

T. rutilans no. 87BY, from Central African Republic
Arrived Edinburgh 26.03.69



G. surdaster 4AT
18.07..69



Stabilate 88
01.08.69
Uncloned



Mice AT18



Mice AT19



Cloning



Stabilate AT18
22.01.96

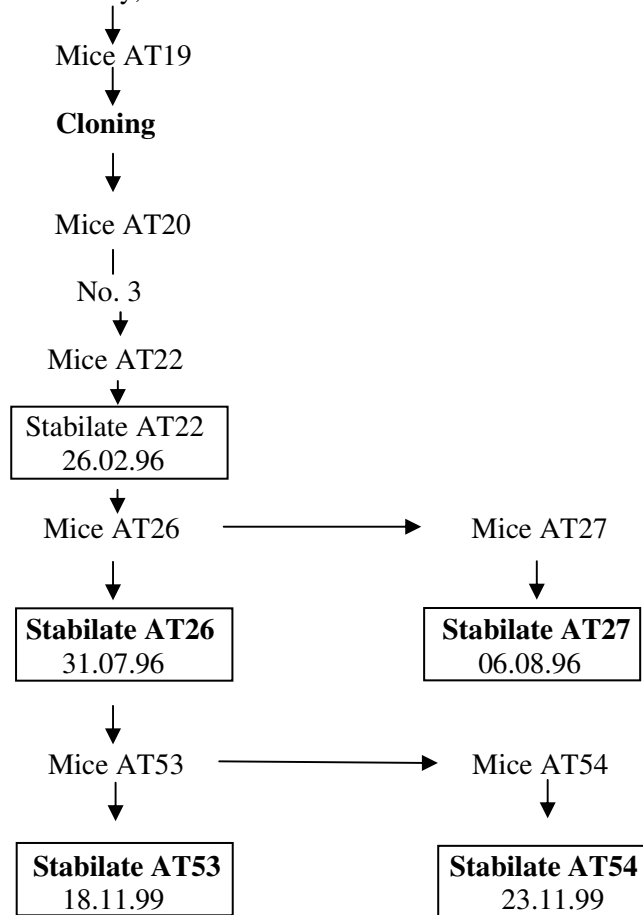


Origin of clone AT 20/3

P. chabaudi chabaudi (Central African Republic)

Clone AT20/3

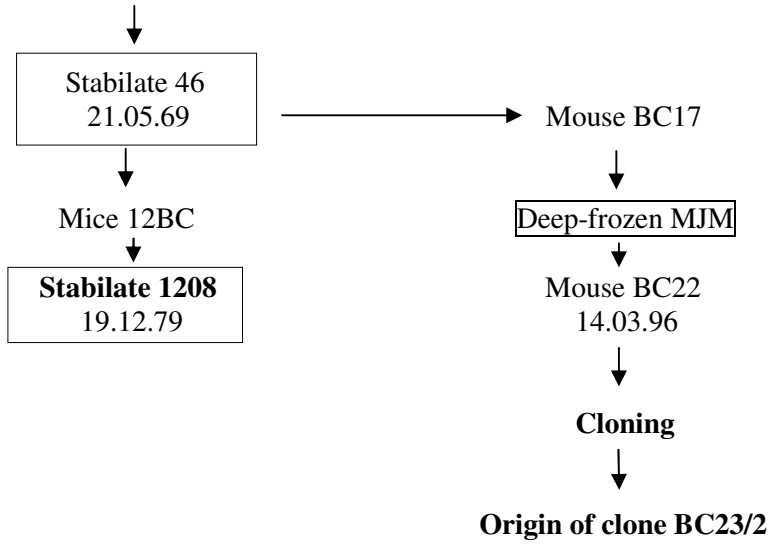
For previous history, see isolate AT



P. chabaudi chabaudi (Central African Republic)

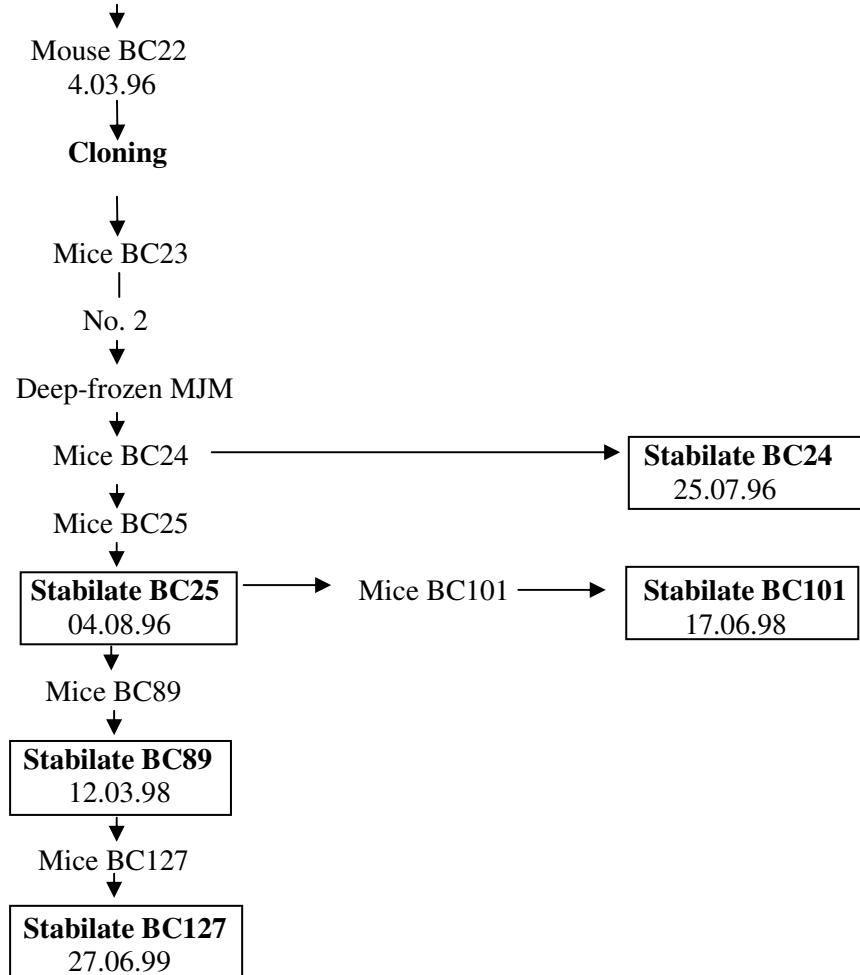
Isolate BC (contains *P.c. chabaudi* and *P.y. yoelii*)

T. rutilans no. 309, from Central African Republic
Sent by I. Landau (Paris), arrived 01.04.69
Named 1BC



P. chabaudi chabaudi* (Central African Republic)*Clone BC23/2**

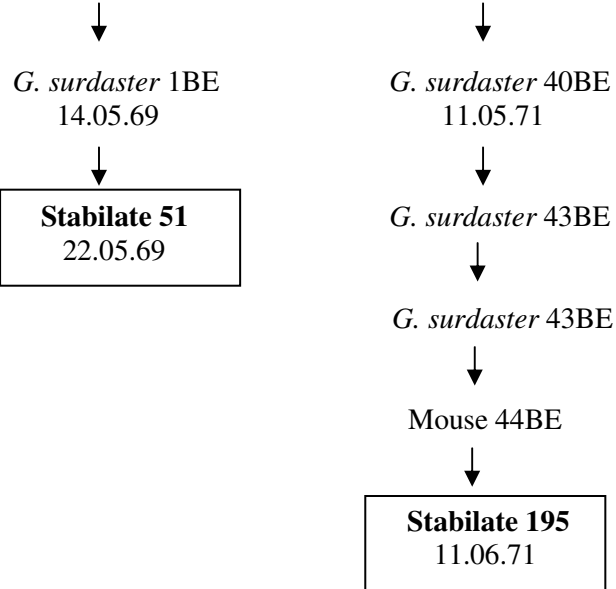
For previous history, see isolate BC



P. chabaudi chabaudi (Central African Republic)

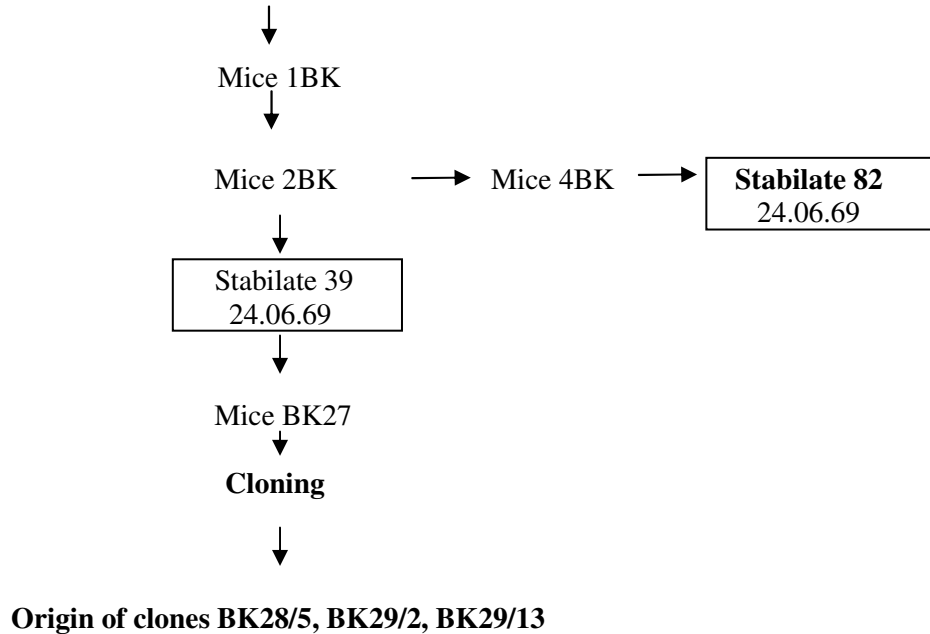
Isolate BE (contains *P.c. chabaudi* and *P.y. yoelii*)

T. rutilans no. 206BY, from Central African Republic
Sent by I. Landau (Paris), arrived 26.03.69.69



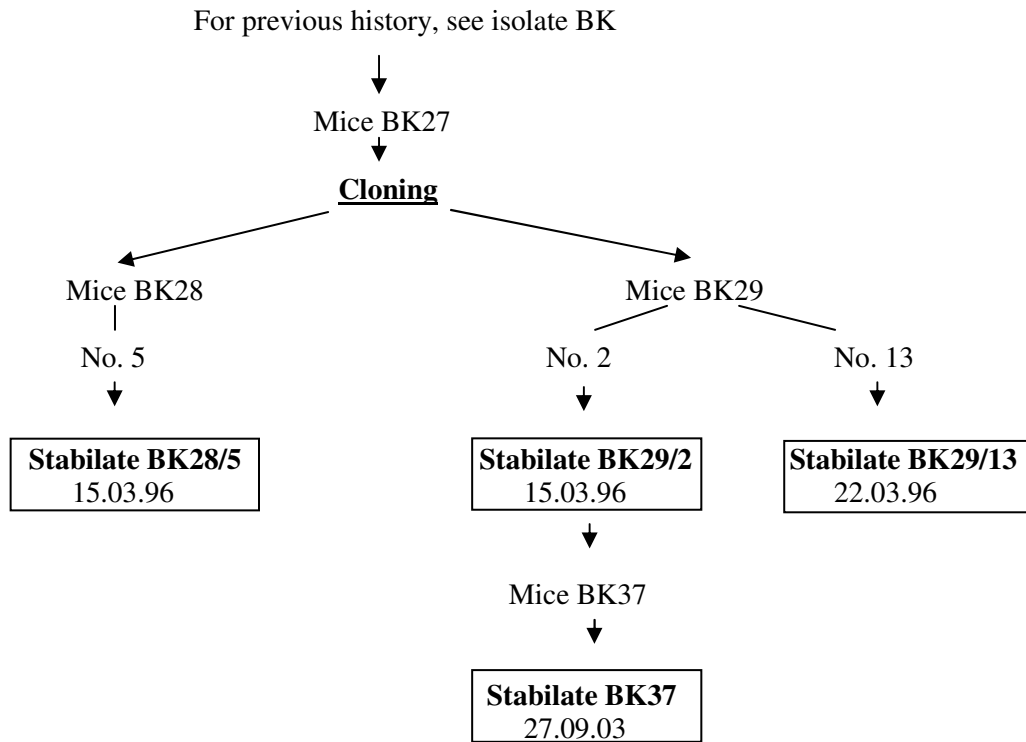
P. chabaudi chabaudi (Central African Republic)**Isolate BK** (only *P.c. chabaudi* visible)

T. rutilans no. 387BY, from Central African Republic
Sent by I. Landau (Paris), arrived 18.04.69



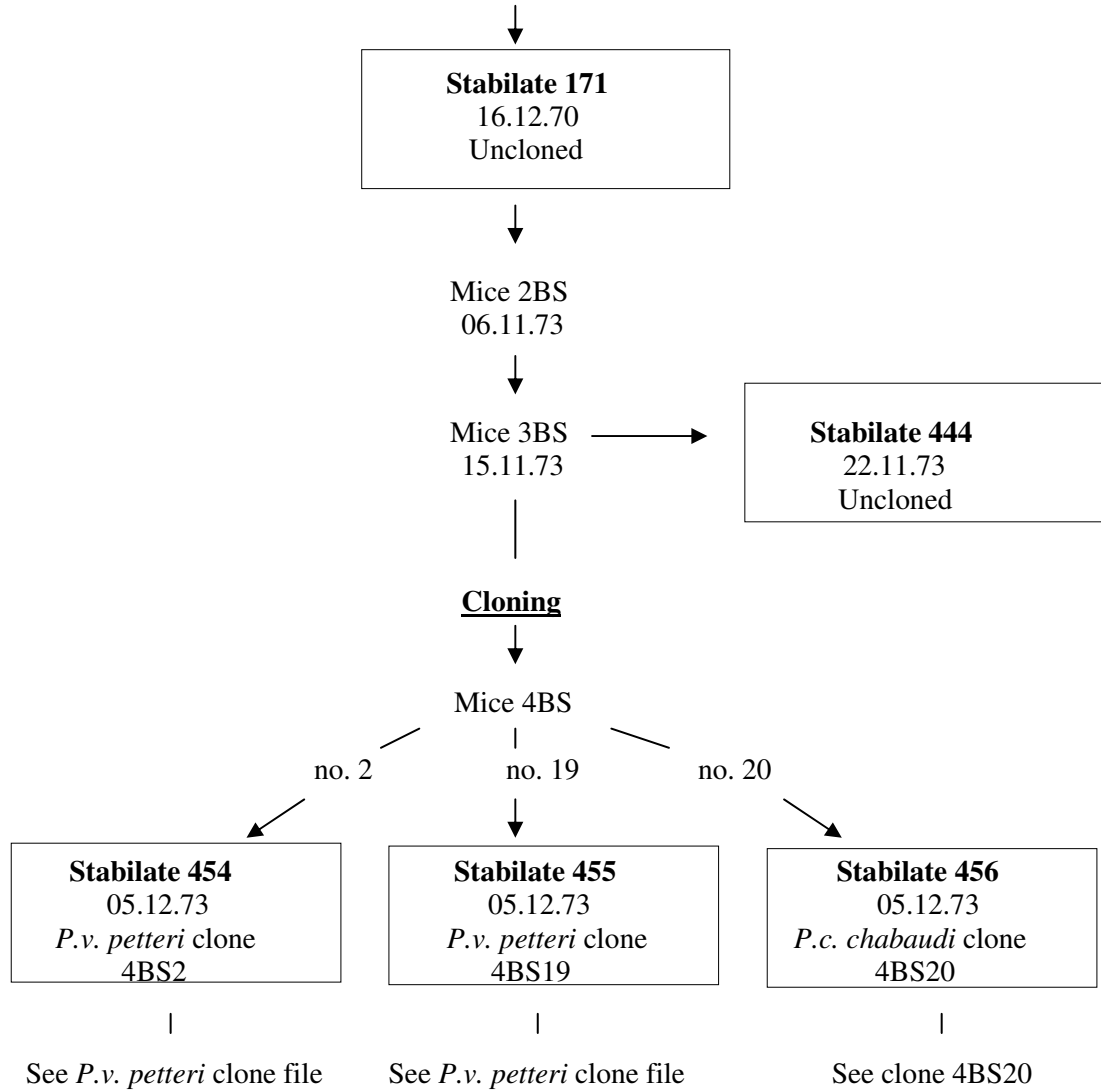
P. chabaudi chabaudi (Central African Republic)

Clones BK28/5, BK29/2, BK29/13



P. chabaudi chabaudi (Central African Republic)**Isolate BS** (contains *P.c. chabaudi* and *P. vinckei petteri*)

T. rutilans no. 3, from Central African Republic
Sent by I. Landau (Paris) 25.09.70
Named 1BS



***P. chabaudi chabaudi* (Central African Republic)**

Clone 4BS20

For previous history, see isolate BS

Stabilate 456

05.12.73

P.c. chabaudi clone

4BS20

P. chabaudi chabaudi (Central African Republic)**Isolate CE** (contains *P.c. chabaudi* and *P.v. petteri*)*T. rutilans* no. 15, from Central African Republic

Sent by I. Landau (Paris) 25.09.70

Named 1CE

Grammomys surdaster 2CE

25.9.70

Stabilate 135

05.10.70

Uncloned

Mice 6CE

21.09.72

3 mouse passages

Mice 10CE

03.11.72

A. stephensi

11.11.72

Mouse 12CE

27.11.72

Stabilate 382

05.12.72

Uncloned

Cloning

Mice 13CE

01.12.72

no. 8

Stabilate 389

19.12.72

Clone - ? *P.v.p.* or *P.c.c.*

no. 11

Stabilate 390

19.12.72

P.c. chabaudi clone 13CE11

no. 23

Stabilate 391

19.12.72

Clone - ? *P.v.p.* or *P.c.c.*

no. 39

Stabilate 392

19.12.72

Clone - ? *P.v.p.* or *P.c.c.*

no. 37

Stabilate 393

19.12.72

Clone - ? *P.v.p.* or *P.c.c.*

no. 41

Stabilate 394

19.12.72

Clone - ? *P.v.p.* or *P.c.c.*

See clone 13CE11

***P. chabaudi chabaudi* (Central African Republic)**

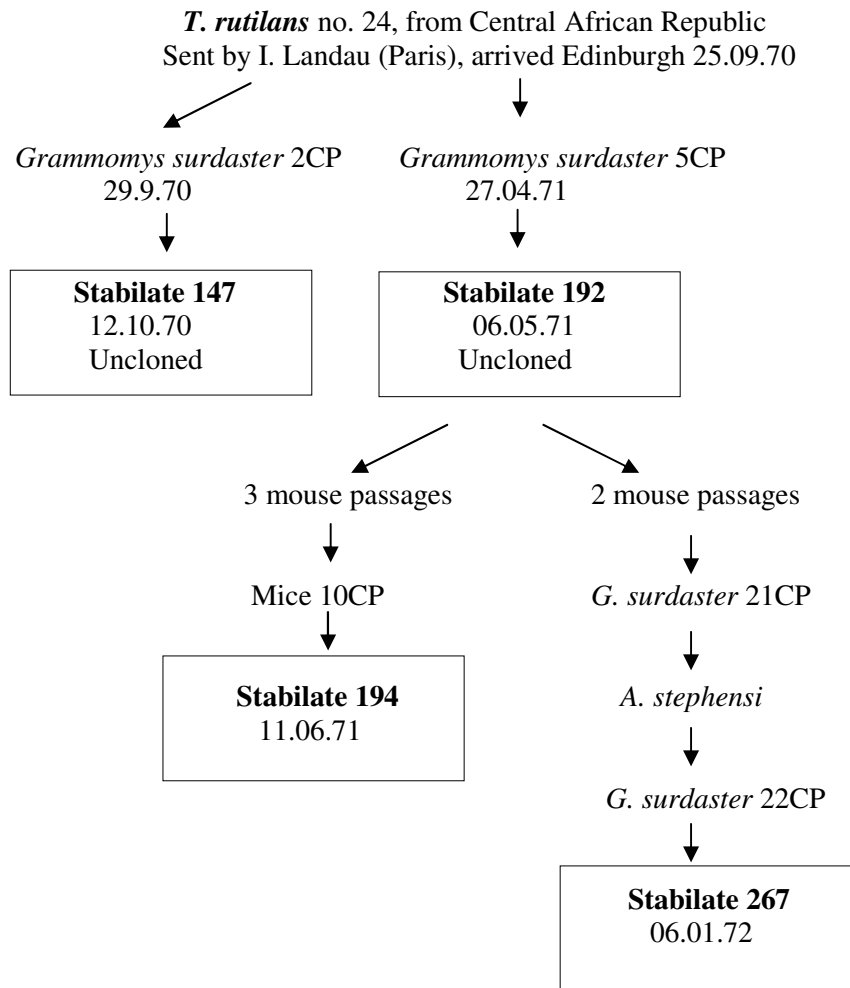
Clone 13CE11

For previous history, see isolate CE

<p>Stabilate 390 19.12.72 <i>P.c.chabaudi</i> clone 13CE11</p>

***P. chabaudi chabaudi* (Central African Republic)**

Isolate CP (contains *P.c. chabaudi*, *P. v. petteri* and *P.y. yoelii*)



P. chabaudi chabaudi (Central African Republic)

Isolate CQ (may contain *P.c. chabaudi* and *P. v. petteri*)

T. rutilans no. 25, from Central African Republic

Sent by I. Landau (Paris) 25.09.70

Named 1CQ



Grammomys surdaster 2CQ

25.9.70



Stabilate 147

12.10.70

Uncloned



Mice CQ20



Stabilate CQ20

16.04.98



Mice CQ21



Mice CQ22

15.05.98



Cloning

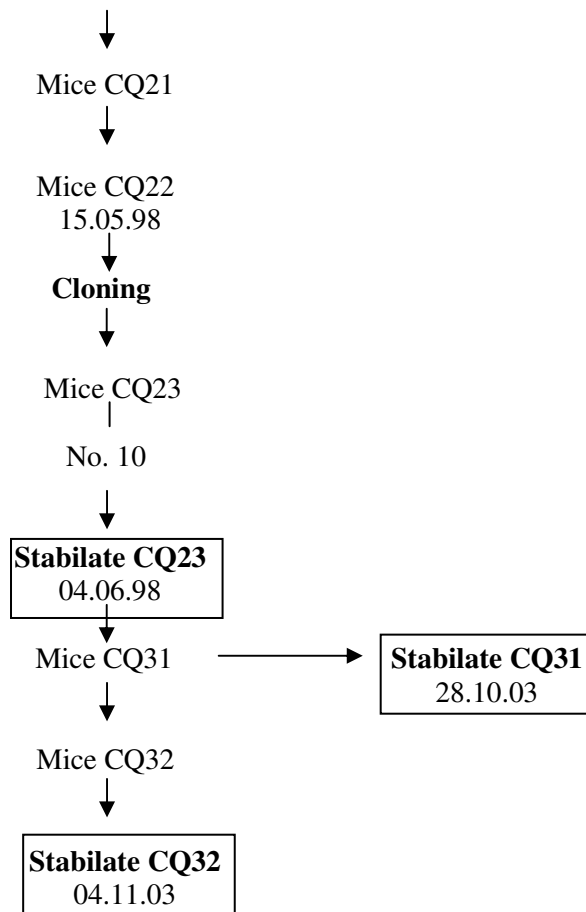


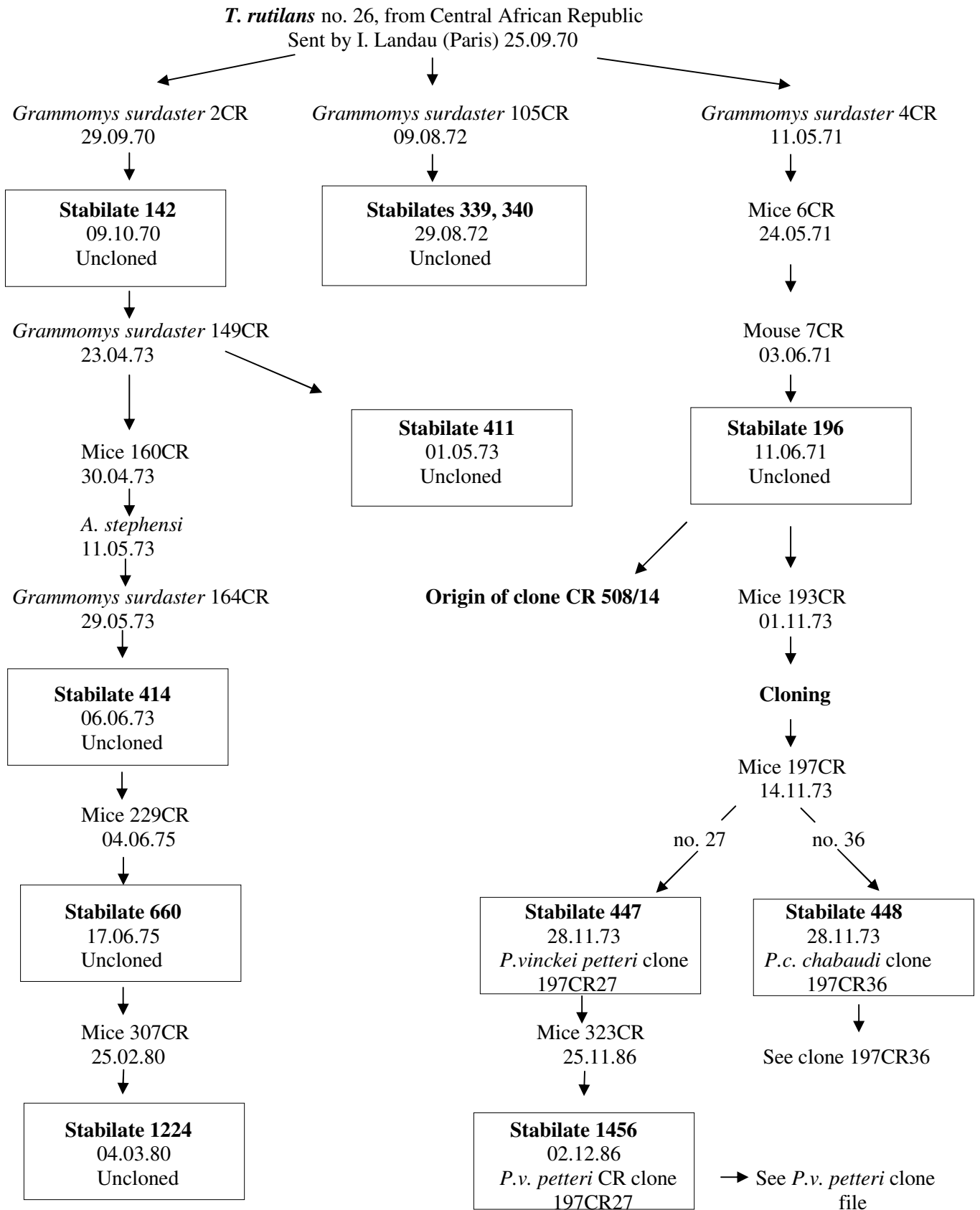
Origin of clone CQ23/10

P. chabaudi chabaudi (Central African Republic)

Clone CQ23/10

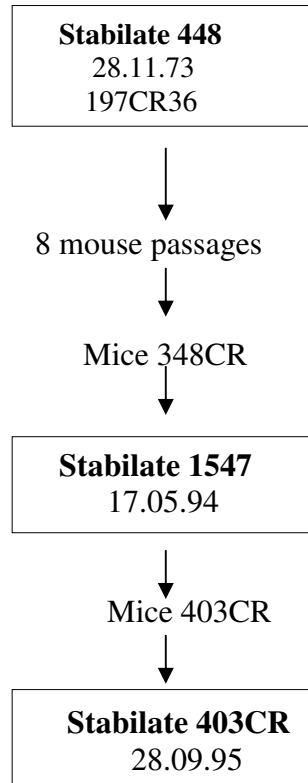
For previous history, see isolate CQ



P. chabaudi chabaudi (Central African Republic)**Isolate CR** (contains *P.c. chabaudi* and *P. v. petteri*)

P. chabaudi chabaudi* (Central African Republic)*CR clone 197CR36**

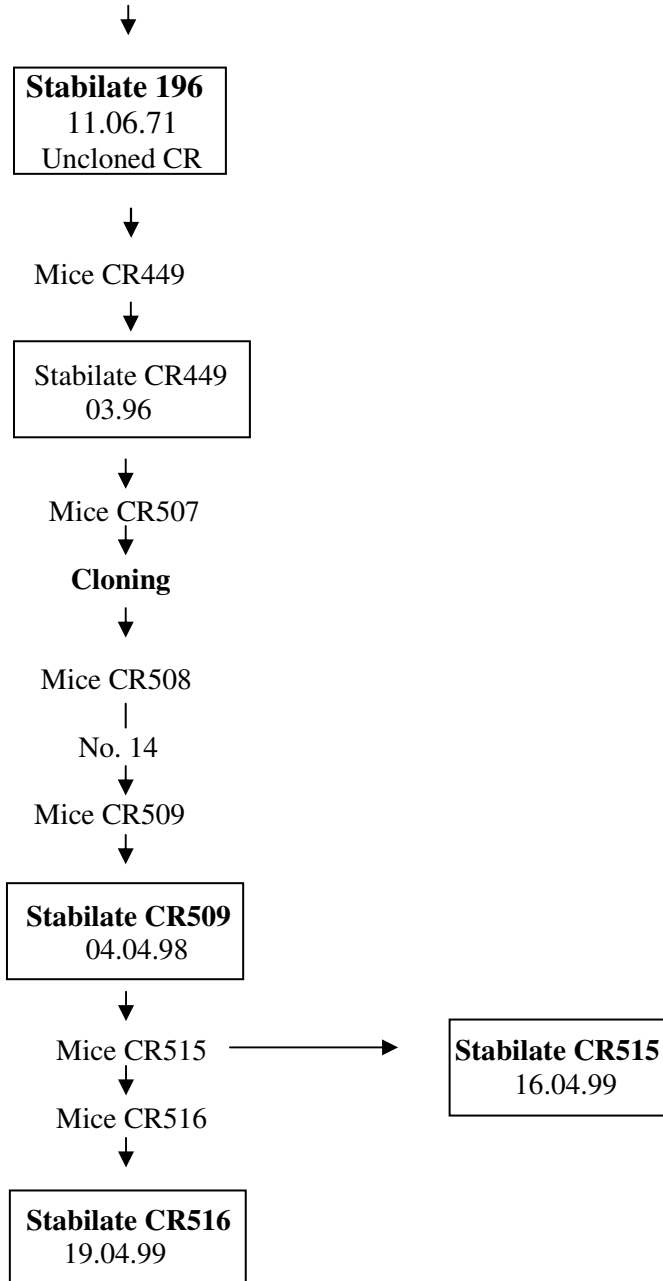
For previous history, see isolate CR



P. chabaudi chabaudi (Central African Republic)

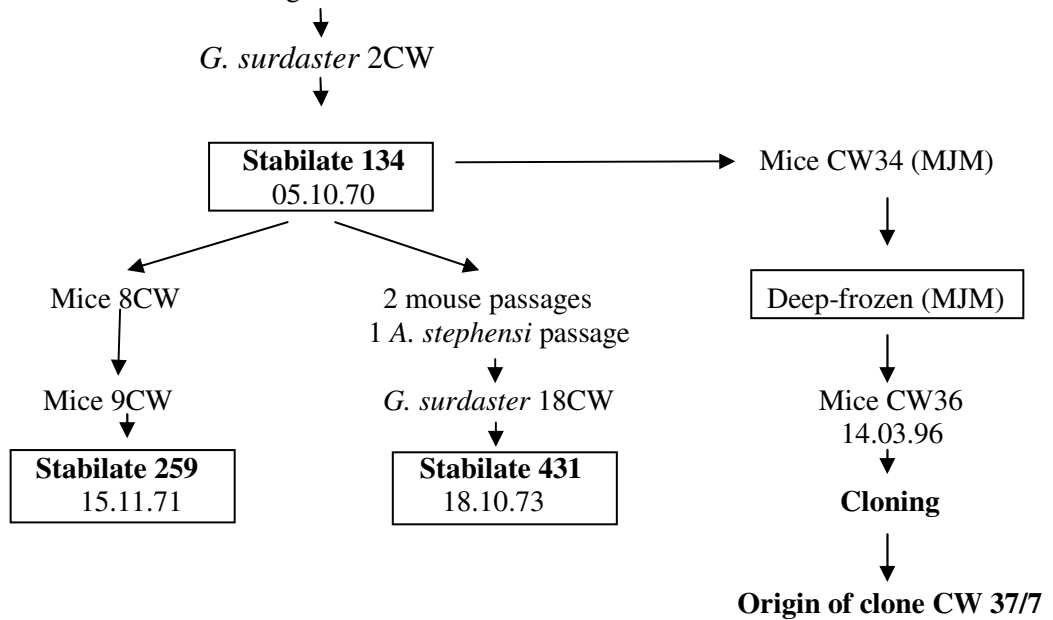
Clone CR508/14

For previous history, see isolate CR



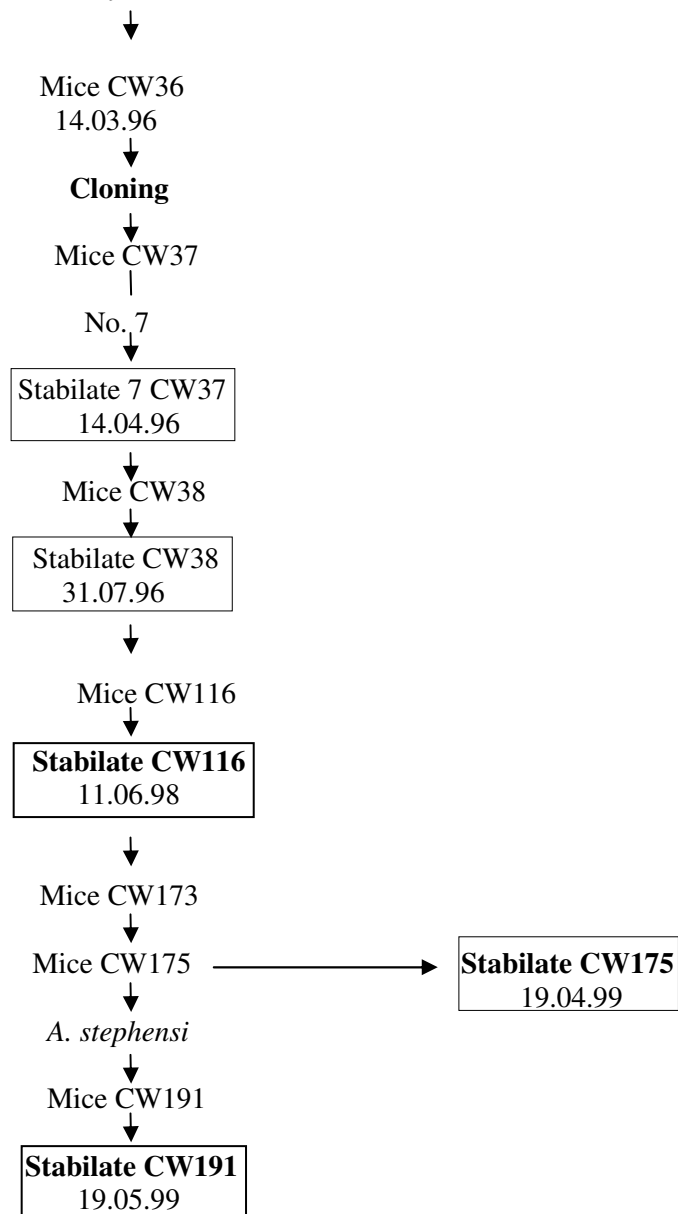
P. chabaudi chabaudi (Central African Republic)**Isolate CW** (*P.c. chabaudi* and *P.y. yoelii* visible)

Thamnomys rutilans, from Central African Republic.
Arrived Edinburgh 25.09.70. Denoted 1CW



P. chabaudi chabaudi (Central African Republic)**Clone CW37/7**

For previous history, see isolate CW



***P. chabaudi chabaudi* (Central African Republic)**

Isolate DR ("Red line"):

Mice sent to Edinburgh from Liverpool by W. Peters.
Arrived Edinburgh 03.10.73. Mice denoted 1DR



Stabilate 430 03.10.73

***P. chabaudi chabaudi* (Central African Republic)**

Isolate DT (=864VD)

T. rutilans 864VD, captured in Central African Republic, La Maboké Field Station, 28.04.70.
Frozen blood from I. Landau (Mouse 1205LS), passaged into mice 28.09.73, then passaged
into mice 12.10.73, sent to Edinburgh from Liverpool.
Arrived Edinburgh 18.10.73. Mice denoted 1DT



Stabilate 433 19.10.73

***P. chabaudi chabaudi* (Central African Republic)**

Isolate DY (=54X):

T. rutilans 54X, captured in Central African Republic, La Maboké Field Station, April 1965
Infected mice sent to Edinburgh by Frank Cox, King's College London
Arrived Edinburgh 07.12.73. Mice denoted 1DY



Stabilate 461 14.12.73

***P. chabaudi chabaudi* (Central African Republic)**

Isolate EC (rat-adapted line):

Said to be 'original strain of Landau (1965)'

Obtained by Graham Coombs, University of Kent at Canterbury, from P. Trigg, NIMR, Mill Hill, and adapted to rats. See Coombs, G.H. and Gutteridge (1975) *J. Protozool.* 22, 555-560.

Enzyme typing shows this strain to be distinct from other *P.c. chabaudi* isolates

Infected rats sent to Edinburgh by Graham Coombs,
Arrived Edinburgh 16.05.74. Rats denoted 1EC

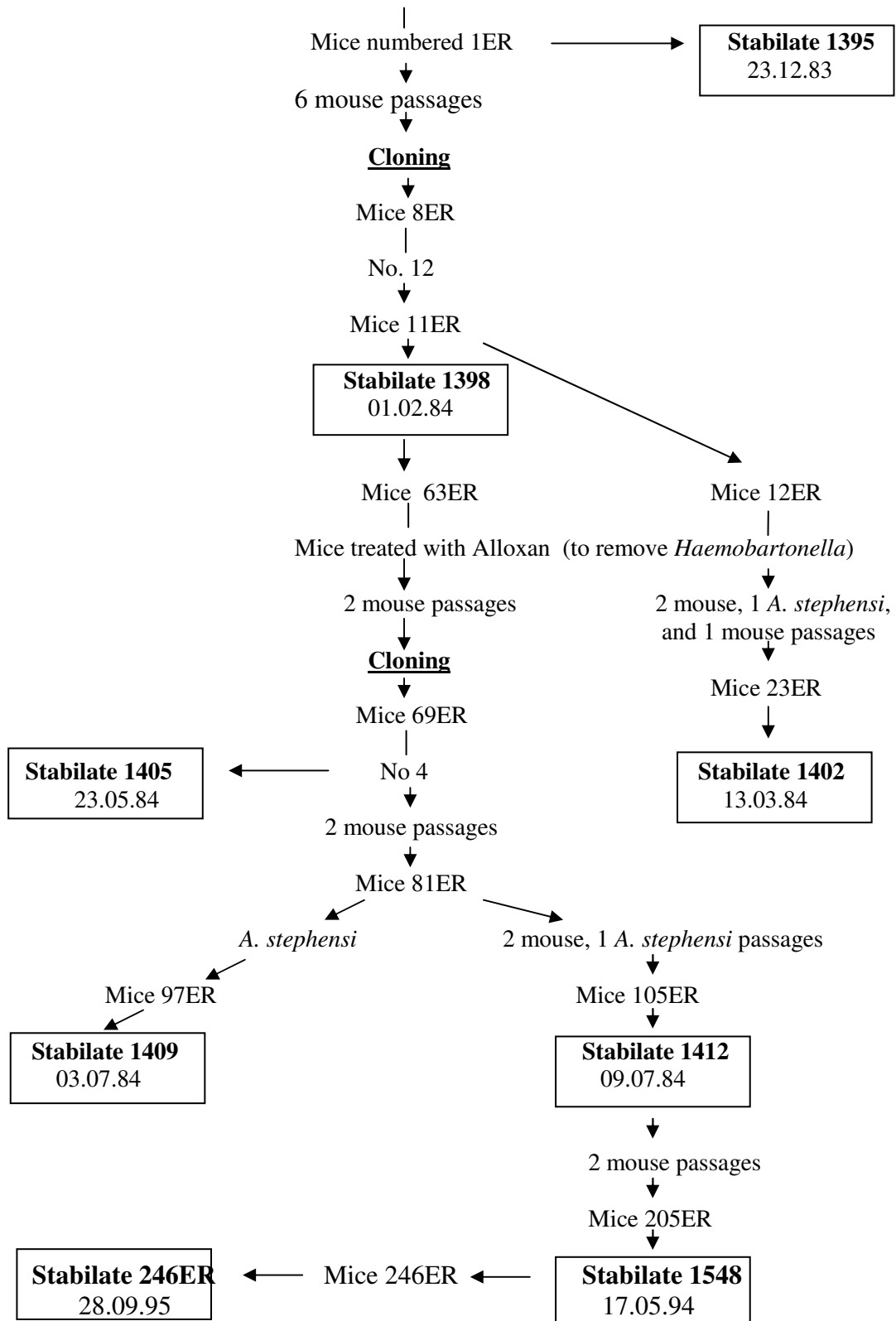


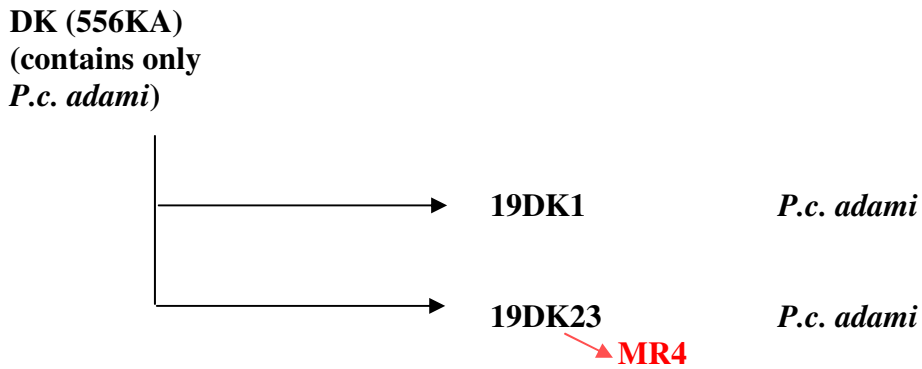
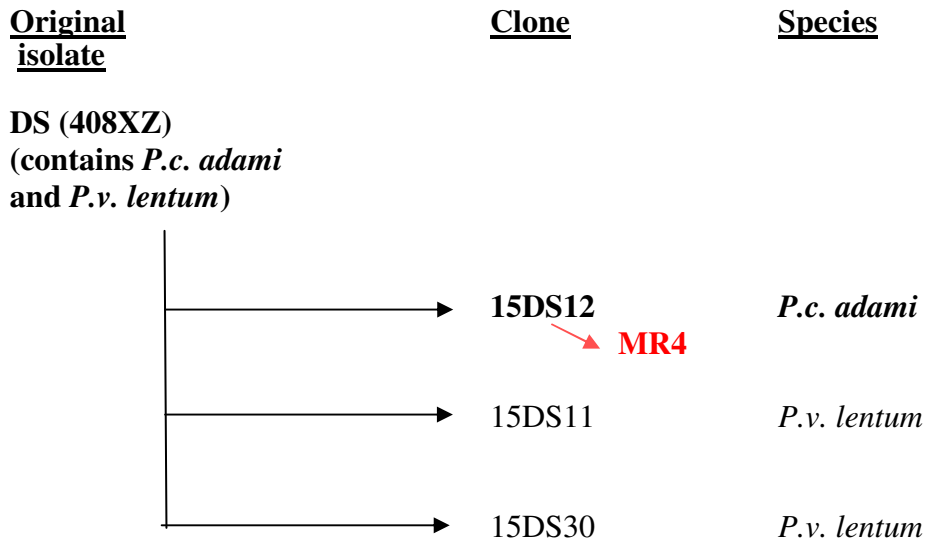
Stabilate 514 17.05.74

P. chabaudi chabaudi (Central African Republic)**Isolate ER (=56L) and clone 8ER12**

Originally isolated from *Thamnomys rutilans*, La Maboké field station, CAR.

Mice obtained from Dr C. Hamers-Casterman, Brussels, 20.12.83



***P. chabaudi adami* (and *P. vinckei lentum*) (Congo Brazzaville): clones**

P. chabaudi adami (Congo Brazzaville)

Isolate 408XZ (DS) (Contains *P. chabaudi adami* and *P. vinckei lentum*)

Isolated Congo-Brazzaville, 28.10.72 from *Thamnomys rutilans*
 Frozen blood sent to Liverpool STM by Irene Landau.
 Inoculated into CFW mice in Liverpool 28.9.73

↓
 Mice inoculated 12.10.73,
 sent to Edinburgh 18.10.73
 Mice numbered 1DS

↓

Stabilate 432 19.10.73 Uncloned
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↓
 Mice 14DS
 19.07.74

↓
Cloning

↓
 Mice 15DS
 24.07.74

↙
 15DS11

↓
 15DS30

↘
 15DS12

↙

Stabilate 545 06.08.74 <i>P.v. lentum</i> clone 15DS11

↓

Stabilate 546 06.08.74 <i>P.v. lentum</i> clone 15DS30

↘

Stabilate 544 06.08.74 <i>P.c. adami</i> clone 15DS12
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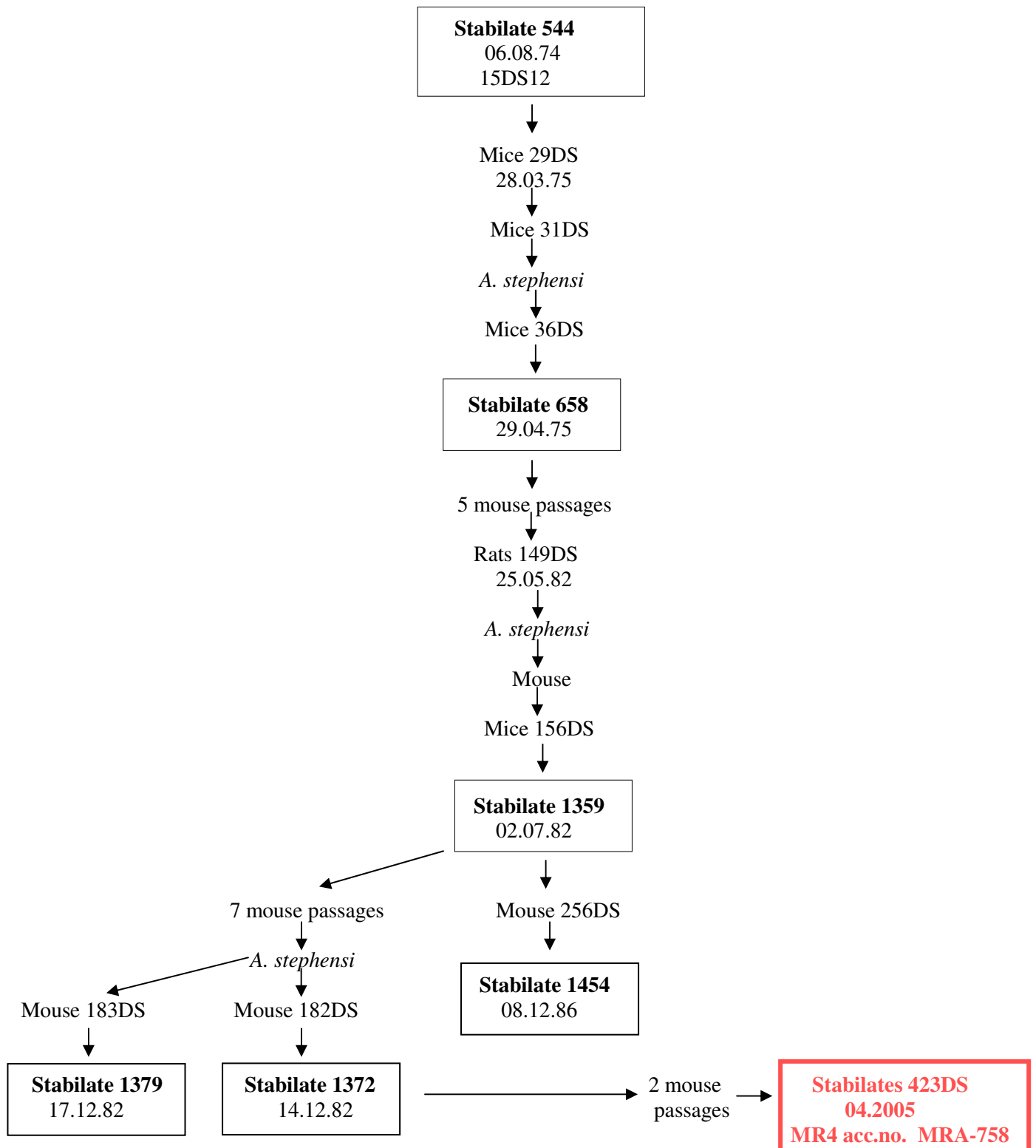
↓
 See *P. vinckei lentum* clone file

↓
 See clone 15DS12

P. chabaudi adami* (Congo Brazzaville)*Clone of isolate 408XZ (DS): 15DS12**

For previous history, see isolate 408XZ (DS).

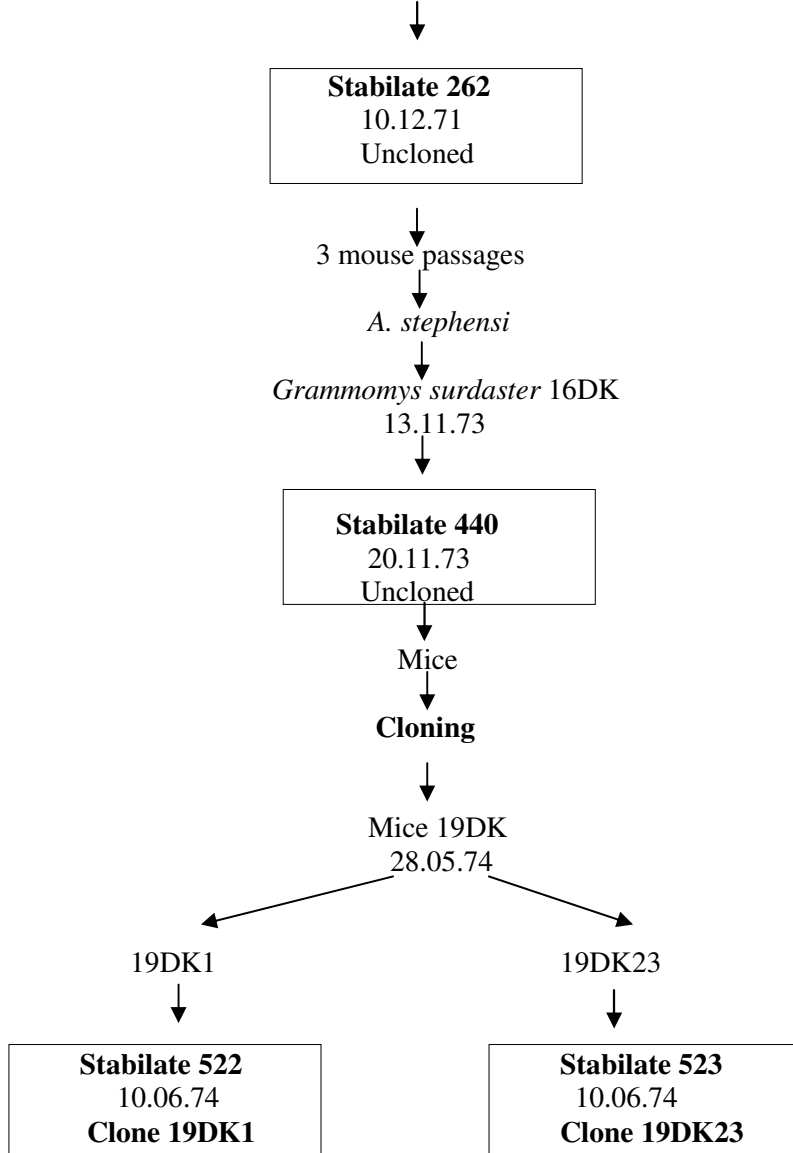
Note: this clone is virulent, compared to *P.c. adami* clone 19DK23 from isolate 556KA



P. chabaudi adami (Congo Brazzaville)**Isolate 556KA (DK)**

Isolated Congo-Brazzaville from *Thamnomys rutilans* 556KA

History: *T. rutilans* 556KA → 2 mouse passages → Deep-freeze → 4 mouse passages →
Mice sent to Edinburgh 04.12.71
Mice numbered 1DK



P. chabaudi adami (Congo Brazzaville)**Clones of isolate 556KA (DK)**

For previous history, see isolate 556KA (DK).

Clone 19DK1

Stabilate 522
10.06.74

Clone 19DK23

Note: Avirulent, compared to clones of isolate 408XZ (DS)

Stabilate 523
10.06.74

Mice 63DK

Mice 64DK

Stabilate 1354
06.05.82

Mice 96DK

Stabilate 1546
22.04.94

Mice 104DK

Mice 105DK

Stabilate 104DK
A.Read D5/2I-6I
21.03.04

2 mouse passages

Stabilate 121DK
04.2005
MR4 acc.no. MRA-759

Stabilate 105DK
A.Read D3/5I-9I
04.04.04

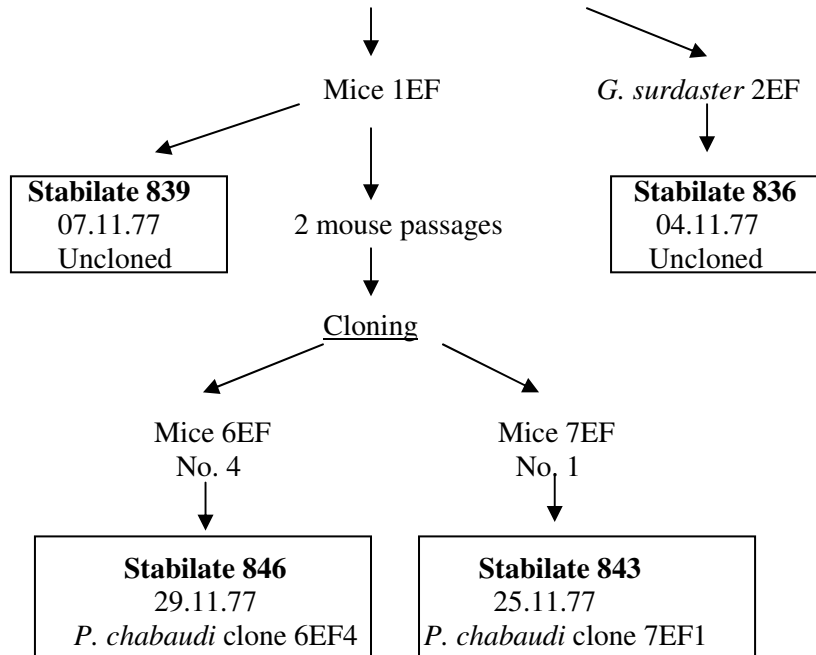
P. chabaudi subsp. (Cameroon)

Isolate Biboto 37 (EF)

(Only *P. chabaudi* visible)

Original Biboto 37 isolate from *T. rutilans* in Cameroon in August 1973 made by J..M. Bafort.

History since isolation:- In Antwerp, 3 passages through mice → *A. stephensi* → mice → deep-frozen 18.10.73, ampoule 2218 sent to Edinburgh 24.10.77 by Marc Wéry



| |
See clones 6EF4 and 7EF1

P. chabaudi* subsp. (Cameroon)*Clones of isolate Biboto 37 (EF)**

See isolate Biboto 37 for previous history

Clone 6EF4**Stabilate 846**

29.11.77

P. chabaudi clone 6EF4**Clone 7EF1****Stabilate 843**

25.11.77

P. chabaudi clone 7EF1

References

These references represent a small selection of papers, books, etc. concerning some of the *P. chabaudi* isolates, lines and clones included in this file.

Early references

1. Overall summary:

Killick-Kendrick, R. and Peters, W. eds (1978) *Rodent Malaria*. Academic Press, 1978

2. *P. c. chabaudi* (Central African Republic)

Carter, R. and Walliker, D. (1975) New observations on the malaria parasites of rodents of the Central African Republic - *Plasmodium vinckei petteri* subsp. nov. and *Plasmodium chabaudi* Landau, 1965. *Annals of Tropical Medicine and Parasitology* **69**, 187 - 196

3. *P. c. adami* (Congo Brazzaville)

Carter, R. and Walliker, D. (1976) Malaria parasites of rodents of the Congo(Brazzaville): *Plasmodium chabaudi adami* subsp. nov. and *Plasmodium vinckei lentum*. *Annales de Parasitologie Humaine et Comparée* **51**, 637-646.

4. *P. chabaudi* (Cameroon)

Lainson, F.A. (1983) Observations on the morphology and electrophoretic variation of enzymes of the rodent malaria parasites of Cameroon, *Plasmodium yoelii*, *P. chabaudi* and *P. vinckei*. *Parasitology* **86**, 221-229.

References concerning specific clones

1. *P.c. chabaudi*

Clones AS(Sens) and AS(15MF/3) :

Cravo, P.V.L., Carlton, J.M-R., Hunt, P., Bioni, L., Padua, R.A. and Walliker, D. (2003) Genetics of mefloquine resistance in the rodent malaria parasite *Plasmodium chabaudi*. *Antimicrobial Agents and Chemotherapy* **47**, 709-718.

Clones AS(Pyr1) and AS(50S/P) :

Hayton, K., Ranford-Cartwright, L.C. and Walliker, D. (2002). Sulfadoxine-pyrimethamine resistance in the rodent malaria parasite *Plasmodium chabaudi*.

Clones 3030AJ/12 and AS8793/2.

Mackinnon, A.J. and Read, A.R. (1999). Genetic relationships between parasite virulence and transmission in the rodent malaria parasite *Plasmodium chabaudi*. *Evolution* **53**, 689-703.

Clones 96AJ15 and AS(3CQ):

Carlton, J., Mackinnon, M. and Walliker, D. (1998). A chloroquine resistance locus in the rodent malaria parasite *Plasmodium chabaudi*. *Molecular and Biochemical Parasitology*. **93**, 57-72.

Clone AS(30CQ):

Padua, R.A. (1981) *Plasmodium chabaudi*: genetics of chloroquine resistance. *Experimental Parasitology* **52**, 419-426.

2. *P.c. adami*Clones 19DK23 and 15DS12 :

Crewther, P.E., Matthew, M.L.S.M., Flegg, R.H. and Anders, R.F. (1996) Protective immune responses to Apical Membrane Antigen 1 of *Plasmodium chabaudi* involve recognition of strain-specific epitopes. *Infection and Immunity* **64**, 3310-3317.