Professor Hans Georg Zachau

Würdigung eines langjährigen Freundes

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„Appreciation of Professor Hans Georg Zachau“ würde ich diesen Text auf Englisch überschreiben. Die Würdigung einer Persönlichkeit ist den sonst so ‚kühlen' Engländern nicht ungeläufig: man findet diese Art anerkennender Beiträge oft in renommierten Journalen.

Für mich ist es ein Bedürfnis, Hans Georg Zachau eine Erinnerung an sein Leben und Wirken zu widmen. Der aktuelle Anlass ist ein Eintrag über ihn in Wikipedia, der schon seine Lebensdaten und sein Wirken nicht richtig wiedergibt, aber in den *Weblinks* und Einzelnachweisen – trotz der für einen bibliografischen Abriss gebotenen Kürze – einen unzulänglichen und völlig falschen Eindruck hinterlässt. Hätte der Einsteller Mühe darauf verwendet, wenigstens die als *Link* zitierte Webseite von Hans Georg Zachau [1] zu Rate zu ziehen, nur dann wäre er vom Vorwurf der Inkompetenz freizusprechen. Eine Richtigstellung des (erst im Juli 2013 revidierten) Eintrages ist möglich und wird auch in die Wege geleitet. Dennoch genügt auch eine Korrektur nicht meinem Bestreben, ein wenig mehr über Hans Georg Zachau zu sagen.

Hans Georg Zachau ist seit 1999 verdienter Emeritus der Ludwig-Maximilians-Universität in München [2]; das Jahr 1998 verbrachte er als *sabbatical* am *National Health Institute* in Bethesda (USA).

Ich kenne Hans Zachau seit dem Jahre 1962, da er mich frisch gebackenen Postdoktoranden als wissenschaftlichen Mitarbeiter in seine Arbeitsgruppe am Institut für Genetik der Universität zu Köln aufnahm. Dieses Institut war durch Initiative des Kölner Botanikers, Professor Straub, neu gegründet und 1961 eröffnet worden; von 1961 bis 1963 leitete es Max Delbrück als Direktor [4]. Es wurde für mich eine wunderbare Zeit [vgl. 3], in der ich mit der Chemie der Nukleinsäuren bekannt wurde und mich in das durch die Machenschaften im Dritten Reich verpönte und erst durch das neu gegründete Kölner Institut in Deutschland rehabilitierte Fach Genetik einarbeiten konnte: Durch Hans Zachau und vor allem durch Max Delbrück empfing ich die ersten Einblicke in die mir bislang verborgene Molekularbiologie. Das *Team-work* von Hans Zachau's Gruppe gipfelte in der Strukturaufklärung zweier serin-spezifischer Transfer-Ribonukleinsäuren aus Hefe, Arbeiten, die 1966 publiziert wurden [5]. Unsere Kölner Arbeitsgruppe bestand aus einer Handvoll Mitarbeiter um Hans Georg Zachau (Annex 1), den wir Mitarbeiter immer nur „Unser Doktor“ nannten. Wir arbeiteten mit wissenschaftlichem Ernst, aber unser Chef ließ auch genügend Raum für heitere Momente. Jeden Dienstag versammelten wir uns in seinem Arbeitszimmer bei Tee und Kuchen, um über Ergebnisse und Pläne zu „ratschen“; auch Kritik nahm er stets humorvoll auf. Selbst wenn unser Doktor zu Kongressreisen unterwegs war, ließ unser Engagement nichts zu wünschen übrig. Ausspannung vom Arbeitsalltag brachten uns die Vorbereitungen für die häufigen Laborfeste, die Max Delbrück besonders liebte, oder die Karnevalsfeste, die das ganze Institut an jedem Rosenmontag inszenierte und feierte [4; Annex 1].

Ich war glücklich genug, als mir Hans Zachau anbot, mit ihm an die Ludwig-Maximilians-Universität in München zu übersiedeln, wohin er 1967 auf ein Ordinariat für Physiologische Chemie in der Medizinischen Fakultät berufen worden war. Er hatte sich für München unter mehreren Angeboten entschieden, weil ihn diese Stadt und ihre schöne Umgebung, die Nachbarschaft des Instituts für Physiologische Chemie zu seiner früheren Wirkungsstätte, dem Max-Planck-Institut für Biochemie, und die bevorstehende Aufgabe besonders reizten. Ein Porträt von Hans Georg Zachau aus dem ersten Jahr in München erschien 1968 [6; Annex 2]. Über dreißig Jahre haben wir dann zusammengearbeitet, zuerst im ‚alten' Bau an der Goethestraße, seit 1971 in einem neu errichteten Erweiterungsbau, welcher den Gesamtkomplex der Institute für Physiologie, Physiologische Chemie, sowie die beiden Max-Planck-Institute für Biochemie und für Eiweiß und Leder abrundete. Im Jahre 1971/72 siedelten die Max-Planck-Institute in die für sie neu erstellte Anlage in Martinsried um. Später, nach Professor Butenandts Tod, beantragte Hans Georg Zachau beim Bayerischen Kultusministerium, die alten und neu eingerichteten Universitäts-Institute zwischen Schiller- und Goethestraße zum „Adolf-Butenandt-Institut" zusammenzufassen.

Selbst als ich unabhängig wurde und meine eigene Arbeitsgruppe aufbauen konnte, ging die Zusammenarbeit zwischen Hans Zachau und mir weiter: Es verging kaum ein Tag, an dem wir nicht über wissenschaftliche Fragestellungen diskutierten, organisatorische Details des Instituts besprachen oder persönliche Ansichten und Erlebnisse austauschten. Schließlich resultierte daraus eine anhaltende Freundschaft.

Regelmäßig, jede Woche am Donnerstagabend, fand in unserem kleinen Lesesaal das von Hans eingerichtete Literaturseminar statt. Es wurden Arbeiten aus neuester Forschung verteilt, über die ein ausgewählter Mitarbeiter kritisch zu referieren hatte. Hans selber erzählte Neuigkeiten von Kongressen oder Tagungen, die er besucht hatte. Selbst ‚unwillige' Mitarbeiter haben später festgestellt, wie viel Wertvolles sie in diesen Seminaren gelernt hatten.

Das Feiern von runden Geburtstagen oder Doktorexamen war fester Bestandteil unseres Institutslebens. Dazu gehörten auch regelmäßige Ausflüge mit allen Mitarbeitern der einzelnen Arbeitsgruppen: obwohl stets brauchbare Ausflugsziele von den Mitarbeiten vorgeschlagen wurden, entschied sich Hans anfangs meist für Andechs (Annex 3). Von Köln hatten ein paar von uns das Rosenmontagsfest nach München importiert, das nun unter „Faschingsfest" vom ganzen Institut zusammen mit den Physiologen gestaltet wurde. Da Hans vermeiden musste, dass wir unsere Arbeitszeit mit den notwendigen Vorbereitungen verbrachten, haben wir sie wochenlang nach Feierabend im Keller des Nachbarinstituts oder am Wochenende vor Rosenmontag unternommen. Zum Fest, das meist über tausend Feierlustige zählte, erschien Hans immer mit seiner Frau in buntem Kostüm.

Zu den nirgendwo explizit hervorgehobenen, wissenschaftspolitischen Erfolgen von Hans zählen unter anderem die Etablierung der bilateralen Deutsch-Sowjetischen Symposien (später Deutsch-Russische Symposien) für Molekularbiologie, die Beteiligung eines deutschen Teams als ‚dritte Kraft' in der Organisation der „I*nternational Spetses Summer Schools for Molecular and Developmental Biology*", oder die Ausrichtung des Deutsch-Israelischen *4. Gentner* Symposiums im Jahre 1984.

Den Ausgangspunkt für die bilateralen Symposien (Annex 4) bildete die Einladung von hochrangigen russischen Wissenschaftlern des Moskauer Engelhardt-Instituts als Vortragende zum Jahrestreffen der GDCh 1976 in München. In den Jahren von 1977 bis 1995 besuchten deutsche Delegationen (bestehend aus jeweils ca. 20 Wissenschaftlern) in zweijährigem Wechsel Institute in der UdSSR, stets von Moskau ausgehend; im Gegenzug kamen russische Delegationen zu Symposien in deutsche Universitätsstädte, um hiesiges Leben und Forschen kennenzulernen; finanziell unterstützt wurden diese Unternehmen von der Deutschen Forschungsgemeinschaft. Hans gab mir die Chance, diese Treffen mit zu organisieren und die meisten davon mitzuerleben; ich bin ihm sehr dankbar dafür.

Das gleiche gilt für die „*Spetses Summer Schools*“ (Annex 5): Hans wurde 1969 von Marianne Grunberg-Manago und Francis Crick eingeladen, von 1970 an jedes dritte Jahr eine Sommerschule in Spetses unter deutscher Federführung zu organisieren. Dies war gewissermaßen eine Anerkennung seines Engagements, die Molekularbiologie in Deutschland auf einen Stand zu heben, von dem sie seither profitiert. Ich habe ihn bis 1992 bei diesen Unternehmungen unterstützen dürfen, und von da an überließ er mir großzügig die alleinige Initiative für Spetses [7].

Außerordentlich dankbar bin ich Hans auch dafür, dass er mich als jungen Forscher förderte, indem ich Gelegenheit zu Vorträgen bei nationalen Tagungen und internationalen Kongressen erhielt. Er war es auch, der mich zu eigener Initiative in der internationalen Wissenschaftspolitik lenkte.

Seinen nachhaltigen Einfluss auf die Entfaltung freundschaftlicher Beziehungen zwischen Deutschland und anderen Ländern sowie auf viele andere, weltweit wichtige Entwicklungen verdanken wir der Mitwirkung von Hans Zachau in zahlreichen Gremien, seiner Mitgliedschaft in mehreren Akademien [z.B. 8] und vor allem seiner Zeit als Kanzler des Ordens *Pour Le Mérite* [9; Annex 6].

Als wir beide zur gleichen Zeit, im Herbst 1997, das Institut verließen, setzte sich unser persönliches Verhältnis noch intensiver fort als vorher; er sagte einmal: „…. dann können wir uns auf das Bänkchen im Garten setzen und zurückschauen...“. Dazu gab es öfter Gelegenheit, gleichwohl ruhte er nicht aus: Zum Beispiel entwarf er mit mir zusammen (und mit der Hilfe einer seiner Technischen Assistentin, Heike Mitlöhner) die Webseite für sich, die heute noch über die Medizinische Fakultät im Internet besteht [1]. Da Hans sich in den letzten Jahren um deren Aktualisierung nicht selbst kümmern konnte, und außer mir niemand diese Dokumentation verwalten kann, empfinde ich es als vorsorgliche Aufgabe, sie hier anzufügen, wo sie von jeglichen Widrigkeiten unberührt bleibt; ausdrücklich beziehe ich die Seiten zur Analyse der Immunglobulin-Gene von Maus und Mensch ein, da sie das umfangreichste Projekt in Hans’ Forschungstätigkeit bildeten (Annex 8).

Hans Georg Zachau war nie ein Mann der ‚großen Worte’. Neben seinen wissenschaftlichen Veröffentlichungen und seiner Webseite bestehen nur wenige selbstbiografische Publikationen [z.B. 4, 11, 12 und Annex 7], die Auskunft über seine Persönlichkeit, seine Interessen und sein Wirken geben. Eines seiner *Hobbys* bestand darin, seine Erinnerungen zahlreichen, eigenhändig bebilderten Bänden anzuvertrauen, und so nehme auch ich

Zuflucht zu Zitaten und Bildern, letztere vor allem aus unserer gemeinsamen Zeit, und in den Annexen zusammengestellt.

Da wir jetzt im Alter weiter von einander entfernt sind, vermisse ich Hans sehr. Ich hoffe, dass er meine Eigenmächtigkeit, Persönliches über ihn zu schreiben, wohlwollend akzeptiert. Mein weiterer Wunsch ist es, dass auch seine Familie und viele Bekannte, die ihn geschätzt haben, diese etwas andersartige Biografie begrüßen werden.

Literaturzitate

[1] Webseite von Hans Georg Zachau. http://biochemie.web.med.uni-muenchen.de/zachau/
[2] Vorlesungsverzeichnis der Luwig-Maximilians-Universität München
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[5] List of Publications in ref. 1], refs. 37 bis 43
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[11] Who is who? http://www.whoswho.de/templ/te_bio.php?PID=19033&RID=1
[12] Zachau, H.G. 'Life with tRNA, chromatin, immunoglobulin genes: recollections of a German molecular biologist'. In: Comprehensive Biochemistry, Vol.41, pp. 635-666 (G. Semenza and R. Jaenicke, Eds.) Elsevier Science BV, Amsterdam 2000

„Leitfaden" zu den Annexen

Annex 1: Erinnerungen an die Kölner Zeit und das Institut für Genetik in Köln. Illustrationen wie aus refs. [3] und [4]
Annex 2: „Wer ist's" – Hans Georg Zachau, ref. [6]
Annex 3: Erinnerungen an die Münchner Zeit
Annex 4: Von den Deutsch-Russischen Symposien
Annex 5: Von den „Spetses Summer Schools"
Annex 6: Bilder von Hans Georg Zachau im Orden, refs. [9,10]
Annex 7: Titelseite aus ref. [12]
Annex 8: Hans Georg Zachau's Homepage, ref. [1]

Annex 1

Erinnerungen an die Kölner Zeit

Hans Zachau's Arbeitsgruppe im Kölner Institut für Genetik. Von oben nach unten und von links nach rechts: Susanne Notz, Hans Zachau, Fritz Melchers, Dieter Dütting; Horst Feldmann; Anita Mosch, Hugo Gottschling, Gisela Schultz, Paula Prüfert, Rainer Thiebe, Wolfgang Karau; Gudrun Patzelt, Heidi Heusinger [3].

Nach Max Delbrücks Abschied von Köln im Sommer 1963 standen dem Institut schwere Zeiten bevor [4].

Annex 2

Wer ist's ?

HANS GEORG ZACHAU

Wenn von einem Ordinarius und Institutsdirektor die Rede ist, denkt man leicht an den Typ des Professors, den man selten zu Gesicht bekommt, weil er sich z.B. hinter einer Doppeltür und einer energischen Sekretärin verschanzt. Dieses gerade in den letzten Jahren etwas strapazierte Bild trifft ganz und gar nicht für H. G. ZACHAU zu, der seit 1967 einen Lehrstuhl für Physiologische Chemie an der Universität München innehat. Das liegt sicher nicht nur daran, daß er erst 38 ist, sondern daß jene Vorstellung weder seiner Art noch seinen Absichten entspricht.

H. G. ZACHAU, erster Träger der neuen Richard-Kuhn-Medaille für Biochemie der GDCh, wurde 1930 in Berlin geboren und hat dort ein humanistisches Gymnasium besucht, über das er viel lobendes sagt. Sein Studium hatte er recht breit angelegt: Chemie, Medizin, Philosophie und Volkswirtschaftslehre. Formale Schwierigkeiten, die solch einer „interdisziplinären" Ausbildung damals wie heute entgegenstanden, hat er irgendwie umschifft. Nach den ersten acht Semestern in Frankfurt ging er zur Diplom- und Doktorarbeit („Beiträge zum Sexuallockstoff des Seidenspinners *Bombyx mori* L.") zu Professor BUTENANDT nach Tübingen. Nach 14 Semestern wurde er promoviert mit dem zumindest für Biochemiker ungewöhnlichen Nebenfach Betriebswirtschaftslehre. Nach einem Assistentenjahr am MPI für Biochemie in Tübingen ging ZACHAU nach den USA, zunächst für ein Jahr zu Prof. J. C. SHEEHAN an das MIT. Hier gelang ihm, zusammen mit W. B. LAWSON, die Strukturaufklärung des cyclischen Peptidantibioticums Etamycin. Das zweite Jahr in den USA, bei Prof. F. LIPMANN am Rockefeller Institut in New York, war für die weitere Arbeit bestimmend. Hier war ZACHAU an Arbeiten auf dem sich damals neu entwickelnden Gebiet der Proteinbiosynthese und der Transfer-Ribonucleinsäuren (tRNS) beteiligt. Zusammen mit G. ACS und F. LIPMANN fand er, daß die Aminosäuren mit dem terminalen Adenosin der tRNS verestert sind.

Unternehmungslustig war ZACHAU wohl immer gewesen. Er unternahm ausgedehnte Fahrradtouren durch Frankreich und Italien während der Studienzeit und große Autotouren durch die USA, Kanada und Mexiko. Für die Rückkehr nach Deutschland kaufte er eine Flugkarte über Japan und Indien und blieb solange unterwegs, wie das in Amerika ersparte Geld reichte — ein gutes Vierteljahr.

Nach seiner Rückkehr 1959 gab ihm Professor BUTENANDT die Gelegenheit, am MPI für Biochemie in München eine eigene Arbeitsgruppe aufzubauen. Zwei Japaner kamen, ein Amerikaner und zwei deutsche Diplomanden. Bearbeitet wurde vor allem das Problem, aus dem natürlich vorkommenden Gemisch der Transfer-Ribonucleinsäuren chemisch einheitliche, aminosäurespezifische tRNS zu isolieren. Es wurde ein Lösungsmittelsystem entwickelt, mit dem man die Nucleinsäuren in Form der Tri-n-butylammoniumsalze durch Gegenstromverteilung fraktionieren kann.

Im Jahre 1961 holte Professor M. DELBRÜCK ZACHAU als Leiter der Abteilung für Genetische Biochemie an das neugegründete Institut für Genetik nach Köln, wo er 1962 habilitiert wurde. Mit einer kleinen Gruppe von zwei bis drei Assistenten, zwei bis drei Doktoranden und einigen ausländischen Gästen entstanden weitere Arbeiten zur Proteinbiosynthese und Untersuchungen über UV-Bestrahlung von Nucleinsäuren. Am wichtigsten war die Strukturaufklärung zweier serinspezifischer tRNS aus Hefe (mit F. MELCHERS, D. DÜTTING, H. FELDMANN). Es handelt sich dabei um zwei sehr ähnliche Moleküle, die je 85 Nucleotide enthalten, davon 14 ungewöhnliche Nucleotide. Zwei der „seltenen" Nucleotide waren bis dahin nicht in Nucleinsäuren gefunden worden und mußten in ihrer Struktur aufgeklärt werden. Die Sequenzanalyse war eine mühevolle Angelegenheit, zumal vielfach erst die Methoden entwickelt werden mußten. Nach etwa vierjähriger Arbeit wurden die Untersuchungen abgeschlossen [diese Nachr. *14*, 173 (1966)], wenig später als die Strukturaufklärung einer alaninspezifischen tRNS durch HOLLEY, der damit die erste Sequenz einer Nucleinsäure überhaupt vorlegte.

Rufe nach Berlin und Köln schlug ZACHAU zugunsten der Berufung auf einen Lehrstuhl für Physiologische Chemie in München aus. Die Raumstruktur von tRNS steht nun im Mittelpunkt des Interesses, daneben stärker funktionelle Fragestellungen: Welche Teile der tRNS-Moleküle sind für die Erfüllung der verschiedenen Funktionen verantwortlich? Die Frage nach aktiven Zentren und Probleme der Nucleinsäure-Proteinwechselwirkungen werden berührt.

Was ZACHAU an der Übersiedlung nach München bedauert, ist die Tatsache, daß ihm nur noch wenig Zeit für die eigene experimentelle Tätigkeit bleibt. Die Pflichten des Ordinarius beanspruchen viel Zeit. Nach wie vor aber werden alle Experimente mit den Mitarbeitern sorgfältig geplant, aufeinander abgestimmt und bis in Einzelheiten durchgesprochen. Immer findet sich Zeit zu einer Diskussion der Ergebnisse oder interessanter Neuigkeiten aus dem engeren oder weiteren Arbeitsgebiet. Bezeichnend ist die stets offene Tür seines Arbeitszimmers, die nicht in das Sekretariat, sondern in das eigene Labor führt. Gespräche verlaufen fast immer in ruhiger Konzentration (meist wird für diese Gelegenheit eine Pfeife Tabak unter Dampf gesetzt); ungeduldig kann er nur werden, wenn ihm etwas ganz und gar nicht „in den Kram" paßt. Im Labor herrscht ein ungezwungener Ton, der sich bei den allwöchentlichen Teestunden noch lockert. Es darf nach Herzenslust kritisiert und „gefrotzelt" werden.

Nicht nur innerhalb der eigenen Gruppe erscheinen ihm Kontakte wichtig. Häufig sind auswärtige und ausländische Kollegen im Labor zu Gast, die über ihre Arbeiten berichten und Erfahrungen austauschen. Was aktuell ist, erfährt man meist nicht aus den Journalen, sondern im persönlichen Gespräch, aus Briefen, oder ZACHAU bringt es von Reisen mit. Traditionsgemäß findet bei den Besuchen der Kollegen die „Nachsitzung" bei ZACHAUS zu Hause statt, wo man dann von der Gastgeberin verwöhnt wird.

Was an freier Zeit bleibt, verwendet ZACHAU gern für die Lektüre zeitgeschichtlicher oder literarischer Werke, zu Theaterbesuchen, zu gelegentlichen Bergtouren im Sommer oder Skiausflügen im Winter.

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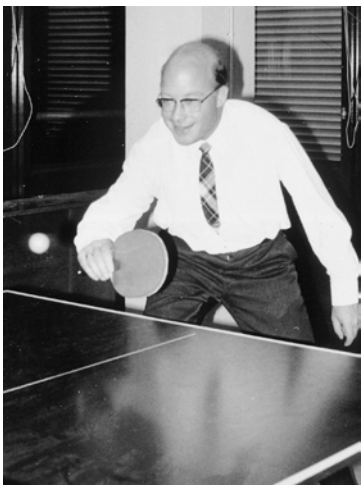
Annex 3

Erinnerungen an die Münchner Zeit

Das ‚Zachau-Labor' vor dem neuen Erweiterungsbau 1971



Ja, der Hans, der kann's

Gruppenausflug des „6. und 7. Stocks" im Jahre 1980, hier am Maisinger See. Im Vordergrund Hans Zachau mit Sonnenbrille und Rucksack.

Ausflug nach Andechs, 1982

…. und wieder nach Andechs, 1985

Gruppenausflug 1987 auf den Wank

.... und Ruhepause nach dem Gipfel: Gabi Combriato, Hans Zachau und Inge Oppermann (seine Sekretärin).

Glückwunsch zum 60. Geburtstag

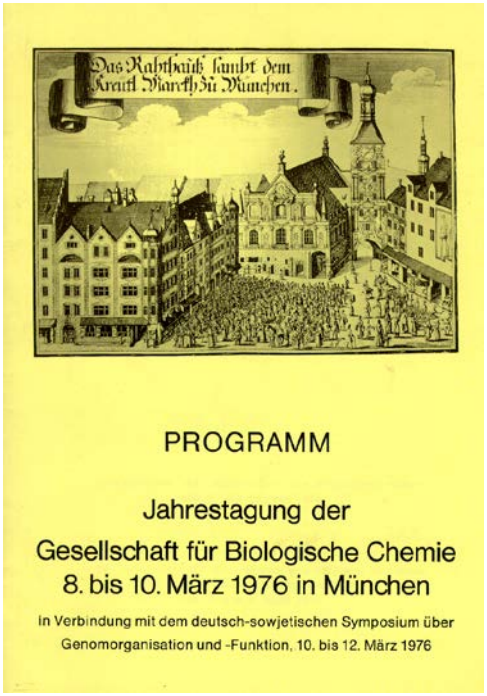
Große Geburtstagsfeier zu Hans' 60. Geburtstag in der Blutenburg (München-Pipping) 1990. Hans sitzt ganz links; auf dem Gehwege Professor Adolf-Butenandt mit seiner Frau.

Sommerfest 1993 im Hof des Adolf-Butenandt-Instituts

Verabschiedung vom Werkstattleiter, Sebastian Mann, 1996. Herr Mann links von seinem Chef und dessen Sekretärin.

Annex 4

Von den Deutsch-Russischen Symposien



Der Auftakt zu den Deutsch-Sowjetischen Symposien

Zuhörer beim 4.. Symposium in Jerewan. Linkes Bild: Vorne, von rechts nach links: Werner Goebel, Hans Zachau, Günter Schütz, Walter Doerfler; aus der Menge hinter Hans Zachau herausragend: Thomas Trautner und Ekkehard Bautz. Rechtes Bild: Vorne, Wolfram Zillig, 2. Reihe: Guido Hartmann und Walter Doerfler (verdeckt), 3. Reihe: Hermann Bujard und Peter Starlinger

‚Frühstück im Freien', auf dem Wege von Moskau nach Irkutsk zum 7. Deutsch-Russischen Symposium 1989.

Die deutsche Delegation vor dem Flughafen in Irkutsk 1989. Von links nach rechts: Albrecht Sippel , Benno Müller-Hill, Hans Günter Gassen, Rolf Knippers, Michael Reth, Klaus Rajewsky, XX, Dr. Klofat (DFG), Alfred Northeim, Ingrid Grummt, Ekkehart Bautz, Peter Starlinger, Guido Hartmann, sitzend Dieter Gallwitz; Hans und ich fotografieren.

Russische Teilnehmer des 8. Deutsch-Russischen Symposiums in Konstanz (1991), Ausflug zur Wallfahrtskirche Birnau. Am Bodensee. Links, Hans Zachau, rechts Guido Hartmann; fast ganz in weiß, Tatjana Venkstern, die langjährige ‚Mutter der Russen'

Zwischenstopp auf der Busfahrt von Moskau nach Suzdal zum 9. Deutsch-Russischen Symposium (1993). Hans Zachau fotografiert die Teilnehmer.

Einige der Teilnehmer am 9. Deutsch-Russischen Symposium in Suzdal (1993), bei einem Ausflug nach Wladimir : Von links nach rechts namentlich zu erkennen: Hans Günter Gassen (dritter), Walter Doerfler (fünfter), Rolf Knippers (siebter), Ekkehard Bautz (achter), Hans Gross (zehnter); ganz rechts Hans Zachau.

Annex 5

Von den „Spetses Summer Schools“

Ankunft in Spetses 1988: Feldmann, Frau Zachau, Frau Oppermann

Hans Zachau an der Büste des College-Gründers

Sommerschule Spetses 1992. In der Mitte links stehend, Hans Zachau.

Sommerschule Spetses 1988. Vierter von links vorne, Hans Zachau

Die Überreichung von Ehrenplaketten an die Organisatoren der Spetses Summer Schools anlässlich ihres 30-jährigen Jubiläums durch den Bürgermeister von Spetses wird mit Spannung verfolgt

Professor Thanos Evangelopoulos überreicht die Ehrung Hans Zachau

Aufbruch zu einer Inselrundfahrt, Spetses 1996

Annex 6

Bilder von Hans Georg Zachau im Orden Poir le mérite

Verleihung des Ordenszeichens an H.G. Zachau

Sitzung des Ordenskapitels

Festsitzungen des Ordens in Anwesenheit von Bundespräsident Roman Herzog (links) und Bundespräsident Johannes Rau (rechts)

Annex 7

Titelseite aus Hans Georg Zachau's Autobiografie

G. Semenza and R. Jaenicke (Eds.)
Selected Topics in the History of Biochemistry: Personal Recollections VI
(Comprehensive Biochemistry Vol. 41) © 2000 Elsevier Science B.V.

Chapter 12

Life with tRNA, chromatin, immunoglobulin genes: recollections of a German molecular biologist

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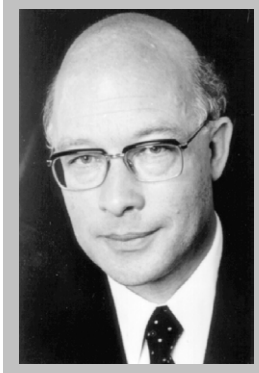
I am one of those lucky individuals who have witnessed the emergence of molecular biology from early on and have participated in its endeavors. Why do I want to write about that and for whom? The 'why question' is easily answered: autobiographical writing is fun for the writer and it is an appropriate pastime for a retired professor. But who may want to read the article? Perhaps some other scientists, younger or older ones. When I was a student or young scientist I probably would not have looked at what an old professor has written about his life in science. However, I became interested in biographies and books on history, after I had reached middle age. Now a good part of my spare time reading is spent with biographies, not only of geniuses, but also of normal people, scientists and others. I like to read, how people, ideas, situations develop. Maybe some of my colleagues are similarly inclined and take an interest in my recollections.

Annex 8

Homepage Professor Hans G. Zachau



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CURRICULUM VITAE OF HANS GEORG ZACHAU

Personal data:

Born May 16, 1930 in Berlin
German citizen
Since 1960 married to Elisabeth Z., nee Vorster
Three children, Martin, Ulrich, Thomas

Professor emeritus of Molecular Biology, Adolf-Butenandt-Institut der Universität München

Education:

1948 Abitur at a classical gymnasium in Berlin
1948-50 Study of preclinical Medicine in Frankfurt, Physikum
1948-53 Study of Chemistry in Frankurt, Diploma exam
1952-55 Diploma and doctoral theses at the Max-Planck-Institut (MPI) fuer Biochemie in Tübingen
1955 Dr.rer.nat. in Chemistry; Business Administration (BWL) as the elective subject
1955-56 Postdoctoral work at the same MPI in Tübingen
1956-57 Postdoctoral work at MIT, Cambridge, MA
1957-58 Postdoctoral work at Rockefeller University, New York

The theses were under the direction of Professor A. Butenandt on the sex attractant of the silk moth. The first postdoctoral year was devoted to synthetic chemical work, the second to structural work on the cyclic peptide antibiotic Etamycin (Professor J. C. Sheehan) and the third to work on protein biosynthesis and tRNA (Professor F. Lipmann).

Professional Record:

1958-61 MPI fuer Biochemie , then in München; start of independent research work
1961-66 Institut fuer Genetik in Köln, founded by M.Delbrück in 1961; group leader
1962 Habilitation in Physiological Chemistry
1965/66 Offers of professorships for Physiological Chemistry in Berlin, Genetics in Köln and Physiological Chemistry in München
since 1967 Professor of Physiological Chemistry in München and Codirector of the Institute for Physiological Chemistry
1995/98 Renaming of the Institute (Adolf-Butenandt-Institut) and the Chair (Molecular Biology)
1999 Emeritus professor

Memberships, Honors, Awards:

Gesellschaft Deutscher Chemiker: member since 1952
Gesellschaft Deutscher Naturforscher und Ärzte: member since 1954
Gesellschaft für Biologische Chemie: member since 1954
European Molecular Biology Organization (EMBO): member since its foundation, 1964
Deutsche Akademie der Naturforscher Leopoldina: member since 1967
Richard Kuhn-Medaille of Gesellschaft Deutscher Chemiker 1968
Bayerische Akademie der Wisenschaften: member since 1976
American Society for Biochemistry and Molecular Biology: honorary member since 1978
Orden Pour le mérite: member since 1981, chancellor since 1992
Großes Bundesverdienstkreuz mit Stern 1983
Österreichische Akademie der Wissenschaften: corresponding member 1985
Academia Europaea: member since 1989
The Human Genome Organisation (HUGO): member since 1989
Bayerischer Verdienstorden 1989
Otto-Warburg-Medaille of Gesellschaft für Biologische Chemie 1989
Bayerischer Maximiliansorden für Wissenschaft und Kunst 1991
Fogarty Scholar-in-Residence at the NIH, 1994 - 2000
Russian Academy of Sciences: Foreign Member since 1994

Councils, Boards, Advisory Committees:

Member of Editorial Boards:
Biochim. Biophys. Acta, 114-672, 1966-1981
Hoppe-Seylers Z. Physiol. Chem., 344-374, 1966-1993
Eur. J. Biochem., 1-102, 1967-1979
Arch. Biochem. Biophys., 152-188, 1972-1978
Nucl. Acids Res., 2-10, 1975-1982
GENE, 1-189, 1976-1997
Mol. Biol. and Med., 1-3, 1983-1985
Molecular Immunol. 23-27, 1986-1990
Nachr. Chem. Techn. Lab., 35-41, 1987-1993

Res. Immunol. 140-142, 1989-1991

Deutsche Forschungsgemeinschaft:
Reviewer in biochemistry for two election periods, 1967-1976
Member and chairman of various review boards in "Schwerpunkt" programs
Member of the board of Sonderforschungsbereiche, 1969-1976 and 1984-1988
Chairman of Forschergruppe "Genomorganisation München", 1978-1984

Minerva Committee for Israeli-German Scientific Cooperation (Gentner Committee): member 1969-1984.
Robert Bosch Stiftung: Trustee and member of the board 1969- 2003.
European Molecular Biology Conference (EMBC): delegate 1970-1983
European Molecular Biology Organization (EMBO): member of Council 1971-1976
European Molecular Biology Laboratory (EMBL), delegate (1974-1983) to and vicepresident (1979-1983) of the Council.

Member of Recombinant DNA Committees:
European Molecular Biology Organization, 1974-?
European Science Foundation, 1975-1976
International Council of Scientific Unions, 1975-1876
DFG (Deutsche Forschungsgemeinschaft), Senatskommission für Sicherheitsfragen bei der Neukombination von Genen, 1975-1993
Bundesministerium für Forschung und Technologie, 1976-1978.

Gesellschaft für Biologische Chemie (GBCh/GBM): President 1975-1977; vice president 1973-1975 and 1977-1979;
member of Council 1979-1989.
Federation of the European Biochemical Societies (FEBS): member of Council 1975-1989.
Gesellschaft Deutscher Naturforscher und Ärzte (GDNÄ): member of Scientific Committee 1976-1982; member of Council 1982-1988
Max-Planck-Institut für Biophysikalische Chemie, Göttingen: Fachbeirat, chairman 1979-1995; member 1996-1991.
Ad hoc committees, e.g. Beraterkommission des Bundesministeriums für Forschung und Technology für die öffentlich geförderte Großforschung auf dem Gebiet der Biotechnologie, 1983, chairman;
Review Committee at Deutsches Krebsforschungszentrum, Institute of Cell and Tumor Biology, Heidelberg, 1984, chairman.
Alexander von Humboldt-Stiftung: member of the committee for the US Special Program 1980-1989.
Gesellschaft Deutscher Chemiker (GDCh): member of Council 1984-1991.
Institute for Molecular Biology of the Austrian Academy of Science, Member of the Board 1988-2002 .
Academia Europaea: member of Council 1989-1995.
Orden Pour le merite: chancellor 1992- 2005.
Volkswagen-Foundation: Committee on "Cooperation with Eastern European Scientists and Engineers", Member 1992- 1991.
W. Engelhardt Institute for Molecular Biology of the Russian Academy of Science, Member of the International Advisory Board 1993-2002 .
Boehringer Mannheim GmbH, member of the board, 1993- 1998.

Meetings organized or chaired:

Summer Schools on Molecular Biology at Erice 1971, 1974 and at Spetsai 1977, 1980, 1984, 1988.
Annual Meeting of GBCh in München 1976.
German-Soviet or German-Russian Symposia on Molecular Biology in München 1976; Baku (with A.Bayev et al.), 1977; München 1979; Erewan (with A.Bayev et al.), 1981; Köln (with P. Starlinger et al.), 1983; Leningrad (with A.Mirzabekov et al.), 1985; Heidelberg (with E. Bautz et al.), 1987; Irkutsk (with A. Mirzabekov et al.) 1989; Konstanz (with R. Knippers) 1991; Susdal, Riga, (with A. Mirzabekov et al., E.Gren et al.) 1993; Köln (with W. Doerfler et al.), 1995.
Fourth German-Israeli (Gentner) Symposium on Biology "Molecular andCellular Diversity of Gene Expression", Rottach-Egern 1984.

RESEARCH ACTIVITIES AND PUBLICATIONS

(Numbers refer to papers in the list of publications)

RESEARCH ACTIVITIES

tRNA structure and interactions, protein biosynthesis, 1957-1981

My work on tRNA started in 1957 during a potdoctoral year in F. Lipmann's laboratory in New York and continued in Germany until the second half of the seventies, with last publications in 1981. In 1957 tRNA was a newly isolated RNA fraction and some of its basic features still had to be discovered. We were fortunate to find the site at which amino acids are bound to the RNA, i.e. the 3'-terminal adenosine, and to characterize the bond as a reactive ester bond (7).

I started independent research work by choosing for myself and the first coworkers a 'safe' project, i.e. the study of model compounds for the reactive aminoacyl-tRNA esters and a 'risky' one, i.e. attempts at tRNA fractionation. Since 1960 our emphasis was on the isolation of specific tRNAs and subsequent structural work. This led, in 1966, to the elucidation of the nucleotide sequence of tRNA-Ser from yeast (40), second to Holley's tRNA-Ala sequence of 1965. These were the very first nucleic acids to be sequenced which meant that, in the course of the work, the methods of sequencing had to be worked out. The tRNA-Ser sequence has been confirmed later at the DNA level, which cannot be said about all early tRNA sequences.

The known primary structures of several tRNAs served in the following years as the basis of biochemical studies on their conformations, on tRNA-synthetase interactions and on the mechanism of tRNA aminoacylation. Numerous tRNA fragments were prepared and combined by reassociation. These were early attempts to define those parts of the molecule which are important for its functions and/or for the maintenance of its threedimensional structure (54, reviews 57, 127). tRNA-synthetase and tRNA-ribosome interactions were studied also by physicochemical methods, frequently in collaboration with other labs (e.g. 112, 145).

Since 1969 the efforts of our group were divided between work on the relatively simple tRNA systems and the more complex systems of the eukaryotic genome and chromatin.

Repetitive DNA, 1970-1984

The repetitive DNAs turned out to be interesting in their own right and useful for introducing to our laboratory the emerging cloning, mapping and DNA sequencing methods. Structural studies on several simple and complex satellite DNAs allowed conclusions as to the evolution of this class of DNA (e.g. 122, 152). Studies on middle and low repetitive DNAs yielded insight into genomic rearrangement processes (e.g. 187, 194).

Chromatin, 1970-1984

The chromatin work of our group started with a series of frustrating experiments on the then popular so-called chromosomal RNA which supposedly contained dihydrouridine residues as we knew them from our tRNA work; however we found the chromosomal RNA to be an artifact (69). The following studies were more rewarding; they dealt with the mechanisms of histone-DNA binding (e.g. 111), with nucleosome phasing on satellite DNA (review 172) and with the structure of chromatin domains (130). The chromatin structures at expressed and non-expressed immunoglobulin k genes of mouse were compared (e.g. 167, 196). A general review of chromatin research was written in 1982 (176).

The studies on tRNA, tRNA-ribosome interactions, satellite DNA and chromatin were pursued independently by former coworkers.

Immunoglobulin genes, since 1977

The work on the chromatin structure at the expressed and non-expressed immunoglobulin k genes led us to investigate the genes themselves. Germline and rearranged k genes of the mouse were cloned and sequenced. The finding of certain sequence elements, later called signal joints, contributed to the understanding of the mechanism of V-J rearrangements (158). Other early results concerned the problem of allelic exclusion (166) and the generation of antibody diversity by somatic mutations being restricted to the rearranged V genes and their near neighborhood (170). The discovery of the immunoglobulin gene promoters (192) led, in several laboratories including ours, to extensive studies on the expression of these genes.

In 1981 we embarked on an attempt to elucidate the structure of the human k locus. The Ck , the 5 Jk and very few Vk gene segments were known at the time. We reached the goal in 1995 (reviews 260, 265,276). The V, J and C genes were cloned in l phages, cosmids and, in the last years, also in yeast artificial chromosomes. Contigs were constructed by chromosomal walking and a physical map of the locus and its surroundings was determined by pulsed field gel electrophoresis. The gene regions, recombination breakpoints and other regions of interest were sequenced. Our clones were recently sequenced by a Japanese group (277; see "Human k locus 2001").

The human k locus emerged as a 2 Mb structure which contained, in addition to the C and J genes, 76 V genes and pseudogenes, 40 of them in the so-called JC-proximal copy and 36 in a distal copy (review of sequences 258). Most JC-proximal V genes are rearranged by a deletion mechanism, the distal genes by an inversion mechanism (238). Somatic hypermutation as monitored in the transcripts, i.e. in the cDNAs, and in the k chain proteins affected the V genes in zero up to more than 10% of the positions (255). In addition to the Vk genes of the locus 25 so-called Vk orphons were found on different chromosomes (206 and review 260). Medical aspects included collaborative work on the gene(s) of the light chains of *Haemophilus influenzae* antibodies (review 245). Work on the structural variation of the k locus among individuals revealed a haplotype in which the 36 distal Vk genes are deleted (e.g. 241). Studies on the k locus of non-human primates yielded information on the evolution of the k genes; chimpanzees for instance possess only the proximal copy of the k locus, indicating that the duplication of the locus was a rather recent event (263).

In 1992 we resumed the study of the k genes of the mouse, the main experimental animal in immunology. The organization of the Vk genes within the locus is rather different from the one in the respective human locus. We found 140 Vk genes and pseudogenes in the locus and established its size to be close to 3.2 Mb, of which 3.1 Mb were cloned in four contigs. Apparently the mouse has twice as many Vk genes and a locus three times as large as that of man (270 - 273; 275, 276). By now three little gaps are still open in the locus. They will be closed at the latest, once the whole mouse genome has been sequenced some years from now.

A review on the k genes of human and mouse was published (No 278 in Publication List).

THE RESEARCH GROUP

The names of most members of our research group can be taken from the List of Publications. There were long-term and short-term collaborators and numerous foreign guests. For most of the time the majority of the members of our group were diploma and doctoral students. Up to now 29 diploma and 56 doctoral dissertations as well as 11 "Habilitationen" were successfully concluded.

LIST OF PUBLICATIONS

H.G. Zachau

Experimental papers and reviews including own work

1	Butenandt, A., Hecker, E. und Zachau, H.G. (1955) Chemische Berichte 88, 1185-1196. ‘Über die vier geometrischen Isomeren des 2.4-Hexadienols-(1)’
2	Sheehan, J.C., Zachau, H.G. and Lawson, W.B. (1957) J. American Chem. Soc. 79, 3933-3934. 'The structure of etamycin’
3	Sheehan, J.C., Zachau, H.G. and Lawson, W.B. (1958) J. American Chem. Soc. 80, 3349-3355. 'The structure of etamycin’
4	Sheehan, J.C., Zachau, H.G. and Lawson, W.B. (1958) in Ciba Foundation Symposium on Amino Acids and Peptides with Anti-metabolic Activity, J. & A. Churchill Ltd. London, 149-156. 'The chemistry of etamycin’
5	Weiss, S.B., Zachau, H.G. and Lipmann, F. (1959) Arch. Biochem. Biophys. 83, 101-114. 'Esterification of adenosine triphosphate by enzymatically formed andsynthetic tryptophanyl adenylate’
6	Weiss, S.B. and Zachau, H.G. (1958) in Fourth International Congress of Biochemistry, Vol. VIII "Proteins", Pergamon Press London, 217-221. ’On formation of a tryptophan ATP ester with tryptophan activating enzyme, tryptophan and ATP’
7	Zachau, H.G., Acs, G. and Lipmann, F. (1958) Proc. Natl. Acad. Sci. USA 44, 885-889. 'Isolation of adenosine amino acid esters from a ribonuclease digest of soluble liver ribonucleic acid’
8	Zachau, H.G. (1960) Chemische Berichte 93, 1822-1830. 'Reaktionsfähige Aminosäureester als Modelle der Aminoacyl-Ribonucleinsäure, I‘
9	Zachau, H.G. und Karau, W. (1960) Chemische Berichte 93, 1830-1839.

	'Reaktionsfähige Aminosäureester als Modelle der Aminoacyl-Ribonucleinsäure, II'
10	Zachau, H.G., Tada, M., Lawson, W.B. and Schweiger, M. (1961), Biochim. Biophys. Acta 53, 221-223. 'Fraktionierung der löslichen Ribonucleinsäure'
11	Tada, M., Schweiger, M. und Zachau, H.G. (1962) Hoppe-Seyler's Z. Physiol. Chem. 328, 85-93. 'Gegenstromverteilung der löslischen Ribonucleinsäure'
12	Staehelin, M., Schweiger, M. and Zachau, H.G. (1963) Biochim. Biophys. Acta 68, 129-131. Nucleotide sequences in purified soluble ribonucleic acid fractions'
13	Zachau, H.G. (1963) in Symposium "Funktionelle und morphologische Organisation der Zelle", Springer Verlag, 40-55. 'Aspekte der Nucleinsäure-Biochemie'
14	Frank, W. und Zachau, H.G. (1963) Hoppe-Seyler's Z.Physiol. Chem. 331, 258-268. 'Über die Aminosäureesterbindung in Aminoacyl-Ribonucleinsäure'
15	Sonnenbichler, J., Feldmann, H. und Zachau, H.G. (1963) Hoppe-Seyler's Z. Physiol. Chem. 334, 283-286. 'Identifizierung der Aminoacyl-sRNA als 3'-Ester des terminalen Adenosins'
16	Zachau, H.G. (1964) in "Struktur und Funktion des genetischen Materials", Erwin-Baur-Gedächtnisvorlesungen III, 1963, Akademie-Verlag Berlin, 185-189. 'Einige Probleme in der Sequenzanalyse von Ribonucleinsäuren'
17	Zachau, H.G. (1964) Hoppe-Seyler's Z. Physiol. Chem. 336, 176-188. 'UV-induzierte Uracil-Dimerisierung in löslicher Ribonucleinsäure'
18	Feldmann, H. and Zachau, H.G. (1964) Biochem. Biophys. Res. Commun. 15, 13-11. 'Chemical evidence for the 3'-linkage of amino acids to sRNA'
19	Zachau, H.G., Feldmann, H., Frank, W., Karau, W. and Sonnenbichler, J. (1964) in Symposium 'Nucleic Acids, Structure, Biosynthesis and Function', Hyderabad, Council of Scientific and Industrial Research, New Delhi, Pergamon Press, 238-245. 'Studies on the aminoacyl adenosine endgroup of aminoacyl sRNA'
20	Dütting, D. und Zachau, H.G. (1964) Hoppe-Seyler's Z. Physiol. Chem. 336, 132-134. 'Ribonucleinsäurespaltung neben N2-Dimethylguanylsäure-Resten durch T1-Ribonuclease'
21	Karau, W. und Zachau, H.G. (1964) Biochim. Biophys. Acta 91, 549-558. 'Isolierung von Serin-spezifischen Transfer-Ribonucleinsäure- Fraktionen'
22	Melchers, F. und Zachau, H.G. (1964) Biochim. Biophys. Acta 91, 559-572. 'Spaltung von löslicher Ribonucleinsäure und Serin-spezifischen Transfer-Ribonucleinsäure-Fraktionen mit Pankreas-Ribonuclease'
23	Dütting, D. und Zachau, H.G. (1964) Biochim. Biophys. Acta 91, 573-583. 'Spaltung einer Serin-spezifischen Transfer-Ribonucleinsäure-Fraktion mit T1-Ribonuclease'
24	Melchers, F. und Zachau, H.G. (1965) Biochim. Biophys. Acta 95, 380- 381. 'Chromatographie von Seryl-RNA und Cysteinyl-RNA an Säulen aus methyliertem Albumin auf Kieselgur'
25	Thiebe, R. und Zachau, H.G. (1965) Biochim. Biophys. Acta 103, 568-578. 'Zur Fraktionierung der löslichen Ribonucleinsäure'
26	Gottschling, H. und Zachau, H.G. (1965) Biochim. Biophys. Acta 103, 418-430. 'Ultraviolett-Inaktivierung der Phenylalanin- und Lysin-spezifischen Transfer-Ribonucleinsäuren'
27	Zachau, H.G. (1965) Biochim. Biophys. Acta 108, 355-366. 'Oligo- und Polynucleotidtrennungen - IV. Chromatographie von löslicher Ribonucleinsäure und deren Spaltprodukten an Sephadex'
28	Melchers, F., Dütting, D. und Zachau, H.G. (1965) Biochim. Biophys. Acta 108, 182-193. 'Enzymatische Spaltungen von Serin-tRNA-Fraktionen'
29	Dütting, D., Karau, W., Melchers, F. und Zachau, H.G. (1965) Biochim. Biophys. Acta 108, 194-201. 'Nucleotidsequenzen in Serin-spezifischen Transfer Ribonucleinsäuren'

30	Zachau, H.G. and Feldmann, H. (1965) in Progr. in Nucleic Acid Res. and Mol. Biol., Vol. 4, Acad. Press New York, 217-230. 'Amino acid esters of RNA, nucleosides, and related compounds'
31	Sonnenbichler, J., Feldmann, H. und Zachau, H.G. (1965) Hoppe- Seyler's Z. Physiol. Chem. 341, 249-254. 'Kernmagnetische Resonanz-Messungen an Aminoacyladenosin aus Aminoacyl-sRNA und an Modellsubstanzen'
32	Schweiger, M. und Zachau, H.G. (1965) Hoppe-Seyler's Z. Physiol. Chem. 342, 93-91. 'Oligo- und Polynucleotidtrennungen, V. Verteilungschromatographie von löslicher Ribonucleinsäure'
33	Zachau, H.G. (1965) Hoppe-Seyler's Z. Physiol. Chem. 342, 98-105. 'Oligo- und Polynucleotidtrennungen, VI. Weitere Versuche zur Verteilungschromatographie'
34	Zachau, H.G., Dütting, D., Melchers, F., Feldmann, H. and Thiebe, R. (1966) in Proc. 2nd Meeting of the Federation of European Biochem. Soc., Wien, Pergamon Press, 21-21. 'On serine specific transfer ribonucleic acids'
35	Harriman, P.D. and Zachau, H.G. (1966) J. Mol. Biol. 16, 87-403. 'Ultraviolet inactivation of transfer ribonucleic acid functions'
36	Hütter, R., Poralla, K., Zachau, H.G. and Zähner, H. (1966) Biochem. Z. 344, 190-196. 'Stoffwechselprodukte von Mikroorganismen. Über die Wirkungsweise von Borrelidin - Hemmung des Threonineinbaus in sRNA'
37	Zachau, H.G., Dütting, D. und Feldmann, H. (1966) Angew. Chem. 78, 392-393; Int. Ed. 5, 422-423. 'Nucleotidsequenzen zweier Serin-spezifischer Transfer- Ribonucleinsäuren'
38	Zachau, H.G., Dütting, D. and Feldmann, H. (1966) in FEBS Symposium "Properties and Function of Genetic Elements", Warschau, Adademic Press N.Y and PWN, Warschau, 271-285. 'On the primary structure of transfer ribonucleic acids'
39	Biemann, K., Tsunakawa, S., Sonnenbichler, J., Feldmann,H., Dütting, D. und Zachau, H.G. (1966) Angew. Chem. 78, 600-601; Int. Ed. 5, 590-591. 'Struktur eines ungewöhnlichen Nucleosids aus Serin-spezifischer Transfer-Ribonucleinsäure'
40	Zachau, H.G., Dütting, D. and Feldmann, H. (1966) Hoppe-Seyler's Z. Physiol. Chem. 347, 212-235. 'The structures of two serine transfer ribonucleic acids'
41	Feldmann, H., Dütting, D. and Zachau, H.G. (1966) Hoppe-Seyler's Z. Physiol. Chem. 347, 236-248. 'Analyses of some oligonucleotide sequences and odd nucleotides from serine transfer ribonucleic acids'
42	Dütting, D., Feldmann, H. and Zachau, H.G. (1966) Hoppe- Seyler's Z. Physiol. Chem. 347, 249-261. 'Partial digestions of serine transfer ribonucleic acids with pancreatic and T1-ribonucleases'
43	Zachau, H.G., Dütting, D., Feldmann, H., Melchers, F. and Karau, W. (1966) in Cold Spring Harbor Symp. Quant. Biol. 31, 417-424. 'Comparison of nucleotide sequences and secondary structure models'
44	Thang, M.N., Guschlbauer, W., Zachau, H.G. and Grunberg-Manago, M. (1967) J. Mol. Biol. 26, 403-421. 'Degradation of transfer ribonucleic acid by polynucleotide phosphorylase'
45	Zachau, H.G. (1968) in FEBS Symposium *Structure and Function of Transfer RNA and 5S RNA*, Oslo 1967, Universitetsforlaget Oslo and Academic Press N.Y., 169-174. 'Chairman's concluding remarks'
46	Adams, A. and Zachau, H.G. (1968) Eur.J.Biochem.5, 556-558. 'Serine specific transfer ribonucleic acids. 15. Some properties of the aggregates from serine specific transfer ribonucleic acids'
47	Zachau, H.G. (1968) Eur. J. Biochem. 5, 559-566. 'Serine specific transfer ribonucleic acids. 16. Aggregation of serine specific transfer ribonucleic acids'
48	Thiebe, R. and Zachau, H.G. (1968) Eur.J.Biochem.5, 546-555 'A specific modification next to the anticodon of phenylalanine transfer ribonucleic acid'
49	Zachau, H.G. (1970) in Methoden der Enzymatischen Analyse, 2. Aufl., Band II (Bergmeyer, H.U. ed.) Verlag Chemie

	Weinheim, 1828- 1834; Int. Ed. 1557-1563. 'Transfer-Ribonucleinsäuren: Bestimmung der Akzeptor-aktivität für ` Aminosäuren'
50	Thiebe, R. and Zachau, H.G. (1968) Biochem. Biophys. Res. Commun. 33, 260-265. 'The role of the anticodon region in homologous and heterologous charging of tRNAPhe'
51	Philippsen, P., Thiebe, R., Wintermeyer, W. and Zachau, H.G. (1968) Biochem. Biophys. Res. Commun. 33, 922-928. 'Splitting of phenylalanine specific tRNA into half molecules by chemical means'
52	Zachau, H.G. (1967) Antrittsvorlesung München 'Genetischer Code und Anticode - ein Problem der Nucleinsäure-Biochemie' a. (1969) Münchener Med. Wochenschr. 111, 1513-1521. b. (1971) Umschau Jahrbuch, Umschau Verl. Frankfurt, 69-85. c. (1971) Forschung, Fischer Bücherei Frankfurt, 69-85.
53	Igo-Kemenes, T. and Zachau, H.G. (1969) Eur.J. Biochem. 10, 549-556. 'On the specificity of the reduction of transfer ribonucleic acids with sodium borohydride'
54	Thiebe, R. and Zachau, H.G., (1969) Biochem. Biophys. Res. Commun. 36, 1024-1031. 'Acceptor activity in homologous and heterologous combination of half molecules from yeast tRNAPhe and wheat tRNAPhe '
55	Römer, R., Riesner, D., Maass, G., Wintermeyer, W., Thiebe, R. and Zachau, H.G. (1969) FEBS Lett. 5, 15-19. 'Cooperative helix-coil transitions in half molecules of phenylalanine specific tRNA from yeast'
56	Wintermeyer, W., Thiebe, R., Zachau, H.G., Riesner, D., Römer, R. and Maass, G. (1969) FEBS Lett. 5, 23-21. 'Association and dissociation of half molecules of phenylalanine specific tRNAs from yeast and wheat germ'
57	Zachau, H.G. (1969) Angew. Chem. 81, 645-662; Int. Ed. 8, 711-721. 'Zur Struktur und Funktion von Transfer-Ribonucleinsäuren'
58	Thiebe, R. and Zachau, H.G. (1971) in Methods in Enzymology (Moldave, K. & Grossman, L. eds.) Acad. Press N.Y., 20, 179-182. 'Half molecules from phenylalanine specific tRNAs'
59	Hirsch, R. und Zachau, H.G. (1970) Hoppe-Seyler's Z. Physiol. Chem. 351, 563-566. 'Zur Modifizierung Serin-spezifischer Transfer-Ribonucleinsäure durch Jod'
60	Erhardt, F. und Zachau, H.G. (1970) Hoppe-Seyler's Z. Physiol. Chem. 351, 567-570. 'Reversible Inaktivierung von Transfer-Ribonucleinsäuren mit Diketen'
61	Thiebe, R. and Zachau, H.G. (1970) Biochim. Biophys. Acta 217, 294- 304. 'Further studies on amino acid acceptance and physical properties of tRNA'
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SURVEY OF PUBLICATIONS

The numbers refer to papers in the List of Publications. Reviews in journals and articles in methods books, symposium volumes and monographs are underlined. Abstracts, book reviews, popular articles etc. are not included in the List of Publications.

tRNA, 1957-1981

tRNA amino acid esters, model compounds: 7 - 9, 14, 15, 18, 19, 30 , 31

tRNA fractionation, multiplicity, oligonucleotide separation: 10, 11, 21, 14, 25, 27, 32, 33, 81, 82

tRNA structural studies: 12, 16, 20, 22, 23, 28, 29, 34, 37, 38, 39-42, 43, 44, 45,

tRNA irradiation: 17, 26, 35

tRNA aggregates: 46, 47

tRNA conformation, structure-function relationships, recognition sites, chemical modification, tRNA fragments: 48, 50, 51, 53 - 56, 58, 59 - 62, 63, 64 - 66, 68, 71, 72, 73, 76 - 78, 79, 83 - 86, 88,89, 90, 91, 92, 96, 105, 108, 110, 115, 134, 138, 146

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THE IMMUNOGLOBULIN GENES OF MOUSE AND MAN

The immunoglobulin k genes and the k locus of the mouse

The data of our laboratory on the genes and the locus are described in the following reports:

(a) T. Kirschbaum et al., 1998. The 3' part of the locus...; *Eur. J. Immunol*. 1998. 28: 1458 - 1466

(b) T. Kirschbaum et al., 1999. The central part of the locus...; see below

(c) F. Röschenthaler et al., 1999. The 5' part of the locus.... ; see below

(d) R. Thiebe et al., 1999. The variable genes and gene families....; see below

with an Appendix by K. F. Schäble et al.

(e) F. Röschenthaler et al., 2000. The 5' part of the locus... continuously cloned....; see below.

(f) H.G. Zachau (2004) in: Molecular Biology of B Cells (F. Alt, T. Honjo and M. Neuberger Eds.) Elsevier Science, London, pp. 27-36. 'Immunoglobulin k genes of human and mouse'

In the following data are reported, which supplement the printed reports.
Previous publications from our laboratory, see 'List of publications'.

(a) Kirschbaum, T., Pourrajabi, S., Zocher, I., Schwendinger, J., Heim, V., Röschenthaler, F., Kirschbaum, V. and Zachau, H.G.

The 3' part of the immunoglobulin k locus of the mouse. Eur. J. Immunol. 1998. 28: 1458 - 1466.

(b) Kirschbaum, T., Röschenthaler, F., Bensch, A., Hölscher, B., Lautner-Rieske, A., Ohnrich, M., Pourrajabi, S., Schwendinger, J., Zocher, I. and Zachau, H. G.

The central part of the mouse immunoglobulin k locus. Eur. J. Immunol. 1999, 29:2057-2064.

ABSTRACT
At the present state of analysis the central part of the k locus comprises four contigs of together 1.2 Mb and contains 55 Vk genes. It is flanked by the 3' part of the locus with 22 Vk genes in 0.4 Mb (T. Kirschbaum et al., this Journal 1998. **28***:* 1458 - 1466) and the 5' part with 63 Vk genes in six contigs of together 1.5 Mb (F. Röschenthaler et al., accompanying report). The 5' and the central regions have one large contig in common. A part of the central region is linked to the 3' region resulting in a 1.1 Mb contig. The central part of the k locus contains 24 members of the Vk 4/5 gene family, while nine Vk 4/5 genes are located in the 5' part. The Vk 33/34 genes and relics are interspersed among the Vk 4/5 genes. The Vk 4/5 gene containing contigs are flanked at the 3' side by a contig of Vk 12/13 and Vk 23 genes, which is linked in one large contig to the Vk 8, Vk 19/28 and Vk 22 gene region, the Vk 21 genes and Jk Ck . In the latter region also sequences related to an S-adenosyl methionine decarboxylase gene were found.

Addendum: Restriction maps of the contigs in the central part of the k locus

In Fig. 2 of the printed report, an overview of the restriction maps of the contigs of this region comprising 1.2 Mb is shown. Only cleavage sites for some less frequently cutting restriction nucleases are included in the overview. In this file the constituent clones and the maps with sites also for some more frequently cutting nucleases are presented.

The map up to position 430 is documented only in the printed version of ref. (a). Misprints: p. 2059 underneath the legend of Fig. 2: ...only at the 5' side of the BssHII site....; p. 2062: the correct accession number of sad is AJ 132684.

Legend to the detailed restriction maps complementing the data of the printed version:

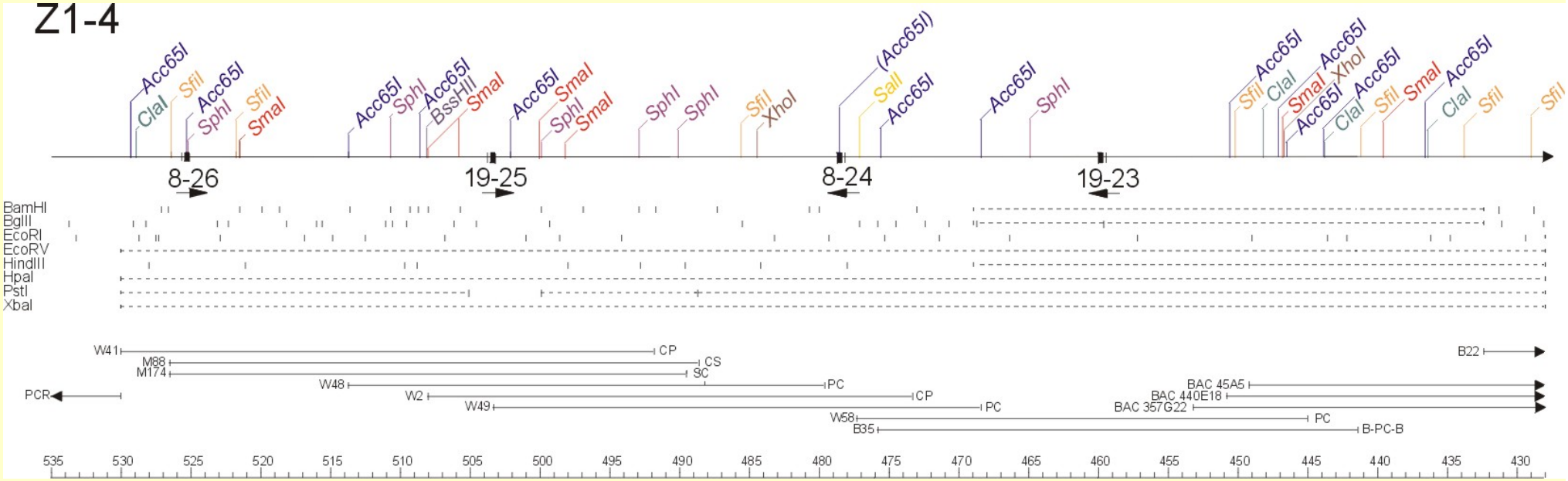
Vk genes are indicated as boxes with the leaders as vertical lines. Arrows underneath the genes designate transcriptional polarities which were assigned by combining the sequence and the map information; details are available from the authors on request. Cleavage sites of less frequently cutting nucleases are shown in the top line of each panel while those of more frequently cutting nucleases are noted underneath as small vertical bars; dotted lines indicate that the nucleases have not been mapped in the respective regions. Both isoschizomers of KpnI, Asp718I and Acc651, were used. Cosmid clones are shown as horizontal lines; for the designations M, B, C, D, E, F, V and W see Fig.1 and section 4.1 of the printed report. The orientation of the cosmid inserts is noted: SC, SalI, ClaI in pHC79; PC, PvuI, ClaI in SuperCos 1; a B at the respective side of the cosmid indicates that a BamHI site has been conserved or created in cloning (B-PC or PC-B). The scale is in kb; in contig Z1 zero is set at Jk Ck ; in Z2 -Z4 zero is set at the 5' end of each contig.

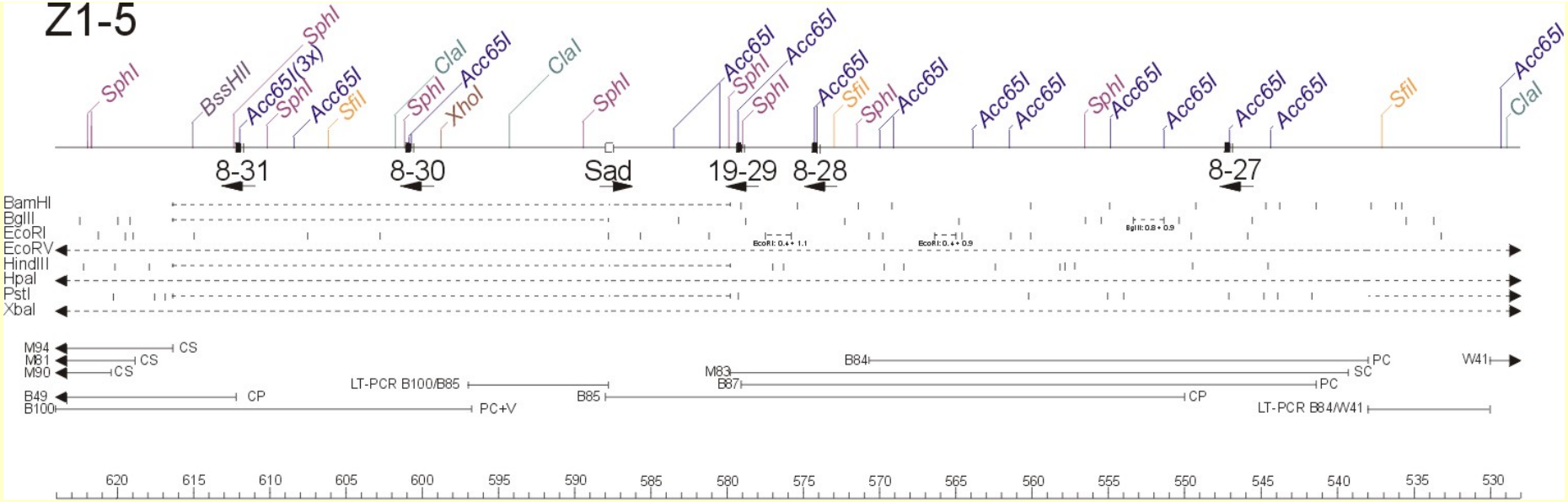
(A) The Vk 4/5 gene region (Z2 – Z4). PCR fragments are indicated. The BACs 2E24, 20P21 and 83M14 were identified with the gene ga33 as hybridization probe. The YAC FEXE10 is described in the printed report.

(B) The region of interdigitated Vk 12/13 and Vk 23 genes and the region of theVk 8 - Vk19/28 - Vk 22 clan (Z1). Among the numerous cosmid clones the ones depicted as dashed lines refer to clones that have not been independently mapped, but have been assigned to the respective region on the basis of known nuclease cleavage patterns. In the cluster of SphI sites at position 890 the two dashed lines indicate alternative positions of one cleavage site. sad refers to a sequence similar to the ones of the gene for a S – adenosyl methionine decarboxylase (see 2.4 of the printed version). The PCR product bridging the Vk 8-26 and Vk 8-27 regions was formed with the help of primers derived from the termini of the cosmid clones W41 and B84 : GAGAAGGTCCCGTGATGTGC and CCGAGGAATACTGAATGGCTG. The Vk 19-29 / Vk 8-30 gap was bridged with the PCR primers GTGCTTTCAGTAAGAGATGTACC and TTGGAGATATAACTGAGCCTGC derived from the cosmid clones B85 and B100, respectively. Cosmids BC330N7 and 14 derived from BAC 330N4 are shown in the region of the Vk gene 22-33. The BACs 45A5, 357G22 and 440E18 were isolated with the help of a 450 bp XbaI - EcoRI fragment located near the 5' end of cosmid B85; this is due to the crosshybridizations described in section 2.4 of the printed report.

Restriction Maps Z1 (Z1-4 to Z1-10); Z2 and Z3

[For the 3' part of Z4, which is described in ref.(b) see below in (e)]




Z1-5
SphI
BssHII
Acc65I(3x)
SphI
Acc65I
SfiI
SphI
ClaI
Acc65I
XhoI
ClaI
SphI
Acc65I
SphI
Acc65I
SphI
Acc65I
SfiI
SphI
Acc65I
Acc65I
Acc65I
SphI
Acc65I
Acc65I
Acc65I
Acc65I
SfiI
Acc65I
ClaI
8-31
8-30
SacI
19-29
8-28
8-27
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
M94
M81
M90
CS
CS
CS
B49
B100
CP
PC+V
LT-PCR B100/B85
B85
M83
B87
B84
PC
SC
PC
CP
LT-PCR B84/W41
W41
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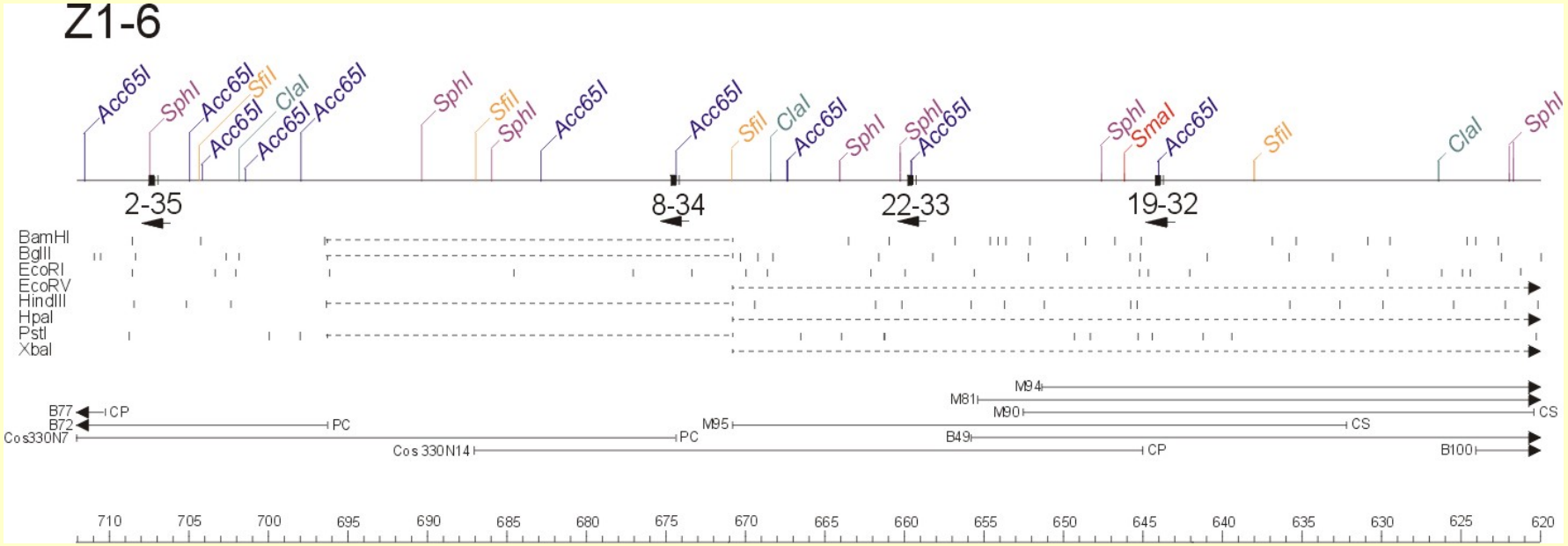
615
610
605
600
595
590
585
580
575
570
565
560
555
550
545
540
535
530


Z1-6
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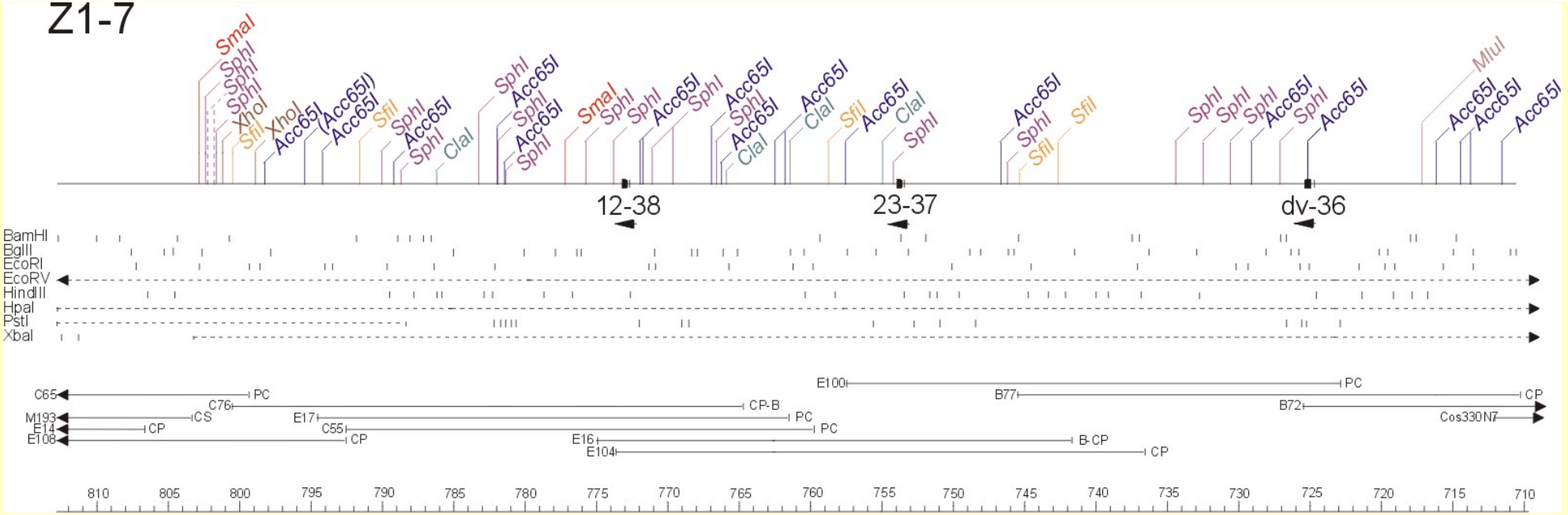
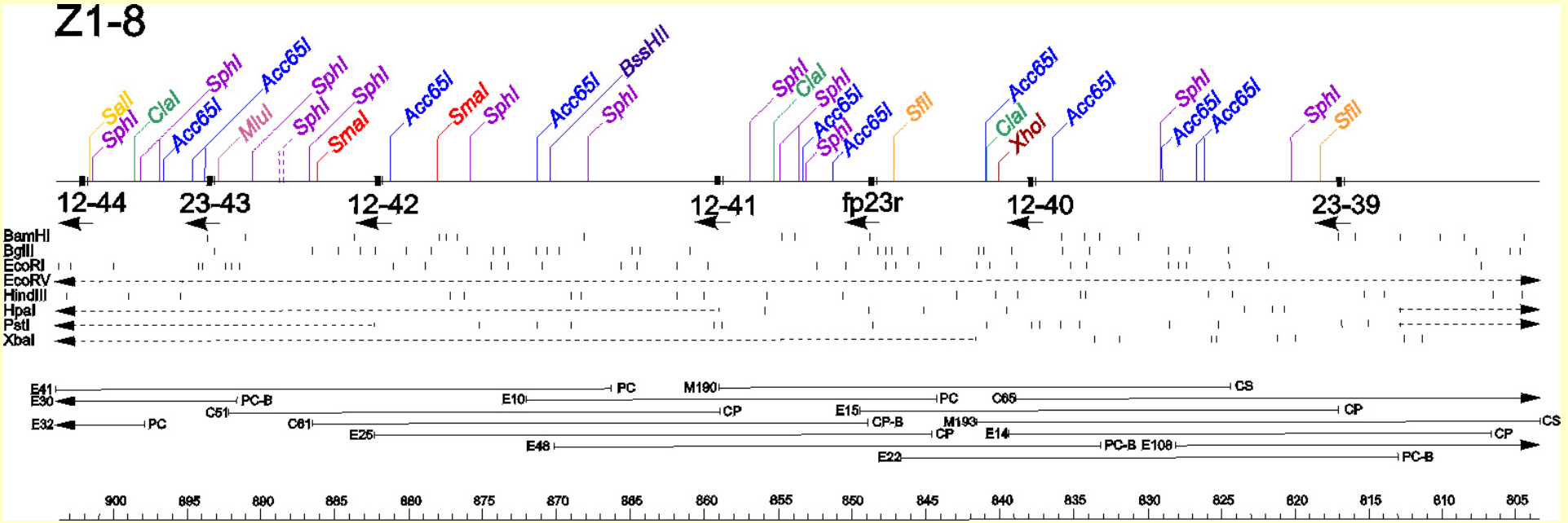
SphI
Acc65I
Acc65I
SfiI
ClaI
Acc65I
SphI
SfiI
SphI
Acc65I
Acc65I
SfiI
ClaI
Acc65I
SphI
SphI
Acc65I
SphI
SmaI
Acc65I
SfiI
ClaI
SphI
2-35
8-34
22-33
19-32
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
M94
M81
M90
CS
B77
B72
Cos330N7
CP
PC
PC
M95
CS
B49
CP
Cos330N14
B100
710
705
700
695
690
685
680
675
670
665
660
655
650
645
640
635
630
625
620


Z1-7
SmaI
SphI
XhoI
Acc65I
(Acc65I)
SfiI
ClaI
MluI
12-38
23-37
dv-36
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
C65
C76
M193
E14
E108
E17
C55
E16
E104
E100
B77
B72
Cos330N7
PC
CP
CP-B
CS
B-CP
810
805
800
795
790
785
780
775
770
765
760
755
750
745
740
735
730
725
720
715
710


Z1-8
SalI
SphI
ClaI
Acc65I
MluI
SmaI
BssHII
XhoI
SfiI
12-44
23-43
12-42
12-41
fp23r
12-40
23-39
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
E41
E30
E32
C51
C61
E25
E48
E10
M190
E15
E22
C65
M193
E14
E108
PC
PC-B
CP
CP-B
CS
PC-B
900
895
890
885
880
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865
860
855
850
845
840
835
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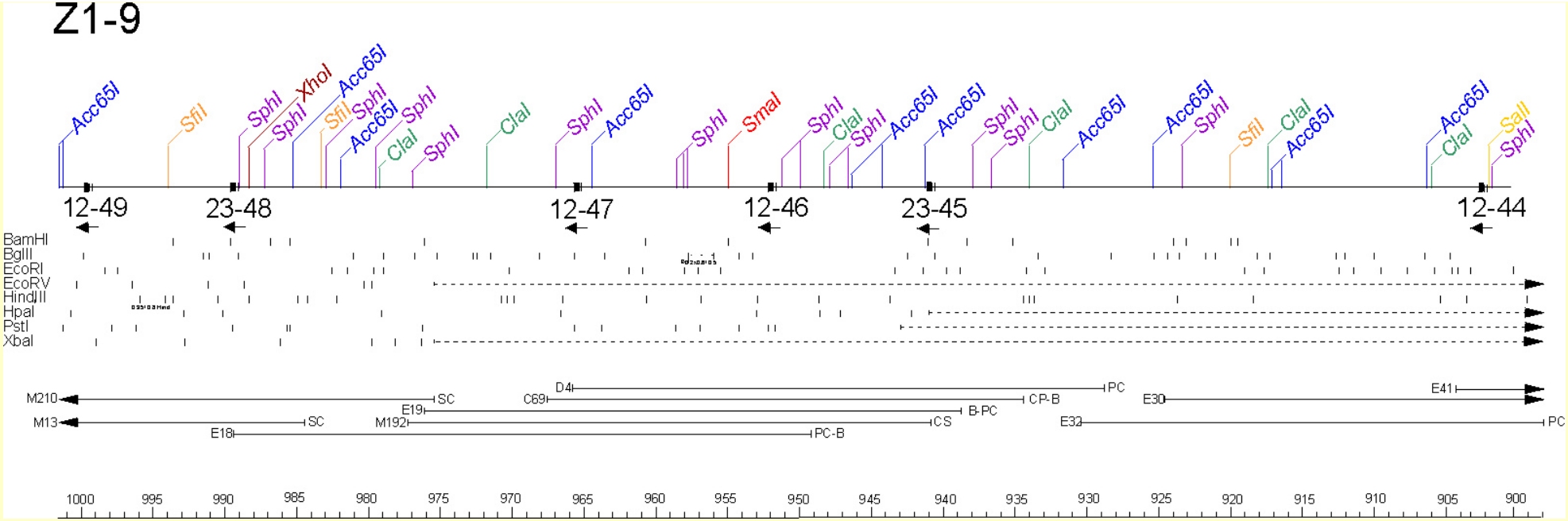
825
820
815
810
805


Z1-9
Acc65I
SfiI
SphI
XhoI
SfiI
ClaI
SmaI
SalI
12-49
23-48
12-47
12-46
23-45
12-44
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
M210
SC
C69
D4
PC
CP-B
E30
E41
M13
E19
B-PC
E18
M192
CS
E32
PC-B
1000
995
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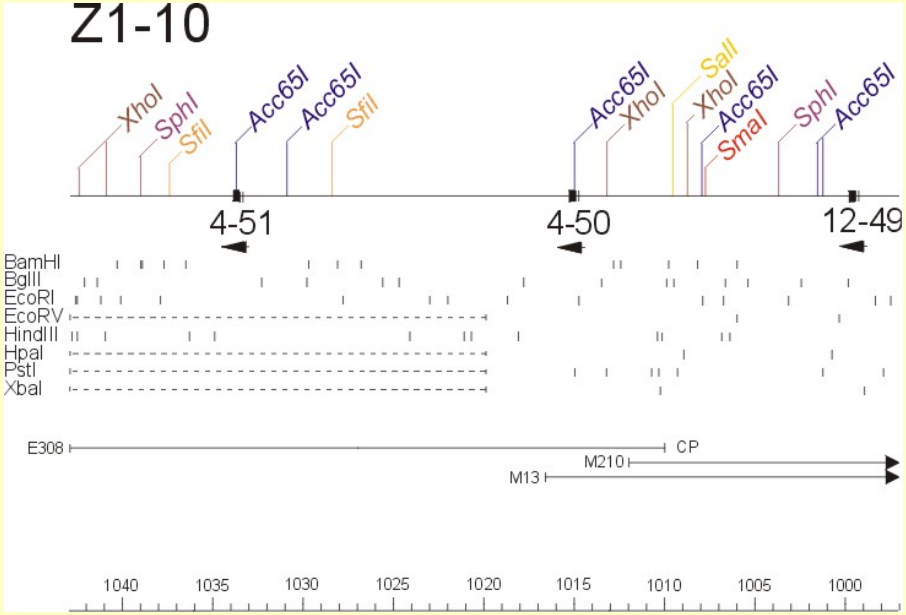
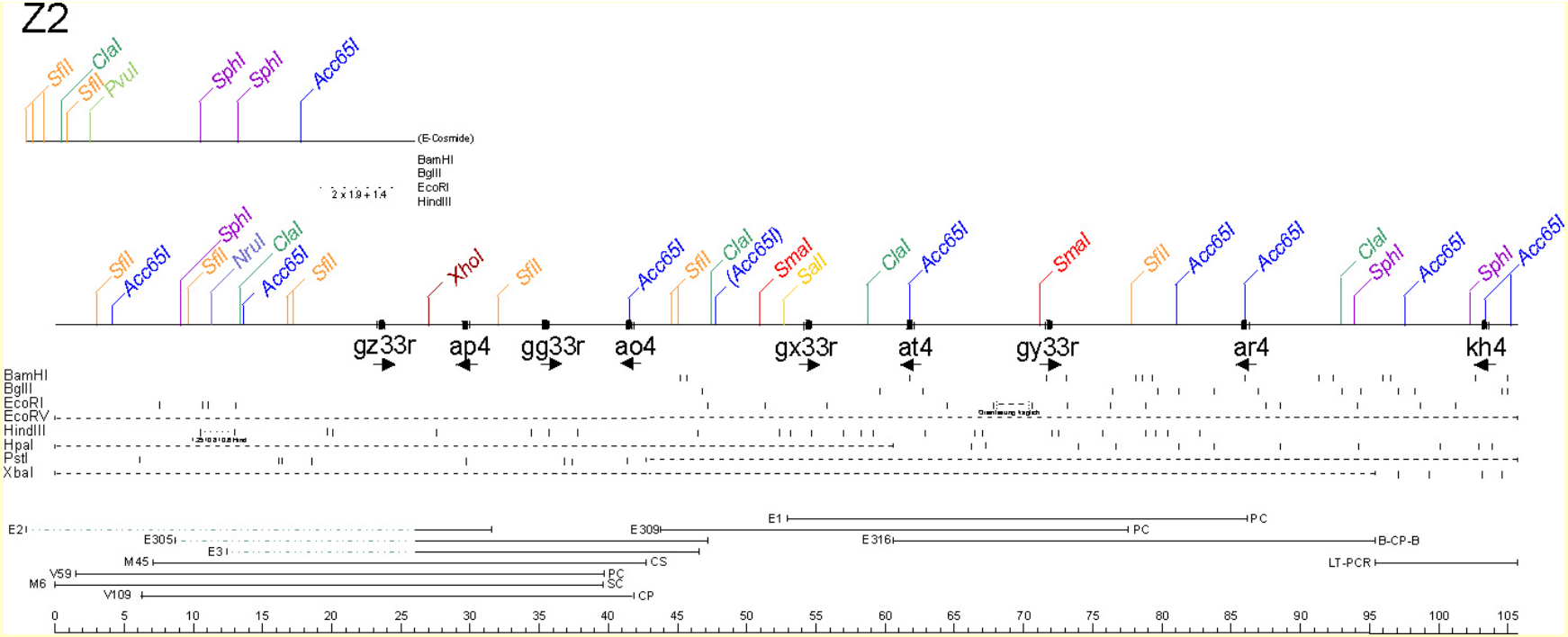
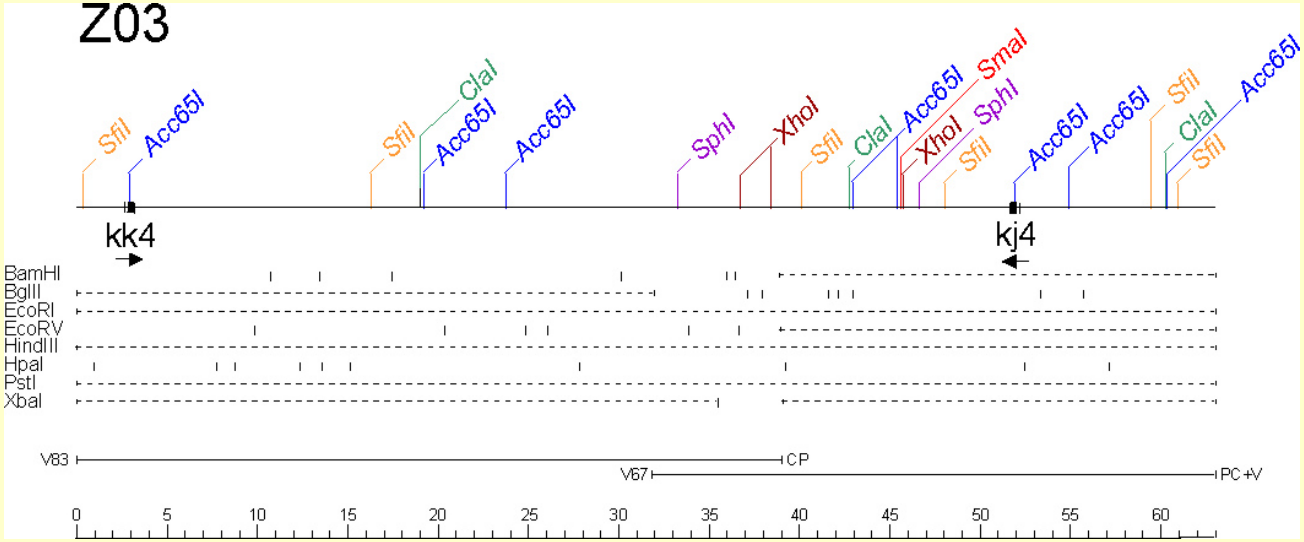
935
930
925
920
915
910
905
900


Z1-10
XhoI
SphI
SfiI
Acc65I
SalI
SmaI
4-51
4-50
12-49
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
E308
CP
M210
M13
1040
1035
1030
1025
1020
1015
1010
1005
1000





The 5' part of the mouse immunoglobulin k locus. Eur. J. Immunol 1999, 29: 2065-2071.

ABSTRACT

The 5' region of the mouse k locus comprises 63 Vk genes in six contigs of together 1.5 Mb, including one which links the region to the central part of the locus. The region of the k locus described here contains Vk1, Vk2, Vk9/10, Vk11, Vk12/13, Vk20, Vk24, Vk32, Vk33/34 and Vk38C genes as well as the VkRF gene and, towards the center of the locus, a number of Vk4/5 genes. Near the 5' end of the locus interspersed a-tubulin gene - like sequences were found. At its 3' side the region borders on the Vk4/5 contigs of the central region of the locus which is described in the accompanying report (T. Kirschbaum et al., 1999). In a concluding section the main features of the structure of the mouse k locus are summarized: nine contigs of together 3.1 Mb were constructed. Assuming about 250 kb of still uncloned DNA in the gaps between the contigs the size of the k locus is estimated to be close to 3.4 Mb, at least 90% of which has been cloned. 140 Vk genes and 18 relics were sequenced, the most 5' situated gene being a functional Vk24 gene. There is evidence for the existence of two to five additional Vk genes in the locus. 56 of the Vk genes are in the same 5', 3' polarity as JkCk, 76 in opposite polarity and for eight the polarity is still undetermined.

For restriction maps of the 5'-part of the locus, see below in (e).

(d) Thiebe, R., Schäble, K. F., Bensch, A., Brensing-Küppers, J., Heim, V., Kirschbaum, T., Lautner-Rieske, A., Mitlöhner, H., Ohnrich, M., Pourrajabi, S., Röschenthaler, F., Schwendinger, J., Wichelhaus, D. P., Zocher, I., and Zachau, H. G.

The variable genes and gene families of the mouse immunoglobulin k locus. Eur. J. Immunol 1999, 29: 2072-2081.

ABSTRACT

118 mouse Vk genes are described which, together with the 22 Vk genes reported previously (T. Kirschbaum et al., this Journal 1998. *28:* 1458 - 1466) amount to 140 genes that had been cloned and sequenced in our laboratory. For 73 of them cDNAs are known, i.e. they have to be considered functional genes, although ten genes of this group have 1bp-deviations from the canonical promoter, splice site or heptanucleotide recombination signal sequences. 20 Vk genes have been defined as only potentially functional since they do not contain any defect, but no cDNAs have been found (yet) for them. 47 of the 140 Vk genes are pseudogenes. In addition 18 relics, i. e. highly diverged and / or truncated genes, and five orphon Vk genes have been sequenced. There are indications for two to five Vk genes or pseudogenes to exist in the k locus which we have not yet been able to clone. This is still very close to the 140 Vk genes of the mouse k locus previously postulated (T. Kirschbaum et al., this Journal 1996, **26:**1613 - 1620). The 140 Vk genes and pseudogenes were assigned to 18 gene families, four of them being one-member families. This differs from previous enumerations of the families only by the combination of the Vk 9 and Vk 10 families and by the addition of the Vk dv gene as a new separate family. Sequence identity usually was 80% or above within the gene families and 55 – 80% between genes of different families. Many of the mouse Vk gene families show significant homologies to the human ones indicating that Vk gene diversification predated in evolution the divergence of the primate and rodent clades.

Note added in proof: the sequencing of an additional Vk9/10 gene, called bv9, is described.

Appendix to the report by R. Thiebe et al.: Karlheinz F. Schäble, Rainer Thiebe, Alexander Bensch, Jutta Brensing-Küppers, Verena Heim, Thomas Kirschbaum, Rosemarie Lamm, Marion Ohnrich, Soheil Pourrajabi, Franz Röschenthaler, Jürgen Schwendinger, Daniel Wichelhaus, Ines Zocher and Hans G. Zachau

Characteristics of the immunoglobulin Vk genes, pseudogenes, relics and orphons in the mouse genome. Eur. J. Immunol. 1999, 29: 2082-2086.

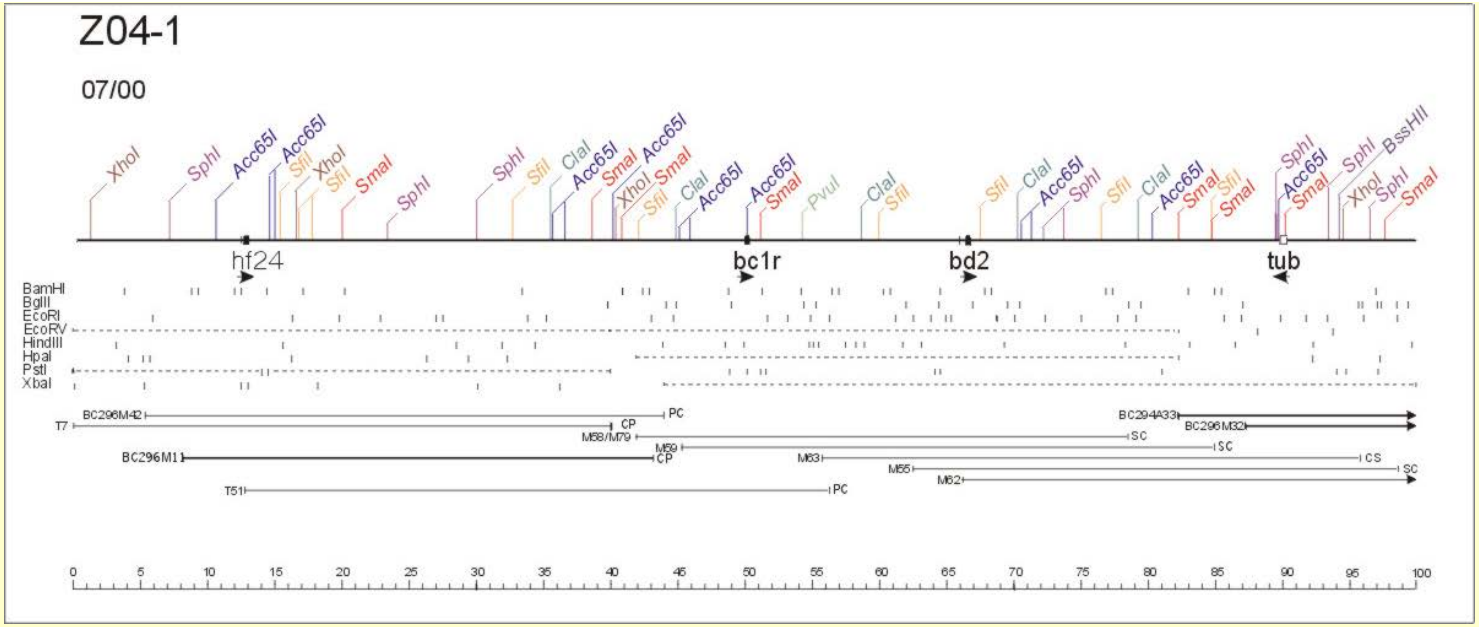
(e) Röschenthaler, F., Hameister, H. and Zachau, H. G. (2000)

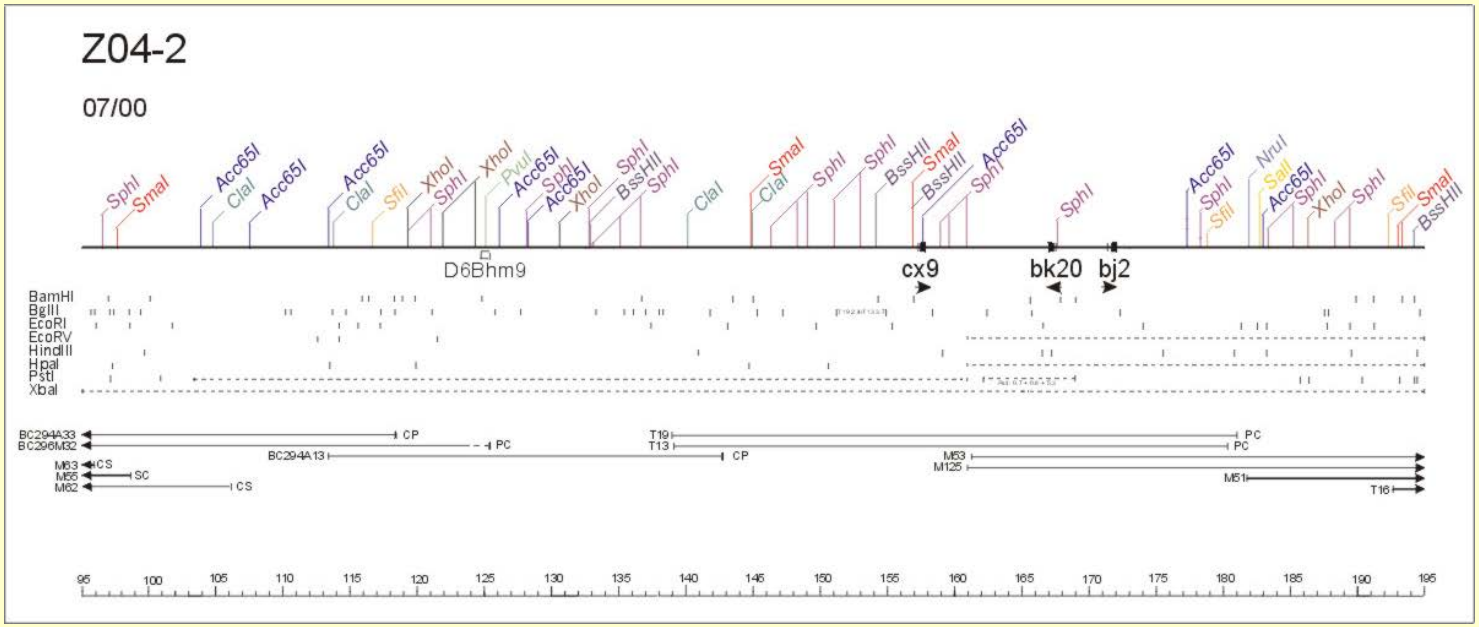
The 5' part of the mouse immunoglobulin k locus as a continuously cloned structure. Eur.J. Immunol. 2000, 30: 3349-3354.

ABSTRACT

Five contigs of the 5' part of the immunoglobulin k locus (F. Röschenthaler et al., 1999) have been linked by cosmid clones prepared from bacterial artificial chromosomes (BACs) and by PCR. One of the previously defined contigs which contains three pseudogenes (Z7) was shown by fluorescence in situ hybridization to be located near the k locus on chromosome 6, but not within the locus. Two additional Vk genes were identified, a potentially functional Vk 24 gene and a pseudogene of the Vk 9/10 family. This brings the number of localized and sequenced Vk genes in the locus to 140. The 5' part of the k locus is now one contig of 1.88 Mb; it comprises 82 Vk genes. Other contigs of the locus are 65kb, 105kb and 1.04 Mb in size and contain 2, 5 and 51 Vk genes, respectively. The contigs are separated by gaps of 10-40 kb each.

Restriction Maps Z04-01 to Z04-05


Z04-1
07/00
hf24
bc1r
bd2
tub
BamHI
BglI
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
BC296M42
BC294A33
BC296M32
BC296M11
T51
M63
M55
M62
M59
M58/M79
T7
CP
PC
SC
CS


Z04-2
07/00
D6Bhm9
cx9
bk20
bj2
BamHI
BglI
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
BC294A33
BC296M32
BC294A13
T19
T13
M53
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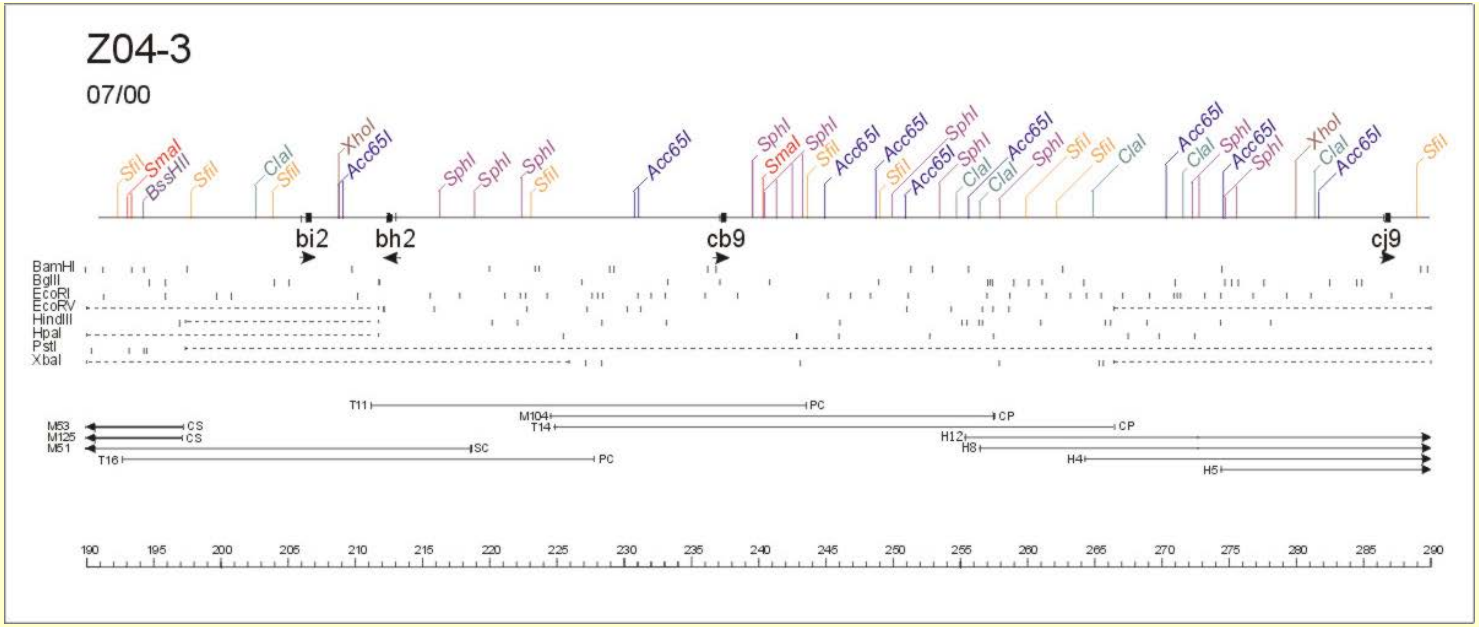
M51
T16
M63
M55
M62
CP
PC
SC
CS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07/00
bi2
bh2
cb9
cj9
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
M53
M125
M51
T16
T11
M104
T14
H12
H8
H4
H5
CS
SC
PC
CP
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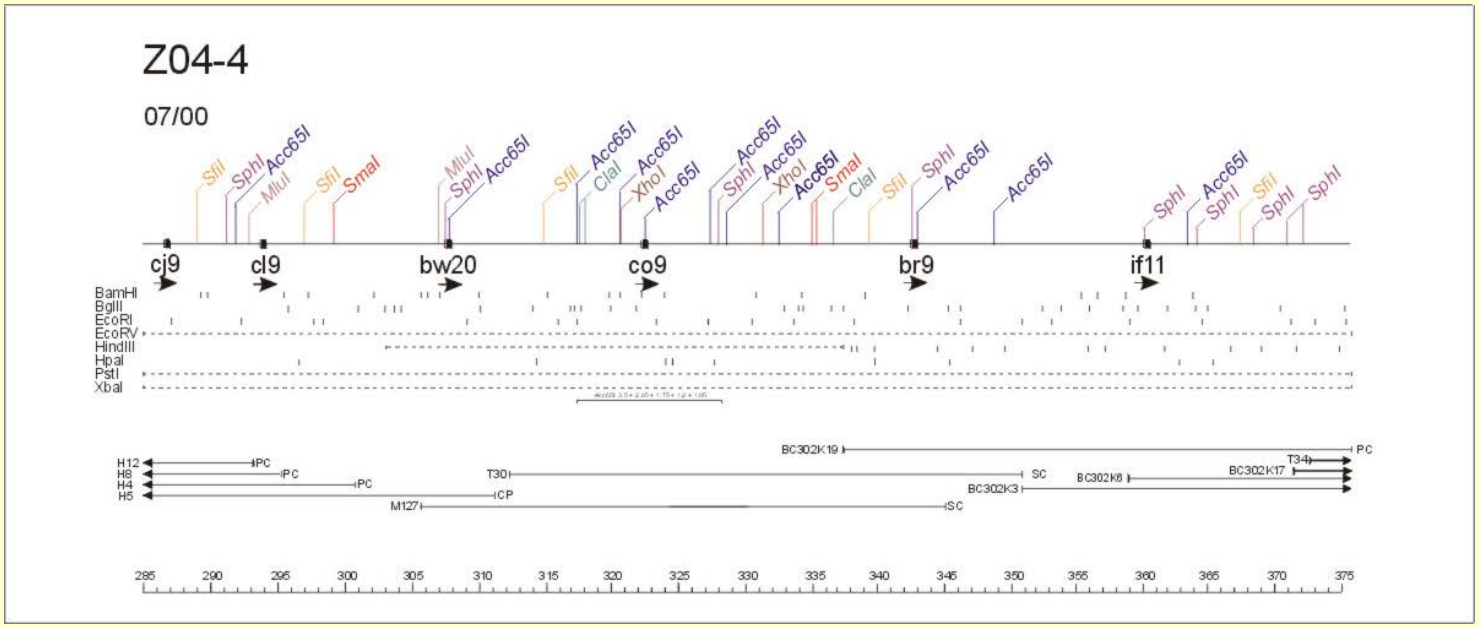
Z04-4
07/00
cj9
cl9
bw20
co9
br9
if11
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
H12
H8
H4
H5
T30
M127
BC302K19
BC302K3
BC302K6
BC302K17
T34
PC
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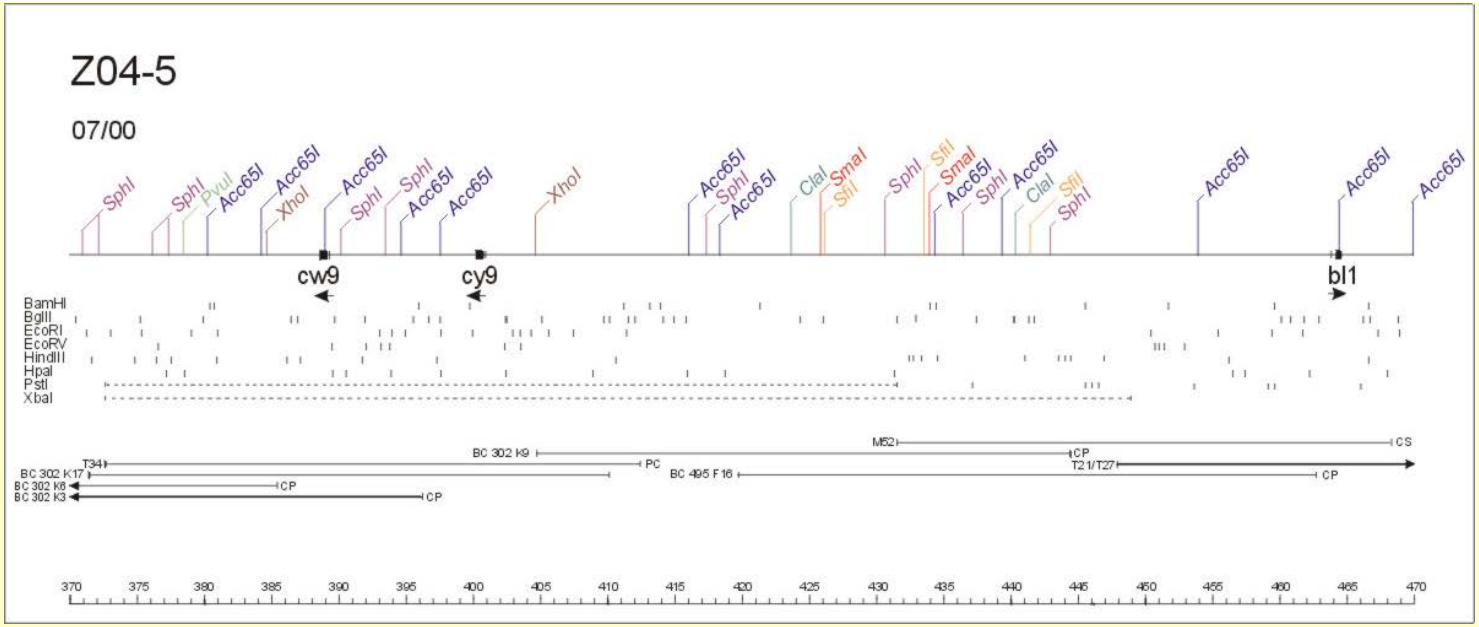
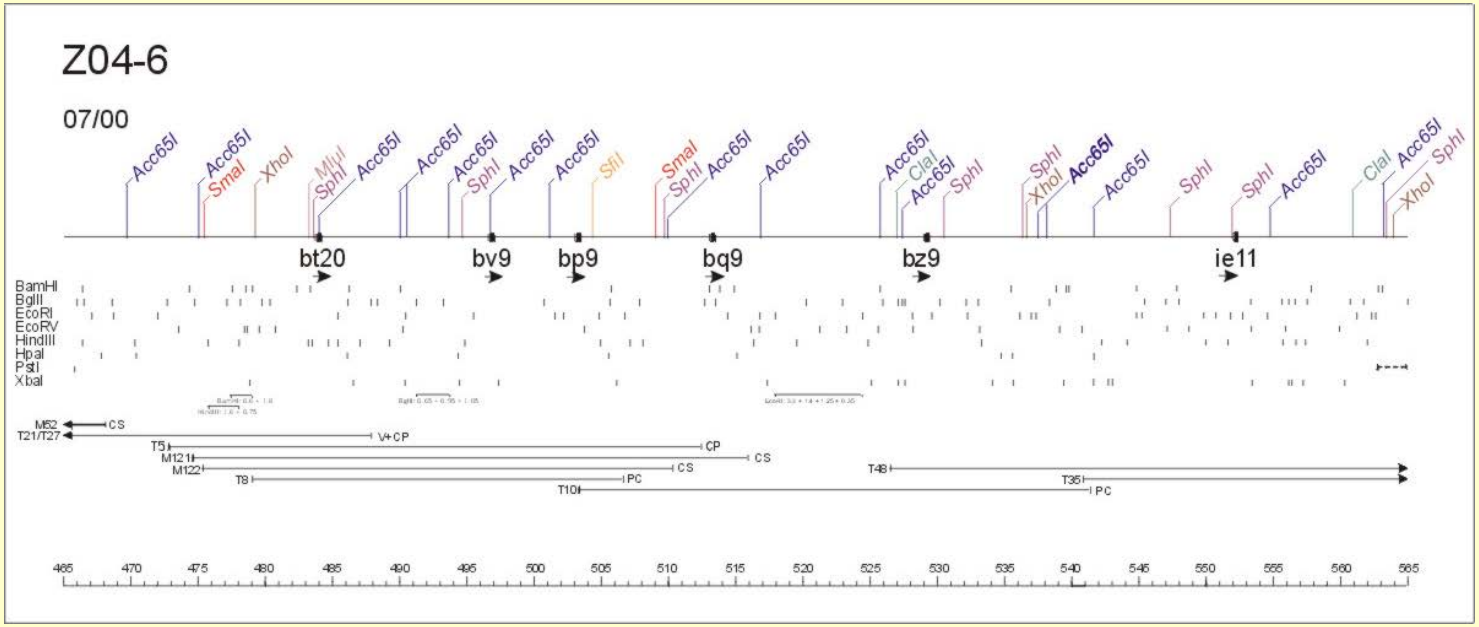
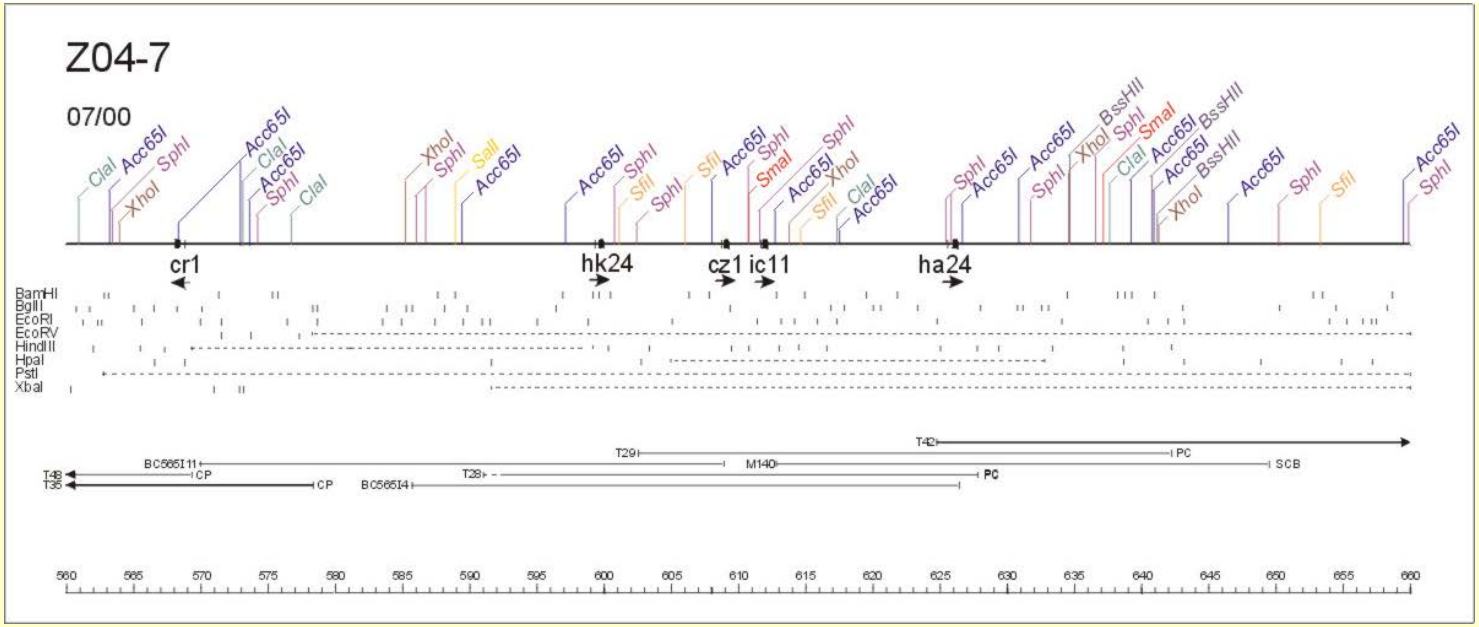


Restriction Maps Z04-06 to Z04-10

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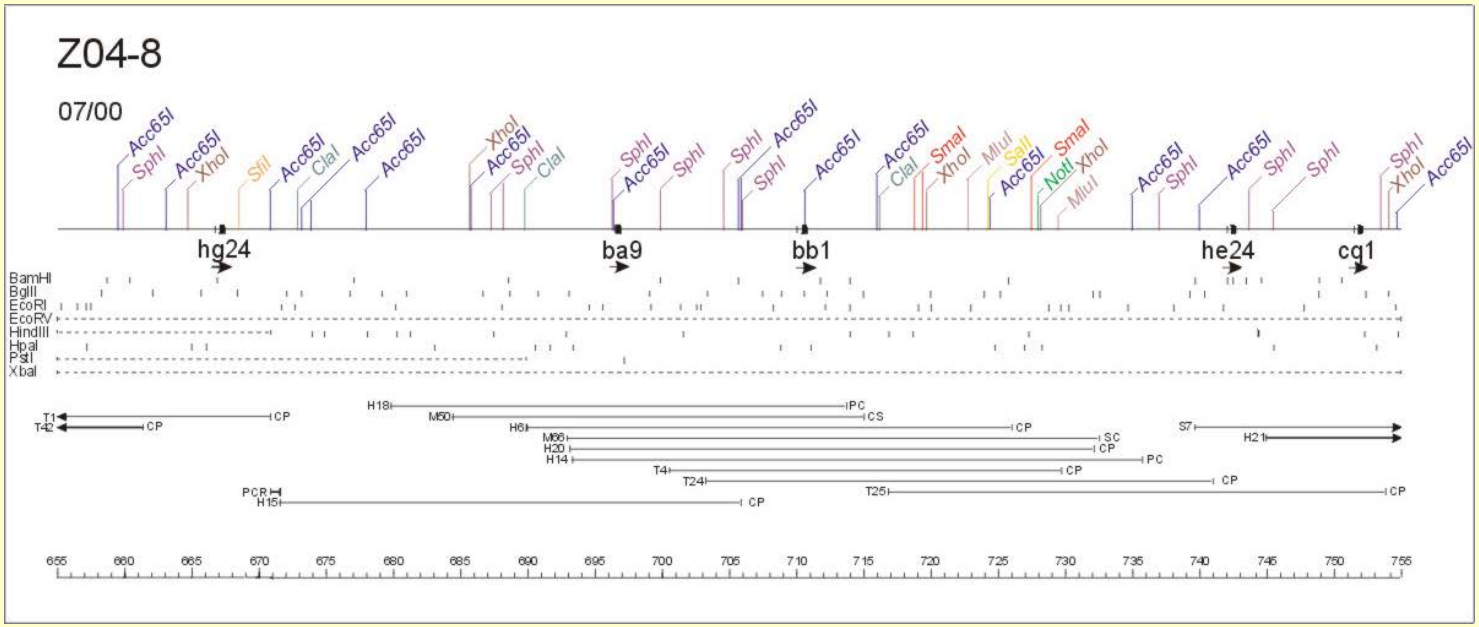
cr1
hk24
cz1 ic11
ha24
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI


Z04-8
07/00
hg24
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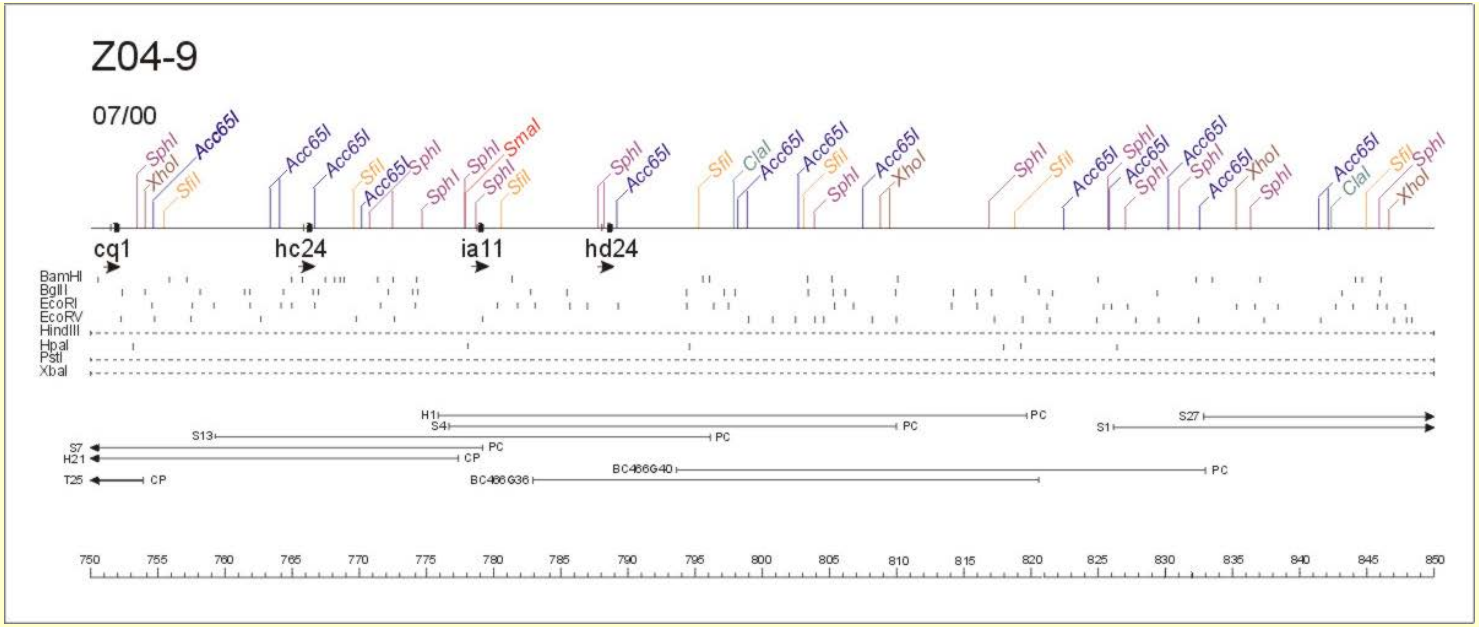
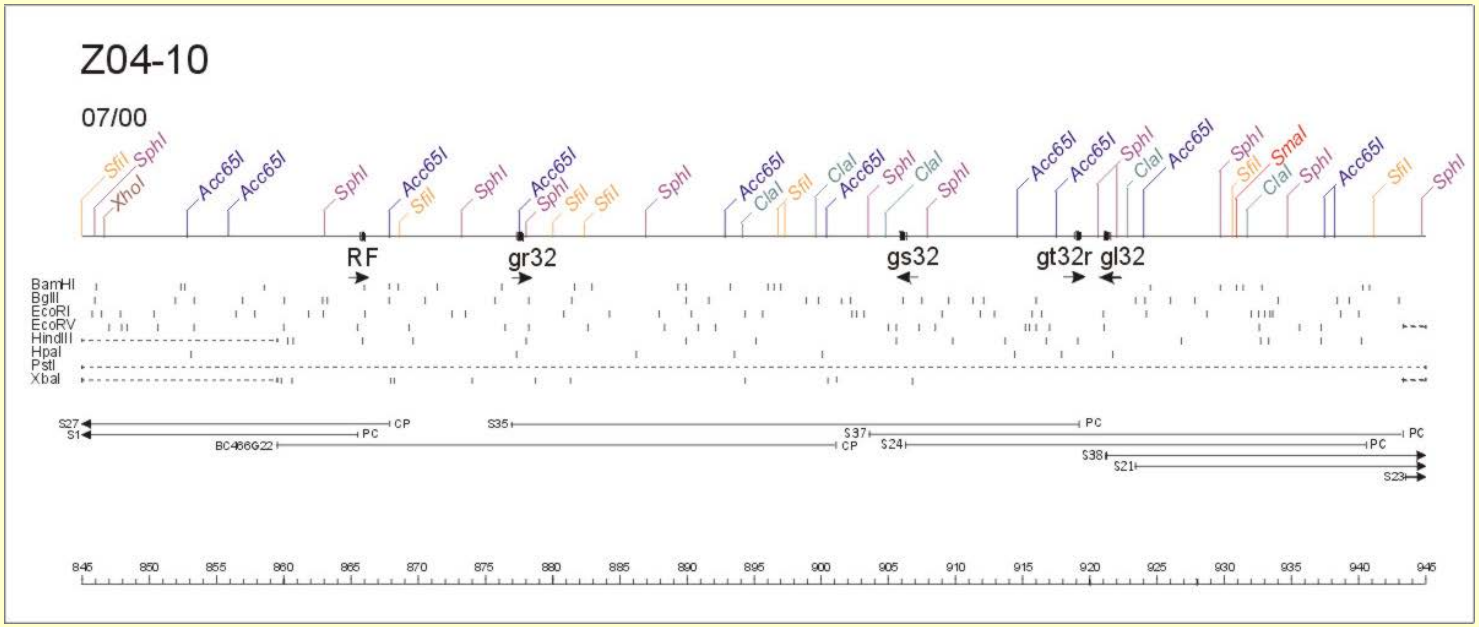
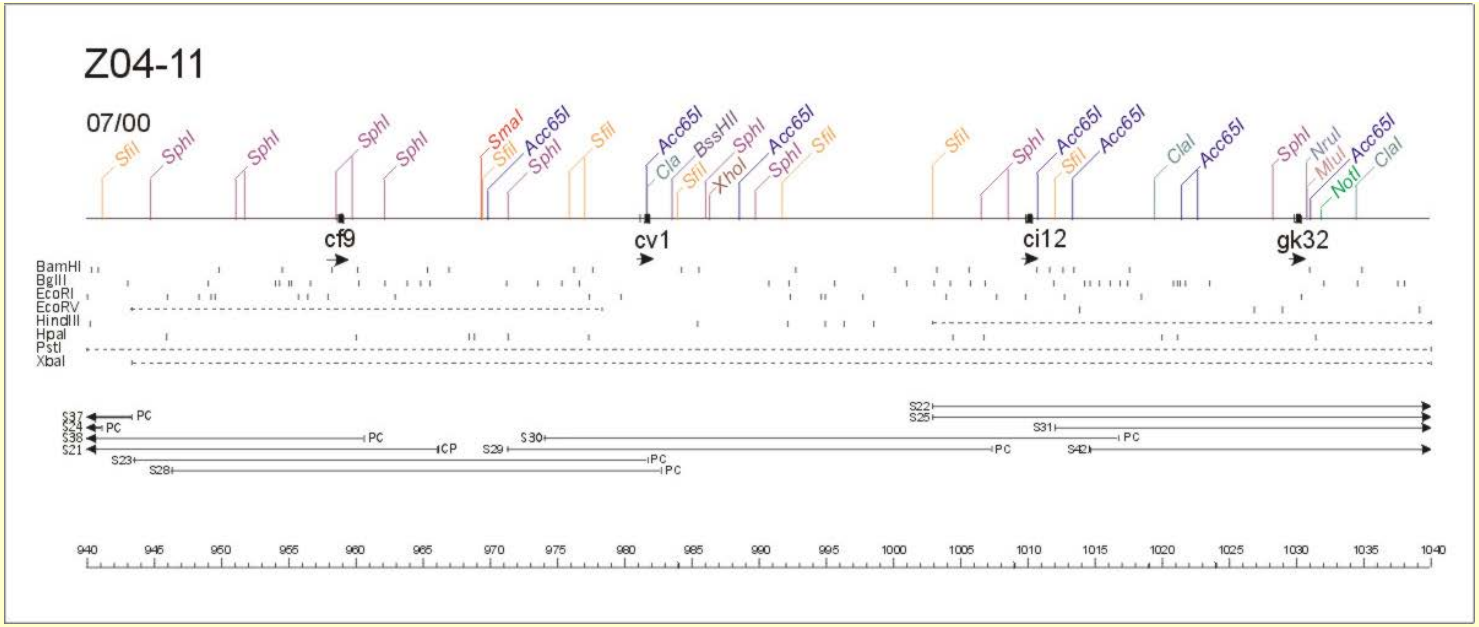
bb1
he24
cg1
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI





Restriction Maps Z04-11 to Z04-15


Z04-11
07/00
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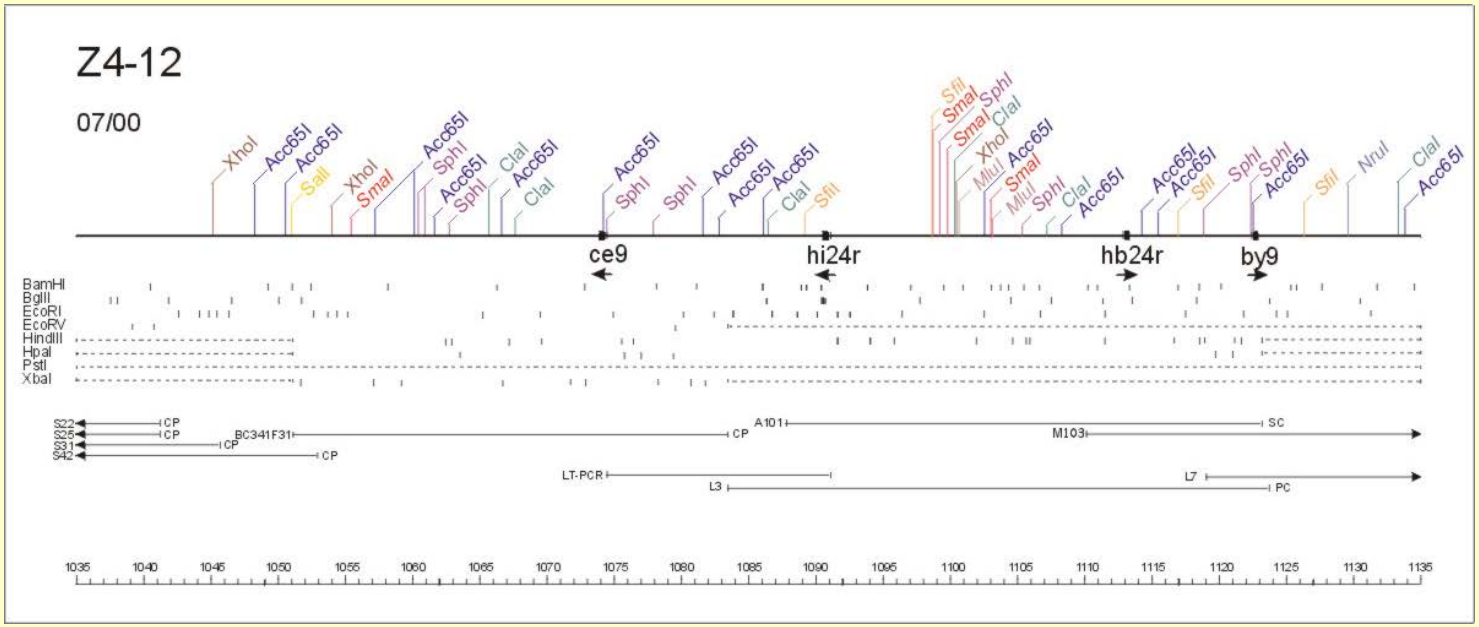
cv1
ci12
gk32
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
940
945
950
955
960
965
970
975
980
985
990
995
1000
1005
1010
1015
1020
1025
1030
1035
1040


Z4-12
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hb24r
by9
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
BC341F31
A101
M103
LT-PCR
L3
L7
1035
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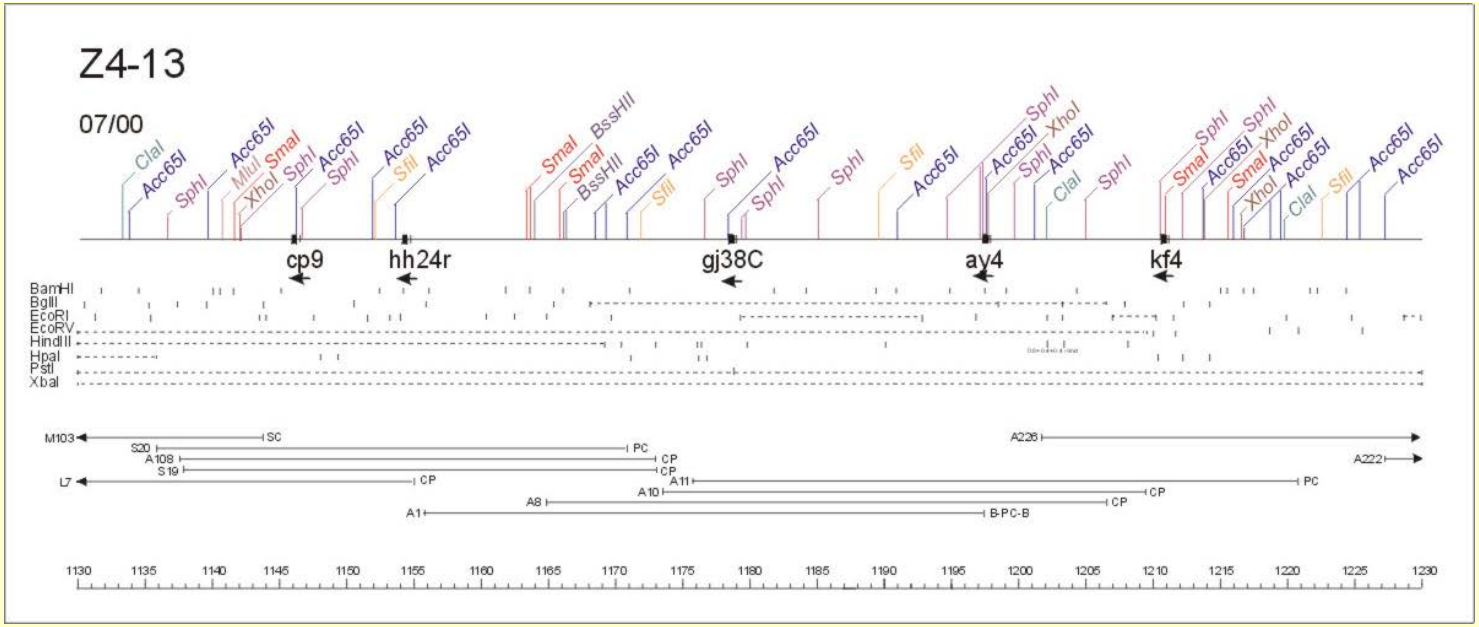
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PstI
XbaI
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S19
L7
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A8
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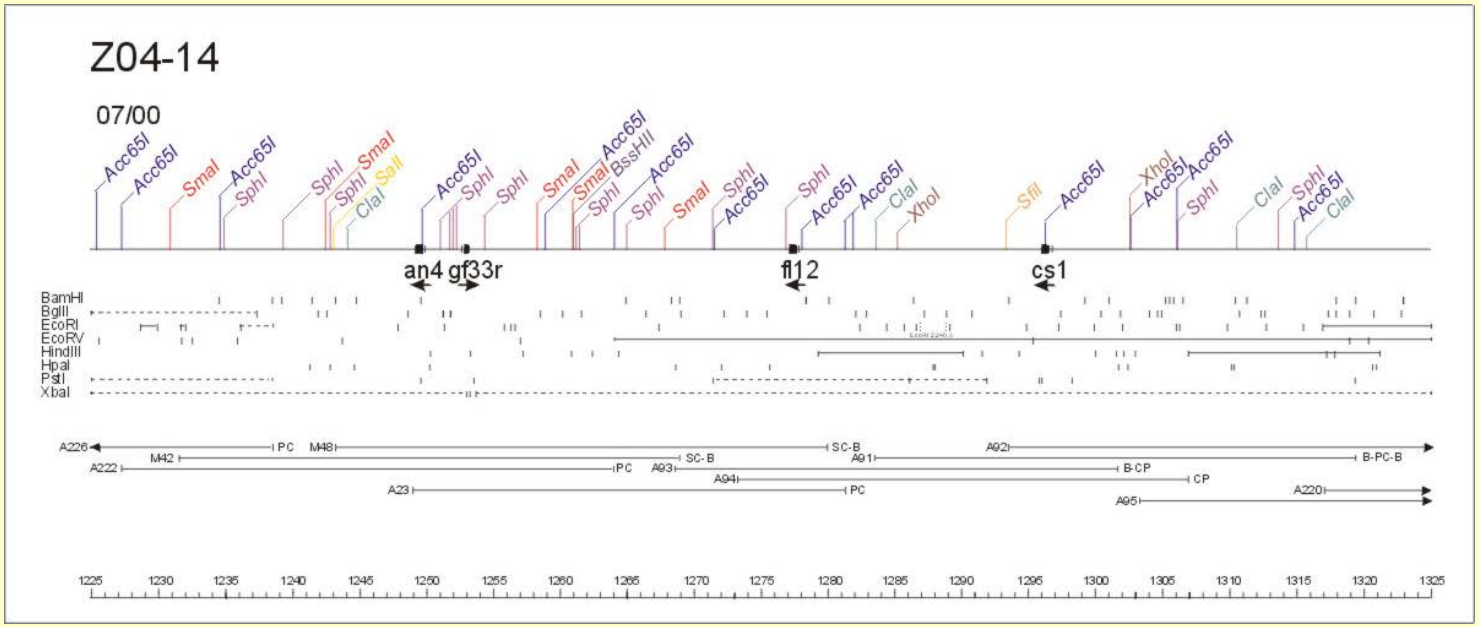
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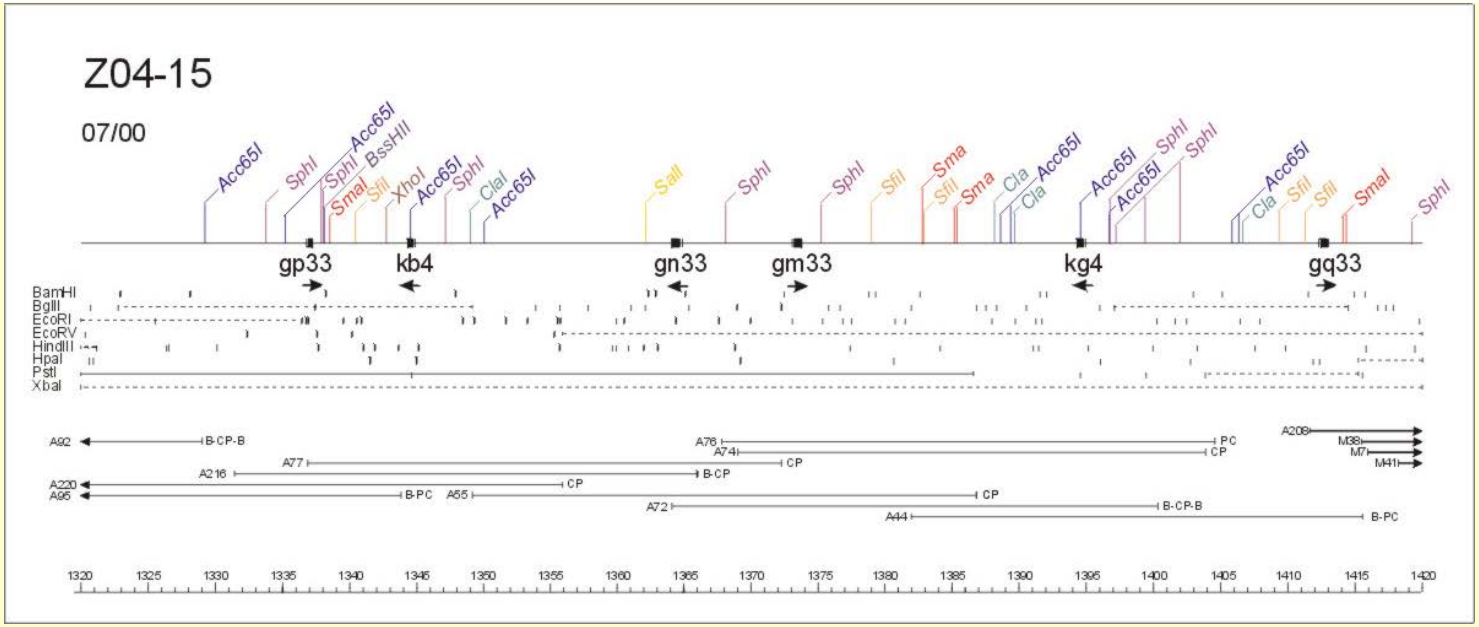
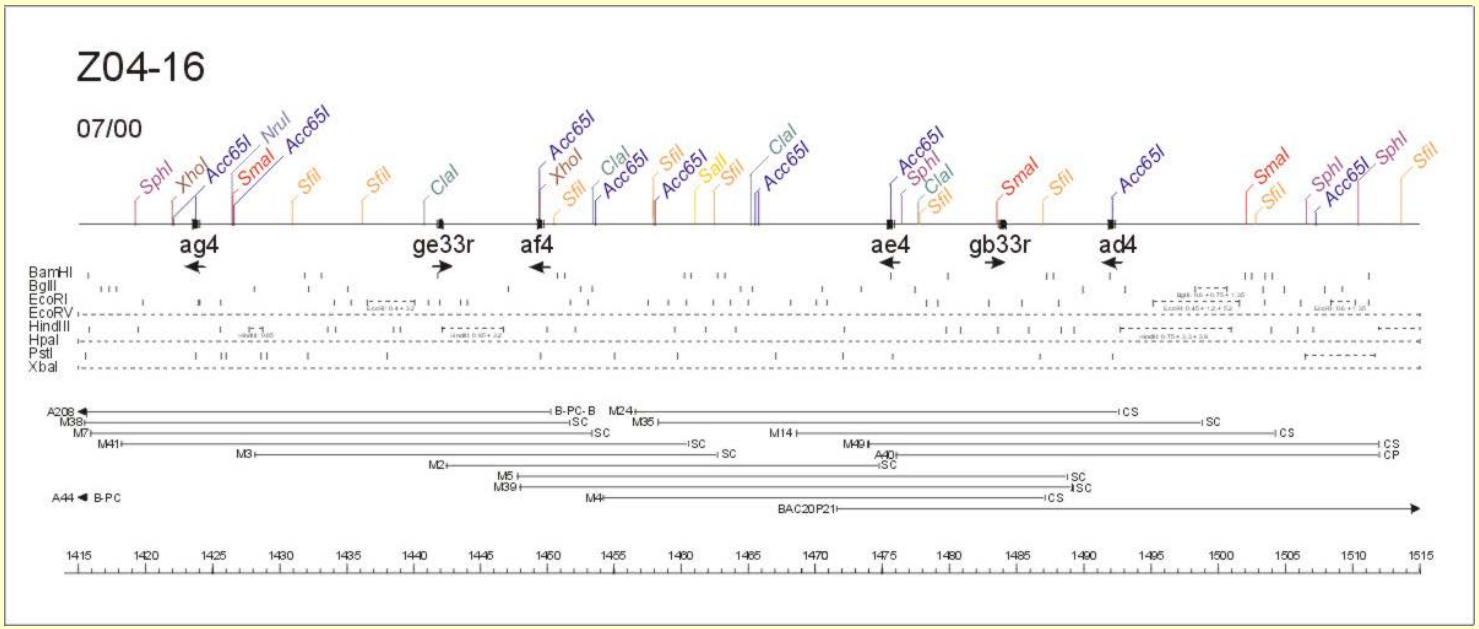
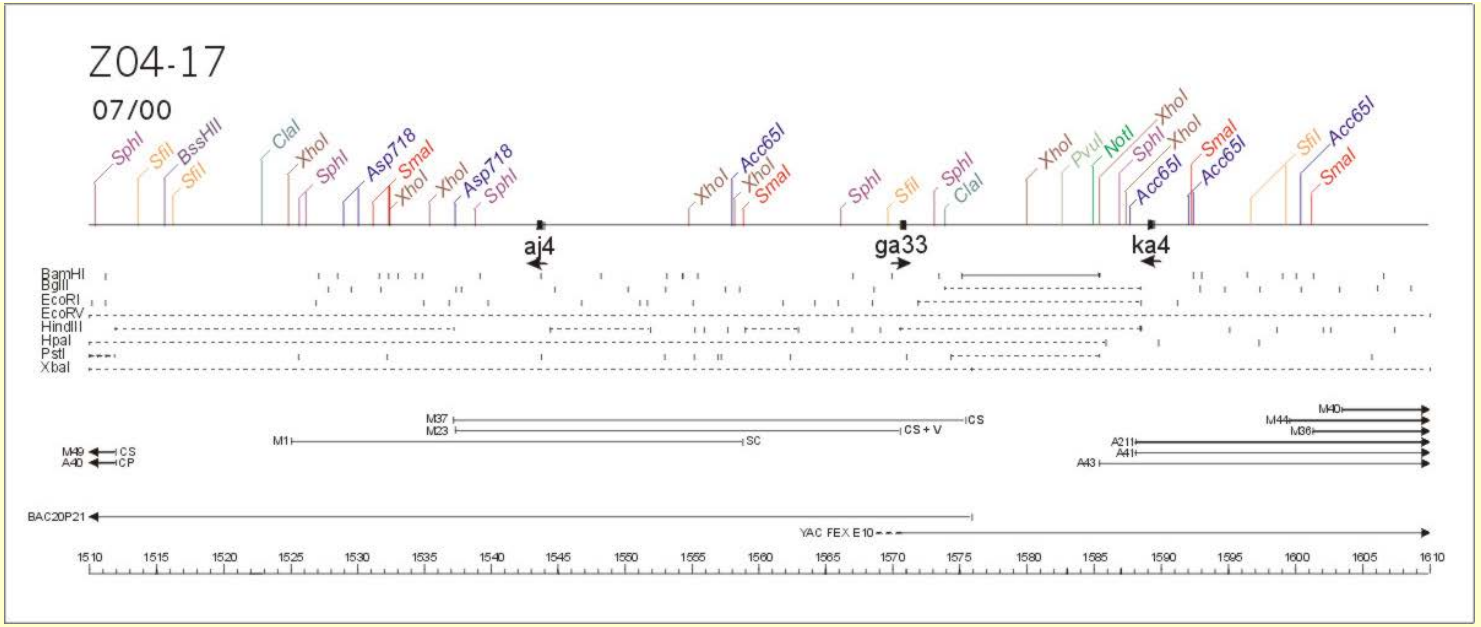


Restriction Maps Z04-16 to Z04-20

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SfiI
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ClaI
XhoI
PvuI
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SphI
XhoI
Acc65I
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SmaI
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ga33
ka4
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
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M23
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M1
SC
M49
A40
CS
CP
M40
M44
M36
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A41
A43
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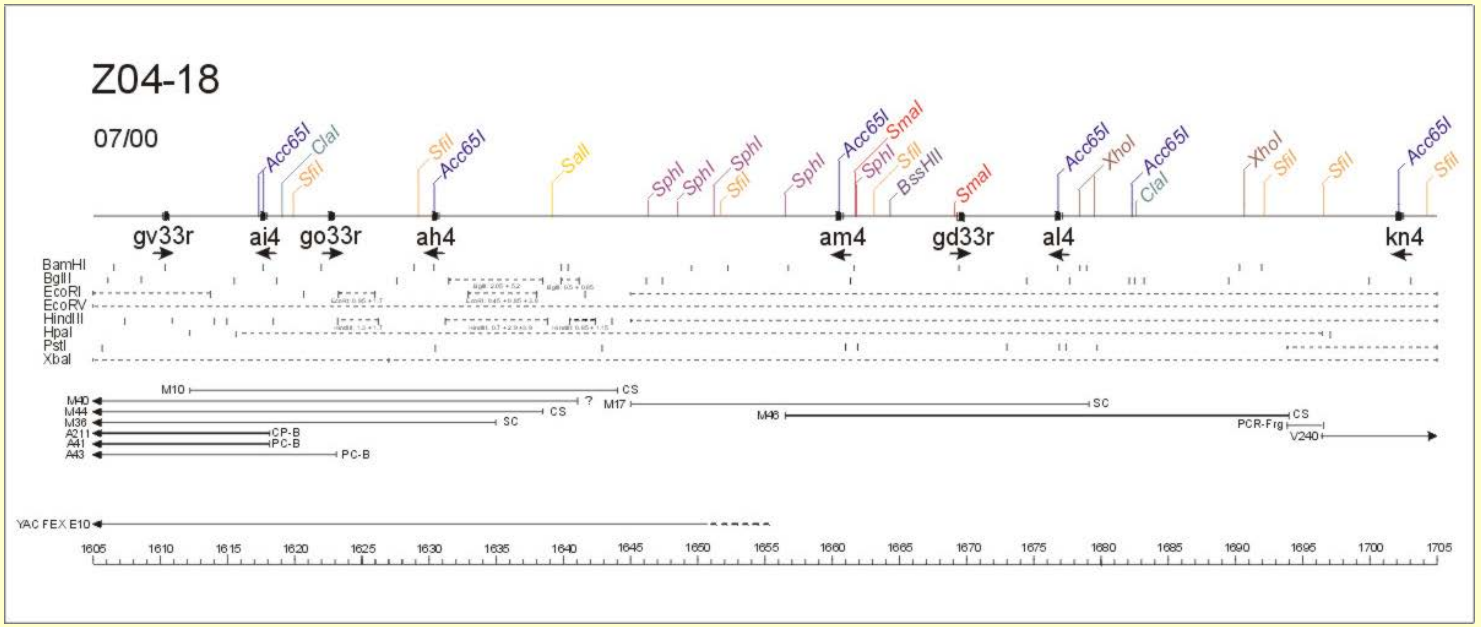
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BssHII
SmaI
Acc65I
XhoI
Acc65I
ClaI
XhoI
SfiI
SfiI
Acc65I
SfiI
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ah4
am4
gd33r
al4
kn4
BamHI
BglII
EcoRI
EcoRV
HindIII
HpaI
PstI
XbaI
M10
CS
M40
M44
M36
A21I
A41
A43
CS
SC
CP-B
PC-B
PC-B
M17
SC
M46
CS
PCR-Frg
V240
YAC FEX E10
1605
1610
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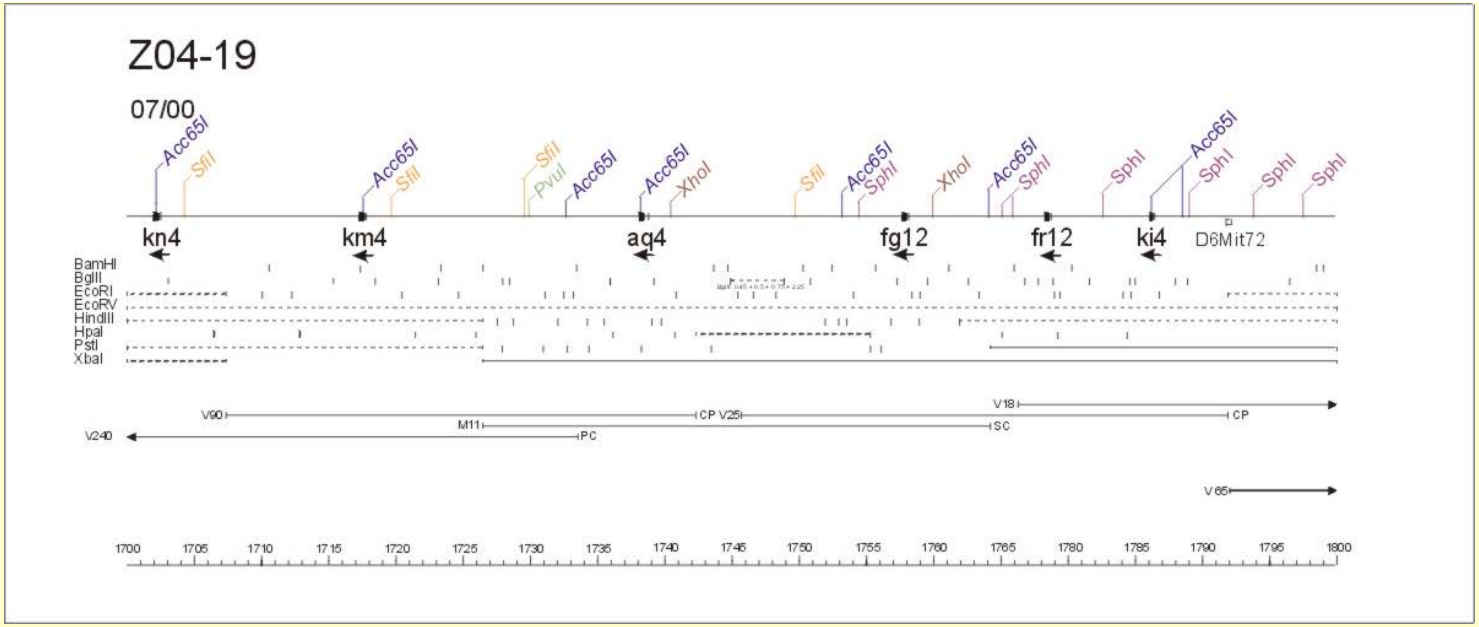

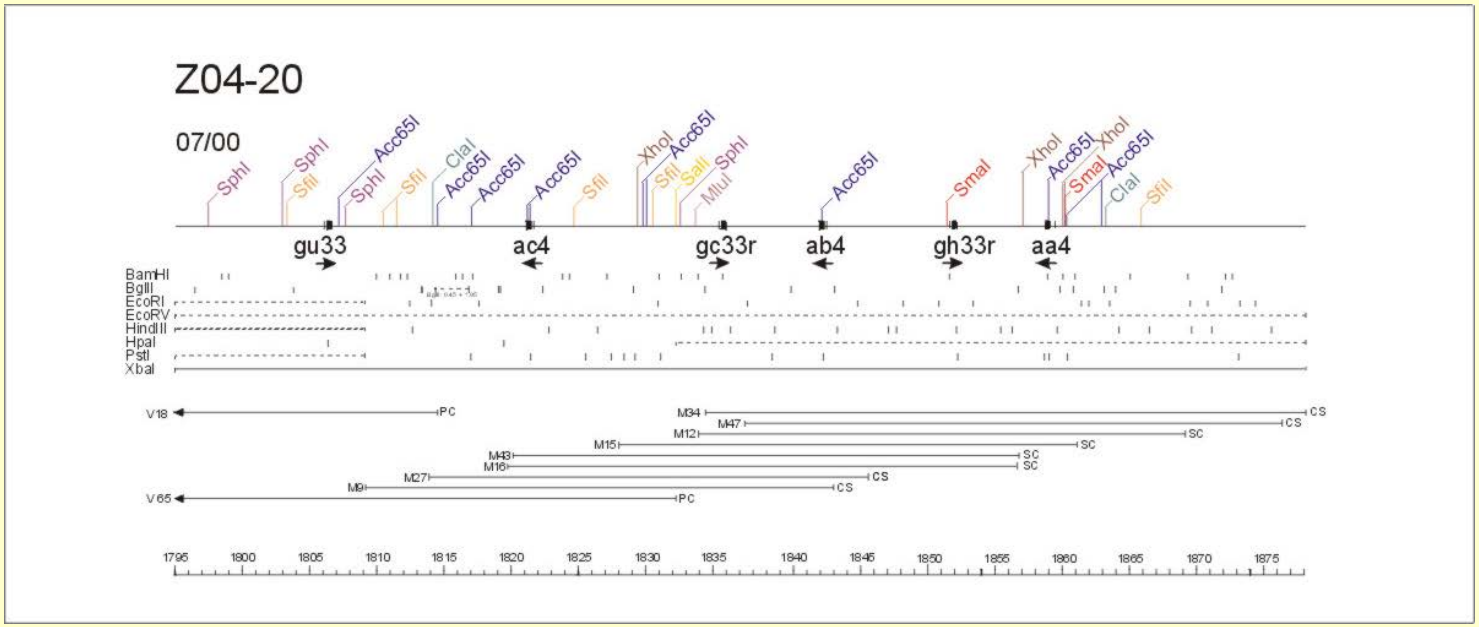

Legend to the detailed restriction maps complementing the data of the printed version

Earlier experimental data on the present contig Z4 are reported in ref. (b) and (c).

The designations and abbreviations are as in the above legend of ref. (b).

Most BACs are shown only in Fig. 1 of the printed version. In the map of the Internet file only those BACs, which are important for contig linking are included; cosmid clones prepared from the BACs carry the first number and the letter of the BAC designation plus our running number of the screening experiment, e. g. BC466G36 or BC466G40.

PCR: the gap near Vk hg24 (Z4-8) was bridged using primers 5'-TAG GTC ACA AAT CAG GCC TCA ACA -3' on cosmid T1 and 5'-AGT TAC ACT GTA GTT ATC TTC AGG-3' on cosmid H15 with BAC 506K14 as template.

The gap on Z4-14 in the Vk ce9/hi24r region was spanned by LT-PCR with primers derived from the two genes and BAC 341F8 as template.

The gap on Z4-21 was closed by LT-PCR with primers derived from the M46 and V240 termini and YAC F1122 as template; a 2.8 kb PCR fragment was obtained; details in ref. (c).

The unique probe mentioned in section 2.4 of ref. (c) is a 0.8 kb EcoRI-HindIII fragment prepared from cosmid A92 (Z4-16) near its PB end.

The Vk genes, relics and orphons described in the above five publications (ref. a-e) are compiled in Tables 1, 2, and 3, respectively. The Tables are updated versions of the ones in the Appendix by Schäble et al. to ref. (d) and include the Vk genes reported in refs. (b) and (e).

Table 1: The Vk gene segments of the mouse k locus

Sub-groups	Gene[a]	Contig[b]	EcoRI [c]	Charact-eristics [d]	--	Acc.no.[e]	Literature [f]	cDNA [g]
vk1	bb1	Z4-8	3.9	+	--	AJ231201	M28131; Vk 1A [7]	S54757
--	bl1	Z4-5	5.3	+	[2]	AJ231203	D00082 (4); K 18.1 [8]	--
--	cq1	Z4-8	6.9	- ex	[3]	AJ231204	--	--
--	cr1	Z4-7	4.2	+	[3]	AJ231205	D00081 (1); K1A5 [8]	--
--	cs1	Z4-14	2.4	+	[4]	AJ231206	--	M64152
--	cv1	Z4-11	12.6	+/- pr	[3]	AJ231207	--	U29595
--	cz1	Z4-7	6.2	- pr, ex	--	AJ231208	--	--
vk2	2-35	Z1-6	5.2	- rss	[1]	AJ231200	--	--
--	bd2	Z4-1	3.2	+	--	AJ231196	Z72384; Vk2 (70/3) [34]	M25996
--	bh2	Z4-3	5.3	- rss	--	AJ231197	--	--
--	bi2	Z4-3	9.0	+	--	AJ231198	--	M34622 (3)
--	bj2	Z4-2	1.8	+	--	AJ231199	Z72382; Vk2 (70/1) [34]	Z17401
vk4/5	4-50	Z1-10	4.4	+	--	AJ235938	M10115 (1); k-(2154) [11];R13[12]	--
--	4-51	Z1-10	10.2	+	[5]	AJ235939	V01565 ; V-L8 [13]; L8 [37]	--
--	aa4	Z4-20	8.0	+	[5]	AJ231209	H4 [37]	X59197
--	ab4	Z4-20	8.0	- rss	[6]	AJ231210	--	--
--	ac4	Z4-20	13.0	+/- rss	[6]	AJ231211	38con [37]	M20464 (3)
--	ad4	Z4-16	6.8	+	[4]	AJ231212	H1 [37]	--
--	ae4	Z4-16	1.8	+	[4]	AJ231214	M25999 (1);4.68 [10];81con(1)[13]	--
--	af4	Z4-16	8.0	+	--	AJ231213	84con (1) [38]	X65009 (5)
--	ag4	Z4-16	4.4	+	--	AJ231215	R11 [37]	--
--	ah4	Z4-18	1.2	+	--	AJ231216	72con [38]	--
--	ai4	Z4-18	1.2	+	--	AJ231217	128con [38]	Z22050
--	aj4	Z4-17	1.0	+/- ex	--	AJ235940	H8 [37]	U54534 (3) [h]
--	al4	Z4-18	11.0	+	--	AJ231218	18con [38]	--
--	am4	Z4-18	6.9	+	--	AJ231219	K01641 (1); 70Z/3 [12]; 67con [38]	M64156
--	an4	Z4-16	3.7	+/- rss	--	AJ231224	R2 [37]	X14098 (1)
--	ao4	Z2	8.5	- ex, sp	[6]	AJ231220	118con [38]	--
--	ap4	Z2	4.2	+	--	AJ231221	76con [38]	AF021872
--	aq4	Z4-19	1.6	+	[5]	AJ231222	H13 [37]	S61341
--	ar4	Z2	8.6	+	[5]	AJ231223	--	--
--	at4	Z2	8.7	+	[5]	AJ231225	nq2.6.1 [37]	M19906 (4)
--	ay4	Z4-13	5.4	+	[4]	AJ231226	--	U73592 (4)
--	ka4	Z4-17	2.8	- ex	[5]	AJ231227	--	--

--	kb4	Z4-15	1.4	+	[5]	AJ231228	X05555; X24 [14]; H6 [13]	--
--	kf4	Z4-13	1.3	+/- rss	[5]	AJ231229	--	X14099
--	kg4	Z4-15	8.5	- pr, ex	[4]	AJ231230	--	--
--	kh4	Z2	4.0	+	[5]	AJ231231	M25998; 4.58 [10]	U60468
--	ki4	Z4-19	1.9	- pr, ex, rss	[3]	AJ231232	--	--
--	kj4	Z3	6.9	+	[3]	AJ231233	K00884; S107B [15]; R1 [37]	--
--	kk4	Z3	6.5	+	[3]	AJ231234	S71118; H3 [16]; H3 [37]	M34586
--	kl4	Z3	1.8	-	[3]	AJ235941	--	--
--	km4	Z4-19	8.7	+	[3]	AJ235942	H9 (1) [37]	--
--	kn4	Z4-18	8.7	+	[3]	AJ235943	R9 [37]	--
--	ko4	Z1/Z2	--	+	--	AJ239198	148con (4) [38]	--
vk8	8-16	Z1-3	4.2	+	[1]	Y15977	--	M62929
--	8-18	Z1-3	4.0	- rss	--	Y15979	--	--
--	8-19	Z1-3	9.0	+	[4]	Y15980	--	M34743
--	8-21	Z1-3	15.5	+	[2]	Y15982	--	U62050
--	8-22	Z1-3	4.0	- ex, rss, pr	--	Y15983	--	--
--	8-24	Z1-4	4.0	+	[1]	AJ235944	--	Z22037
--	8-26	Z1-4	4.4	- rss	[1]	AJ235945	--	--
--	8-27	Z1-5	3.7	+/- rss	--	AJ235946	--	X59193
--	8-28	Z1-5	5.2	+	[1]	AJ235947	--	M17488
--	8-30	Z1-5	15.5	+	--	AJ235948	X77142 (5); H8 VL [17]	M34634
--	8-31	Z1-5	1.5	- pr, ex	--	AJ235957	--	--
--	8-34	Z1-5	3.7	+	--	AJ235958	--	--
vk9/10	ba9	Z4-8	3.7	+	--	AJ231235	V01563; L6 [18]	M74713
--	bp9	Z4-6	2.6	- ex	--	AJ231236	--	--
--	bq9	Z4-6	5.7	- ex	--	AJ231237	--	--
--	br9	Z4-4	1.8	- ex, rss	--	AJ231238	--	--
--	bv9	Z4-6	6.1	+	--	AJ242670	V00804 (2); Vk 41 [33]	AF045508 (1)
--	by9	Z4-12	2.5	+/- rss	--	AJ231239	M18407 (1); 3386 5' V [19]	(44)
--	bz9	Z4-6	4.0	-ex	--	AJ277844	--	--
--	cb9	Z4-3	2.4	+	--	AJ231241	--	X96756 (3)
--	ce9	Z4-12	5.3	+/- rss	--	AJ239197	X05795; Vk Id^{CR} [32]	M20281
--	cf9	Z4-11	5.3	+	[3]	AJ231243	--	U18586
--	cj9	Z4-3	6.0	+	--	AJ231244	K00880; MOPC173B [20]	M12191
--	cl9	Z4-4	5.3	- pr, ex	--	AJ231245	--	--
--	co9	Z4-4	5.5	- ex, rss	--	AJ231246	--	--
--	cp9	Z4-13	3.9	+/- rss	[3]	AJ231247	M54906; AJ2 [21]	M36261
--	cw9	Z4-5	12.5	+	--	AJ231248	AF003294; Igk-V9a [22]	X02177 (2)
--	cx9	Z4-2	10.5	- rss, ex, sp	--	AJ231249	Z72385; Vk9B(294A9) [34]	--
--	cy9	Z4-5	3.0	+	--	AJ231250	AF003295; Igk-V9b [22]	U20061
vk11	ia11	Z4-9	5.7	- sp, ex	--	AJ231252	--	--
--	ic11	Z4-7	1.5	- rss, ex	--	AJ231253	--	--
--	ie11	Z4-6	0.9	-rss, ex	--	AJ231255	--	--
--	if11	Z4-4	5.4	+	--	AJ231256	X54753; MSI-N17 [23]	U21579
vk12/13	12-38	Z1-7	10.5	+	--	AJ235951	--	U78500
--	12-40	Z1-8	3.7	- ex	--	AJ235952	--	--
--	12-41	Z1-8	3.0	+	--	AJ235953	M31554 (2); VkRFT2 [24]	L24555
--	12-42	Z1-8	9.8	- ex, rss	--	AJ235954	--	--
--	12-44	Z1-8	3.0	+/- rss	--	AJ235955	--	S61689
--	12-46	Z1-9	12.0	+	--	AJ235956	--	U29621

--	12-47	Z1-9	1.8	- ex, rss	--	AJ235959	--	--
--	12-49	Z1-9	5.0	- ex, pr	--	AJ235960	--	--
--	ci12	Z4-11	2.7	+	[3]	AJ235949	--	Y13991 (2)
--	fg12	Z4-19	4.5	- ex, pr	--	AJ235933	--	--
--	fl12	Z4-14	15.0	+	--	AJ235950	--	X59181
--	fr12	Z4-19	5.5	- pr, sp, ex	[3]	AJ235934	--	--
vk19/28	19-13	Z1-2	14.0	+	[2]	--	J00569; identical to V_{TNP} [43]	X75103
--	19-14	Z1-3	5.9	+	[1]	Y15975	--	M26002
--	19-15	Z1-3	9.2	+	[1]	Y15976	--	M19766
--	19-17	Z1-3	8.5	+	--	Y15978	--	M36250
--	19-20	Z1-3	3.7	+	--	Y15981	--	M31259
--	19-23	Z1-4	9.2	+	--	AJ235961	--	AF045512
--	19-25	Z1-4	5.9	+	--	AJ235962	--	AF004328(3)
--	19-29	Z1-5	3.7	+	[1]	AJ235967	--	--
--	19-32	Z1-6	2.6	+/- pr	[1]	AJ235968	M14360 (3); V-Ser [25]	L30147
vkdv	dv-36	Z1-7	3.6	+	[1]	AJ235966	--	--
vk20	bk20	Z4-2	1.8	- sp, ex	--	AJ231257	Z72386; Vk20(294A9) [34]	--
--	bt20	Z4-6	12.0	+	--	AJ231258	--	M55318
--	bw20	Z4-4	10.5	+	--	AJ231259	--	X16678
vk21	21-1	Z1-1	3.4	+	--	--	X16955; Vk 21G [42]	M31270
--	21-2	Z1-1	20.0	+	--	--	X16954; Vk 21A [42]	M83099
--	21-3	Z1-1	20.0	+	--	Y15967	K0216255; 18.5kb Vk [41]	X65094
--	21-4	Z1-1	8.5	+	--	Y15968	8.5kb Vk [41]	U29629
--	21-5	Z1-1	9.0	+	--	--	K02161; 9.5kb Vk 21C[41]	M21522
--	21-6	Z1-1	6.0	- ex	--	Y15969	6.0kb Vk [41]	--
--	21-7	Z1-1	1.5	+	--	Y15970	K02158; 1.6kb Vk [41]	Z22098
--	21-8	Z1-2	4.3	-	--	Y15971	4.0kb Vk [41]	--
--	21-9	Z1-2	4.3	+	--	Y15972	4.0kb Vk [41]	--
--	21-10	Z1-2	16.0	+	--	--	K02160;16kb Vk , Vk 21B [41]	Z22079
--	21-11	Z1-2	5.8	-	--	Y15973	6.0kb Vk [41]	--
--	21-12	Z1-2	1.4	+	--	Y15974	K02159; 1.5kb Vk , Vk 21E [41]	U39824
vk22	22-33	Z1-6	4.5	+	[2]	AJ235965	AF044198; Vk 22G [40]	U29423
vk23	23-37	Z1-7	10.0	+	--	AJ235963	--	Z17400
--	23-39	Z1-8	11.0	+/- rss	--	AJ235964	M26003 (2); 23.32 [10]	S82437
--	23-43	Z1-8	1.6	+	--	AJ235973	--	M34528
--	23-45	Z1-9	1.6	+	--	AJ235974	X13937; B1P8-7b-2 [26]	X86546
--	23-48	Z1-9	14.5	+	--	AJ235975	V01564; L7 [18]	X70264
vk24/25	ha24	Z4-7	9.0	- ex	--	AJ231260	--	--
--	hc24	Z4-9	1.8	- ex	--	AJ132682	--	--
--	hd24	Z4-9	2.2	- ex, pr	[3]	AJ231262	--	--
--	he24	Z4-8	6.0	+	--	AJ132683	K02418 (2); Vk 24B [31]	S74547
--	hf24	Z4-1	10.0	+	--	AJ231263	--	AF045509
--	hg24	Z4-8	13.5	+	--	AJ231264	J00553; Vk_{167} [27]	M19910 (2)
--	hk24	Z4-7	6.2	+	--	AJ277843	--	--
vk32	gk32	Z4-11	12.0	- ex, rss	[3]	AJ231267	--	--
--	gl32	Z4-10	3.1	- ex, rss	[3]	AJ231268	--	--
--	gr32	Z4-10	3.8	+/- sp	--	AJ231269	U27011 (2); 1-10 [28]	M34636
--	gs32	Z4-10	5.8	- pr , ex	--	AJ231270	--	--
vk33/34	ga33	Z4-17	3.4	- pr, ex, rss	--	AJ231271	--	--
--	gm33	Z4-15	3.4	+	[4]	AJ231273	M35156; Igk-V34c [29]	--
	gn33	Z4-15	4.0	+	[5]	AJ231274	k	U29631 (3)

--								
--							M35154 (4); Ig -V34b [29]	
--	gp33	Z4-15	2.7	- pr, ex, rss	[5]	AJ231275	--	--
--	gq33	Z4-15	9.5	- pr, ex, rss	[5]	AJ231276	--	--
--	gu33	Z4-20	6.7	- ex	[3]	AJ235969	--	--
vk38c	gj38c	Z4-13	9.7	+	[4]	AJ235935	M64442; [30]	M57588
vkRF	RF	Z4-10	3.1	+	--	AJ235936	--	X14621
sad[i]	--	Z1-5	2.1	--	[35]	AJ132684	--	--
tub	--	Z4-1	2.0	--	[36]	AJ235970	--	--

a The designations of the genes in contigs that have not been linked to Jk -Ck are in the order of their discovery (see section 2.1 in the main part of the report by Thiebe et al.). Abbreviated designations are used, e. g. aa4 for a Vk 4/5 gene. For comments on the gene ko4 see section 2.5. of Thiebe *et al*.

b The contig designations are the ones used in refs (a,b,e).

c The EcoRI fragment sizes are in kb.

d +, - and +/- designate, respectively, potentially functional genes, pseudogenes and genes with defects, for which, however, a cDNA can be found in the data base (for definitions see section 2.2 of ref (d) and ref (e)); the location of defects is noted as pr, promoter; sp, splice sites; ex, stop codons, small deletions or insertions in the exons; rss, recombination signal sequences. In the adjacent column, references to theses prepared in our laboratory are given [1 – 6], in which the respective sequencing strategies are described.

e Accession numbers of gene sequences described in refs. (a-e) and Schäble et al. at the EBI data library.

f Accession numbers of and references to the corresponding genomic gene sequences in the literature (including the designations of the genes) are noted. Rearranged genes or excised circular products are listed, if no gene sequences in the germline configuration were found in the data library. If there are several entries in the data library, one has been selected for this Table. There is no additional comment, if the compared genes were identical in their exon 2 sequences; in case differences were found, the number of bp is noted in parenthesis.

g Accession numbers of expression products, usually cDNAs, derived from the germline genes. Only such products are considered which differ from the respective germline sequences in 5 positions or less (see 2.2 Thiebe *et al*.). As in f) only one data base entry is selected and the number of sequence differences is noted in parenthesis. Ref. 44 at by9 refers to the expression at an extremely low level.

h The finding of a cDNA [39] for the gene aj4 which has a stop codon in exon 2 is discussed in 2.5 of Thiebe *et al.*

i The accession number in ref.(b) is misprinted.

Table 2: Relics in the mouse k locus

--	**Relic** [a]	**Contig** [b]	**Characteristic fragments** [c]	**Acc.no.** [d]
vk1	bc1r	Z4-1	6.6 EcoRI	AJ231202
vk23	fp23r	Z1-8	2.8 EcoRI	AJ235976
vk24/25	hb24r	Z4-12	2.3 EcoRI	AJ231261
--	hh24r	Z4-13	--	AJ231265
--	hi24r	Z4-12	1.65 EcoRI	AJ231266
vk32	gt32r	Z4-10	4.8 EcoRI	AJ231251
vk33/34	gb33r	Z4-16	2.6 EcoRI	AJ132671
--	gc33r	Z4-20	6.8 EcoRI	AJ132672
--	gd33r	Z4-18	2.6 EcoRI	AJ132673
--	ge33r	Z4-16	1.25 EcoRI	AJ132674
--	gf33r	Z4-14	4.5 EcoRI	AJ231272
--	gg33r	Z2	13 EcoRI	AJ132675
--	gh33r	Z4-20	2.5 EcoRI	AJ132676
--	go33r	Z4-18	2.7 EcoRI	AJ132677
--	gv33r	Z4-18	3.5 Hind III	AJ132678
--	gx33r	Z2	4.0 EcoRI	AJ132679
--	gy33r	Z2	2.5 EcoRI	AJ132680

--	gz33r	Z2	2.5 EcoRI	AJ132681

a The designation of the relics is analogous to the one of the Vk genes and pseudogenes, except that an 'r' is added.

b The contig designations are the ones used in refs (a-e)].

c The sizes of the characteristic fragments are in kb.

d Accession numbers at the EBI data library.

Table 3: The Vk orphons in the mouse genome

--	Orphon [a]	Contig [b]	EcoRI [c]	Acc.no. [d]	Literature [e]
vk1	gw1	O6	11.0	AJ235937	X58991; VkY 1.7 [9]
vk2	be2	O16	5.1	AJ235971	Z72381; Vk2 (68) [34]
--	bn2	O19	1.2	AJ235972	Z72383; Vk2
vk9/10	bg9	O16	1.0	AJ235977	--
--	ca9	O6	2.6	AJ231240	X58992 (1); VkY 9B.8 [9]
--	cc9	O6	4.5	AJ235977	--
vk20	bf20part1	O16	5.1	AJ235930	--
--	bf20part2	O16	6.5	AJ235929	--
--	bu20part1	O19	--	AJ235931	--
--	bu20part2	O19	--	AJ235932	--

a Designations of the orphons. Parts 1 and 2 of the Vk 20 orphons are separated by a repetitive element (see Schäble et al.).

b Contigs on chromosomes 6, 16 and 19.

c EcoRI fragment sizes in kb.

d Accession numbers at the EBI Data Library.

e Accession number of and references to related genes in the literature.

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The immunoglobulin k genes and the k locus of man

The work of our group on the human k locus has been summarized in the following reviews:

- Zachau, H.G. (1995) In: *Immunoglobulin Genes*, 2nd Edition (Honjo, T. and Alt, F.W., Eds.) Academic Press, London-New York, pp. 173-191. 'The human immunoglobulin k genes'

- Zachau, H.G. (1996) The Immunologist 4, 49-54. 'The human immunoglobulin k genes'

- Zachau, H. G. (2000) Biol, Chem. 381, 951 - 954 . 'The immunoglobulin k gene families of human and mouse: a cottage industry approach'.

- Zachau, H.G. (2004) in: Molecular Biology of B Cells (F. Alt, T. Honjo and M. Neuberger Eds.) Elsevier Science, London, pp. 27-36. 'Immunoglobulin k genes of human and mouse'.

The work was concluded by the sequencing of our clones by a Japanese group. The results of the joint work was published recently. The summary of this publication and one figure are shown here:

Evolutionary dynamics of the human immunoglobulin k locus and the germline repertoire of the Vk genes. Kazuhiko Kawasaki, Shinsei Minoshima, Eriko Nakato, Kazunori Shibuya, Ai Shintani, Shuichi Asakawa, Takashi Sasaki, H. -Gustav Klobeck, Gabriele Combriato, Hans G. Zachau, and Nobuyoshi Shimizu (2001) Eur. J. Immunol. 31, 1017 - 1028.

Summary

We have determined the entire nucleotide sequence of the human immunoglobulin k locus, comprising a total of 1,010,706 nucleotides. The 76 Vk found by a hybridization-based approach and their classification in seven families were confirmed. A Vk orphon located near the locus was also sequenced. In addition, we identified 55 novel Vk relics and truncated pseudogenes, which establish five new families. Among these 132 Vk genes, 46 have open reading frames. According to the databases and the literature, 32 unique Vk genes and five identical gene pairs form VJ-joints, 27 unique genes and four gene pairs are transcribed, and 25 unique genes and four gene pairs produce functional proteins. The Vk gene locus contains a 360-kb inverted duplication, which harbors 118 Vk genes. A comparison of the duplicated Vk genes suggests positive selection on the complementarity determining regions of the duplicated genes by point mutations. The entire duplication unit was divided into 13 blocks, each of which has its distinct nucleotide sequence identity to its duplication counterpart (98.1-99.9%). An inversion mediated mechanism is suggested to generate the high homology blocks. Based on the homology blocks and the mutation rates, the inverted duplication is assumed to have taken place ~5 million years ago. An orphon Vk gene near the k locus and a cluster of five orphons on chromosome 22 have no counterparts within the k locus. This suggests possible mechanisms of the transposition of orphon V k genes.

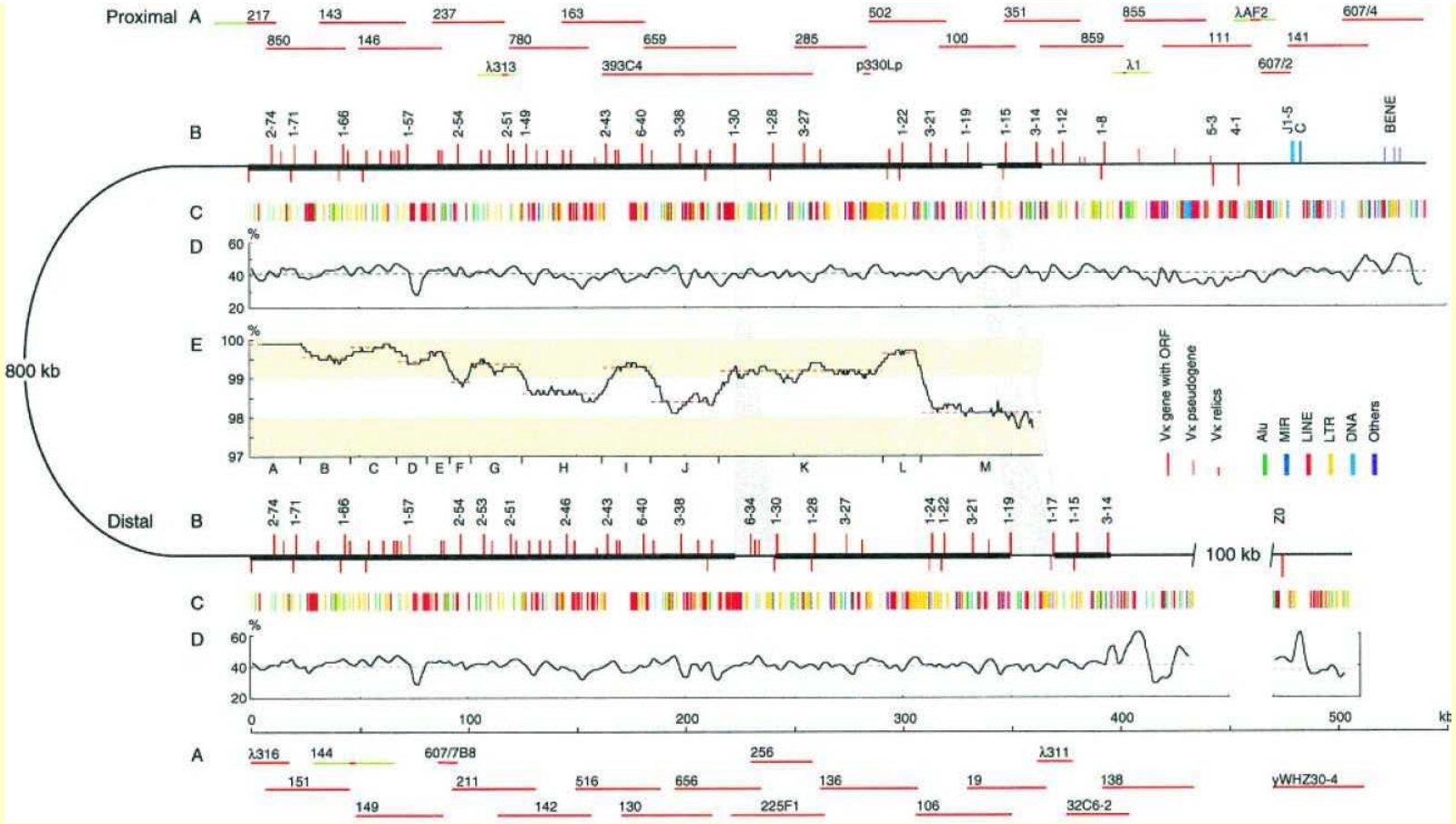

Figure 1: Comprehensive map of the human immunoglobulin κ locus. (A) Locations of the clones used in sequencing. Sequenced regions and unsequenced regions are depicted with red and green lines, respectively. (B) Locations of the κ genes and *BENE* (purple). Vκ (red), Jκ1-5 (sky blue), and Cκ (blue) genes with the same transcriptional polarity are indicated as vertical lines on the same side of the horizontal line; vertical lines pointing in the opposite direction indicate genes with opposite polarity. Lines with full height, 2/3 height, and 1/3 height represent genes with ORFs, pseudogenes with >200-nt, and relics with <200-nt in length, respectively. Relics consisting only of exon 1 are not included. The names of the Vκ genes with ORFs are shown. Thick horizontal lines within the locus represent duplicated regions, while thin horizontal lines indicate regions which exist in either the proximal or the distal unit. The wedge-shaped shadows indicate deletion events, which occurred after the inverted duplication. The 6-kb regions between two wedges show sequence homology (light shadow). However, these two regions do not seem to be the inverted duplication counterparts, but correspond to adjacent block duplicates generated prior to the inverted duplication. (C) Six categories of interspersed repeats are indicated; *Alu* (green), *MIR* (blue), LINE (*L1* and *L2*; red), LTR (yellow), DNA transposons (sky blue), and the others (purple) [25]. (D) The GC content was plotted with a window size of 4,000 nt and with a sliding size of 2,000 nt. (E) Sequence identity without indels between the proximal unit and the distal unit was plotted with a window size of 10,000 nt and with a sliding size of 500 nt. Thirteen homology blocks (A-M) and the average sequence identities (red dashed lines) are indicated. The scale of the homology plot is for the proximal unit; it does not take into account the gaps in the distal unit.