Curriculum Vitae (January 2013)

Name: Jonathan Charles Howard
Date of Birth: 24 June 1943
Nationality: British

Education:

1964	BA (Zoology) Oxford
1964-1965	Royal Society Leverhulme Scholarship, Genetics and Biometry Laboratory (Laboratory of Prof JBS Haldane), Government of Orissa, Agricultural University, Bhubaneswar, India
1969	D. Phil. (Medicine) Oxford „Cellular Aspects of Antibody Formation" Supervisor Prof. JL Gowans, MRC Cellular Immunology Unit, Sir William Dunn School of Pathology, University of Oxford

Employment:

1969-1973	Member of Scientific Staff, MRC Cellular Immunology Unit, Oxford.
1971-1977	Post-Doc, Adjunct Assistant and Adjunct Associate Professor, Department of Pathology, University of Pennsylvania, Philadelphia (Dr DB Wilson)
1974-1994	Member of Staff and from 1986 Head of the Department of Immunology, The Babraham Institute, Cambridge
1994-2011	Professor of Cell Genetics (C4), Institute for Genetics, University of Cologne
2011-present	Professor Emeritus, Institute for Genetics, University of Cologne
2012-present	Director, Instituto Gulbenkian de Ciência, Oeiras, Portugal

Sabbaticals:

1981	Department of Pathology, Stanford University (Dr IL Weissman)
1981	Division of Biology, Cal. Inst. Technology (Dr LE Hood)
1986	Department of Structural Biology, Stanford University (Dr P Parham)
1992	Cell Biology, EMBL Heidelberg (Dr B Dobberstein)
2004	Division of Neurobiology, MRC Laboratory of Molecular Biology, Cambridge (Dr HT McMahon)

Awards:

1971	Fulbright Scholarship
1970-1973	Weir Junior Research Fellowship, University College, Oxford
1974-1979	Research Fellow, Clare Hall, Cambridge
1993	EMBO member
1995	Fellow of Royal Society (FRS)
2007	Member Academia Europaea
2011	Donald Gordon Fellow, Stellenbosch Institute for Advanced Study (STIAS)

Membership of significant decision-making bodies since 1994:

1994-1995	Member, Cell and Molecular Biology Board, Medical Research Council, UK
1996-1999	Member, later Chairman, Sectional Committee 7, Royal Society, London
1996-1999	Molecular Biology Grants Committee, Human Frontiers Science Programme (HFSP), Strassburg.
1996-2011	Member and Chairman, Scientific Advisory Board, CNRS-INSERM Institut d'Immunologie Marseille-Luminy, France
1996-2004	Member, Scientific Advisory Board, Max Planck Institute for Immunobiology, Freiburg
2002-2005	Member, Courses and Workshops Committee, EMBO, Heidelberg
2004-present	Member, Board of Trustees, Max Planck Institute for Plant Breeding, Cologne, Germany
2004-present	Member, Scientific Advisory Board, Gulbenkian Institute of Sciences, Lisbon, Portugal
2004	Max Planck Society Research Field Rapporteur (with Prof. Guenther Schütz)
2005-2007	Member, Sectional Committee 7, Royal Society, London
2007-present	Member, Advanced Independent Fellowship (SNWG) selection committee of the MPG
2008-2012	Member, University Research Fellowships Committee, Royal Society
2009-2012	Member, later Chairman, Scientific Advisory Board, Max Planck Institute for Developmental Biology, Tübingen
2009-present	Member ERC Advanced Grants review committee Immunity and Infection panel LS6.
2011-2012	Member Scientific Advisory Board (Fachbeirat) of the German Society for Genetics (Gesellschaft für Genetik)
2013-	Member of Review Board, Dorothy Hodgkin Research Fellowships of the Royal Society

Research Grants presently held:

SFB680 Molecular Basis of Evolutionary Innovations

TPB3: Recent co-adaptation in the *Toxoplasma*-mouse parasite-host relationship; renewal awarded the period 1/2010-12/2013 (one further 4-year renewal possible)

SFB670 Cell-autonomous Immunity

TP6: The role of p47 (IRG) GTPases in cell-autonomous resistance to protozoal pathogens; renewal awarded for the period 7/2010-6/2014 (one further 4-year renewal possible)

SPP1399 Host-Parasite Co-evolution

Virulence factors and resistance genes in the ecological relationship between *Toxoplasma gondii* and *Mus musculus* 07/2012-06/2015

SFB635 Post-translational Control of Protein Function

TPB2: Regulatory interactions between IRG GTPases: renewed for 07/2011-06/2015

List of Publications

Book:

"Darwin", Oxford University Press, 1st edn **1982**, 2nd edn. **2001**

Papers

Spekker K, Leineweber M, Degrandi D, Ince V, Brunder S, Schmidt SK, Stuhlsatz S, Howard JC, Schares G, Degistirici O, Meisel R, Sorg RV, Seissler J, Hemphill A, Pfeffer K, Däubener W. (**2012**) Antimicrobial effects of murine mesenchymal stromal cells directed against Toxoplasma gondii and Neospora caninum: role of immunity-related GTPases (IRGs) and guanylate-binding proteins (GBPs). Med Microbiol Immunol. 2012 Dec 27. [Epub ahead of print] PMID: 23269418

Fentress SJ, Steinfeldt T, Howard JC, Sibley LD. (**2012**) The arginine-rich N-terminal domain of ROP18 is necessary for vacuole targeting and virulence of Toxoplasma gondii. Cell Microbiol. 2012 Dec;14(12):1921-33. doi: 10.1111/cmi.12022. PMID: 22906355

Fleckenstein, M, Reese, ML, Boothroyd, JC, Howard, JC, Steinfeldt, T. (**2012**) A *Toxoplasma gondii* pseudokinase inhibits host IRG resistance proteins. PloS Biology. PLoS Biol 10(7): e1001358. doi:10.1371/journal.pbio.1001358

Reid, AJ, Vermont, SJ, Cotton, JA, Harris, D, Hill-Cawthorne, GA, Könen-Waisman, S, Latham, S, Mourier, T, Norton, R, Quail, M, Sanders, M, Shanmugam, D, Sohal, A, Wasmuth, J, Brunk, B, Grigg, M, Howard, JC, Parkinson, J, Roos, DS, Trees, AJ, Berriman, M, Pain, A & Wastling, JM **(2012**) Comparative genomics of Coccidian parasites differing in host range and transmission strategy. PLoS Pathogens (3): e1002567. doi:10.1371/journal.ppat.1002567

Traver, MK, Henry, SC, Cantillana, V, Oliver,T, Hunn, JP, Howard, JC, Beer, S, Pfeffer K, Coers, J, Taylor, GA (**2011**) IRGM proteins influence the localization of GBP2 by modulating macroautophagy. J. Biol. Chem. 286(35):30471-80.

Howard, JC, Hunn, JP, Steinfeldt, T, (**2011**) The IRG protein-based resistance mechanism in mice and its relation to virulence in *Toxoplasma gondii*. Current Opinion in Microbiology. Aug;14(4):414-21. PMID: 21783405

Liesenfeld, O, Parvanova, IA, Zerrahn, J, Han, SJ, Heinrich, F, Munoz, M, Kaiser, F, Aebischer, T, Buch,, T, Waisman, A, Reichmann, G, Utermöhlen, O, von Stebut, E, Bogdan, C, Specht, S, Saeftel, M, Hoerauf, A, Mota, M, Könen-Waisman, S, Kaufmann, SHE, Howard, JC (**2011**) Irga6/IIGP contributes to *in vivo* resistance against *Toxoplasma gondii* infection but not to resistance against other intracellular pathogens including *Plasmodium berghei.* PLoS One doi:10.1371/journal.pone.0020568

Nikolaus Pawlowski[1], Aliaksandr Khaminets[1], Julia P. Hunn[1], Natasa Papic[1], Andreas Schmidt[1,$], Revathy C. Uthaiah[1,§], Rita Lange[1], Gaby Vopper[1], Sascha Martens[1,#], Eva Wolf[2,+], Jonathan C. Howard[1] (**2011**) The Activation Mechanism of Irga6, an Interferon-Inducible GTPase Contributing to Mouse Resistance against *Toxoplasma gondii.* BMC Biology 9:7.

Hunn, JP, Feng, CG, Sher, A, Howard, JC. (**2011**) The Immunity-Related GTPases in Mammals - a fast Evolving Cell-Autonomous Resistance System against Intracellular Pathogens. Mammalian Genome, 22(1-2):43-54. Epub 2010 Oct 30. PMID: 21052678

Zeng, J and Howard, JC **(2010)** Spontaneous focal activation of iNKT cells in mouse liver and kidney. BMC Biology *BMC Biology* 2010, **8:**142doi:10.1186/1741-7007-8-142

Tobias Steinfeldt[1], Stephanie Könen-Waisman[1], Lan Tong[1§], Nikolaus Pawlowski[1], Tobias Lamkemeyer[1], L. David Sibley[2], Julia P. Hunn[1], Jonathan C. Howard[1*](**2010**) Phosphorylation of IRG resistance proteins is an evasion strategy for virulent *T. gondii* strains. PLoS Biology 8(12): e1000576. doi:10.1371/journal.pbio.1000576

Melo, M, Kasperowitz, P, Cerny, A, Könen-Waisman, S, Kurt-Jones, E, Lien, E, Beutler, B, Howard, JC, Golenbock, D, Gazzinelli, R. (**2010**) UNC93B1 mediates host resistance to infection with *Toxoplasma gondii.* PLoS Pathogens 6(8): e1001071. doi:10.1371/journal.ppat.1001071

Nikolaus Pawlowski **(2010)** Dynamin self-assembly and the vesicle fission mechanism: structural insights into the large atypical GTPases. BioEssays 32:1033-1039

Hunn, JP, Howard, JC (**2010**) The mouse resistance protein, Irgm1 (LRG-47): a regulator or an effector of pathogen defense? PLOS Pathogens P6(7): e1001008. doi:10.1371/journal.ppat.1001008

Khaminets, A, Könen-Waisman,, S, Hunn, JP, Zhao,, YO, Preukschat, D, Coers, J, Boyle, JP, Ong, YC, Boothroyd, JC, Reichmann, G, Howard,, JC (**2010**) Coordinated loading of multiple IRG resistance GTPases on to the *Toxoplasma gondii* parasitophorous vacuole. Cellular Microbiology 12(7):939-61, PMID: 20109161

Zhao, YO, Könen-Waisman, S, Taylor, GA, Martens, S, Howard, JC (**2010**) Localisation and mis-localisation of the interferon-inducible immunity-related GTPase, Irgm1 (LRG-47) in mouse cells. PLoS One Jan 13;5(1):e8648

Lapaque, N, Muller, A, Alexopolou, L, Howard, JC, Gorvel, JP (**2009**) Brucella abortus induces Irgm3 and Irga6 expression via Type-I IFN by a MyD88-dependent pathway, without the requirement of TLR2, TLR4, TLR5 and TLR9. Microbial Pathogenesis, ePublished 09 September 2009

Zeng, J, Parvanova, IA, Howard, JC (**2009**) A dedicated promoter drives constitutive expression of the cell-autonomous immune resistance GTPase, Irga6 (IIGP1) in mouse liver. PLoS ONE 4(8): e6787. doi:10.1371/journal.pone.0006787

Howard JC **2009** Why didn't Darwin discover Mendel's Laws? J. Biol. 8:15

Henry SC, Daniell XG, Burroughs AR, Indaram M, Howell DN, Coers J, Starnbach MN, Hunn JP, Howard JC, Feng CG, Sher A, Taylor GA. **2009** Balance of Irgm protein activities determines IFN-{gamma}-induced host defense. J Leukoc Biol. Jan 27 PMID: 19176402

Bekpen C, Marques-Bonet T, Alkan C, Antonacci F, Leogrande MB, Ventura M, Kidd JM, Siswara P, Howard JC, Eichler EE **2009** Death and Resurrection of the Human *IRGM* Gene. PLOS Genetics PLoS Genet 5(3): e1000403. doi:10.1371/journal.pgen.1000403

Zhao, YO, Khaminets, A, Howard, JC **2009** Disruption of the *Toxoplasma gondii* Parasitophorous Vacuole by Immunity-related GTPases (IRG proteins) Causes Necrotic Death in IFNγ-induced Cells. PLoS Pathog 5(2): e1000288. doi:10.1371

Zhao YO, Rohde C, Lilue JT, Könen-Waisman S, Khaminets A, Hunn JP, Howard JC. **2009** *Toxoplasma gondii* and the IRG (Immunity-Related GTPase) resistance system in mice: a review. Memorias do Instituto Oswaldo Cruz. 104(2):234-40.

Coers J, Starnbach MN, Howard, JC. **2009** Modeling infectious disease in mice: co-adaptation and the role of host-specific IFNg responses. PLOS Pathogens. 5(5): e1000333. doi:10.1371/journal.ppat.1000333

Papic N, Hunn JP, Pawlowski N, Zerrahn J, Howard JC. **2008**. Inactive and active states of the interferon-inducible resistance GTPase, Irga6, In Vivo. J Biol Chem. 2008 Nov 14;283(46):32143-51

Hunn, J, Koenen-Waisman, S, Papic, N, Schroeder, N, Pawlowski, N, Lange, R, Kaiser, F, Zerrahn, J, Martens, S and Howard JC**. 2008** Regulatory interactions between IRG resistance GTPases in the cellular response to *Toxoplasma gondii*. EMBO Journal, 27(19):2495-509

Howard, JC. **2008**. The IRG proteins: A function in search of a mechanism. Immunobiology 213:367-375

Coers J, Bernstein-Hanley I, Grotsky D, Parvanova I, Howard JC, Taylor GA, Dietrich WF, Starnbach MN. **2008** Chlamydia muridarum evades growth restriction by the IFN-gamma-inducible host resistance factor Irgb10. J Immunol. 180(9):6237-45.

Deverson EV, Gow IR, Coadwell WJ, Monaco JJ, Butcher GW, Howard JC. **2008** Pillars Article: MHC class II region encoding proteins related to the multidrug resistance family of transmembrane transporters. 1990. Nature 348: 738-41. Classical article. J Immunol 180(5):2729-32

Howard, JC (**2007**) Cell-autonomous immunity. Microbes and Infection 9(14-15):1633-5

Könen-Waisman, S and Howard, JC (**2007**) Cell-autonomous immunity to *Toxoplasma gondii* in mouse and man. Microbes and Infection 9(14-15):1652-61

Howard JC, Jack RS. (**2007**) Evolution of immunity and pathogens Eur J Immunol. 37(7):1721-3.

Martens, S and Howard, JC, **2006**. Interferon-inducible GTPases. Annu. Rev. Cell Dev. Biol. In press

Lapaque, N, Takeuchi, O, Corrales, F, Akira, S, Moriyon, I, Howard, JC, Gorvel, JP. **2006**. Differential inductions of TNF and IGTP, IIGP by structurally diverse classic and non-classiclipopolysaccharides. Cellular Microbiology 8:401-413

Bekpen, C, Hunn, JP, Rohde, C, Parvanova, I, Guethlein, L, Dunn, DM, Glowalla, E, Leptin, M, Howard, JC. **2005** The interferon-inducible p47 (IRG) GTPases in vertebrates: loss of the cell-autonomous resistance mechanism in the human lineage. Genome Biology, Published 31.10.05

Martens, S, Parvanova, I, Zerrahn, J, Griffiths, G, Schell, G, Reichman, G, Howard, JC. **2005** Disruption of Toxoplasma gondii parasitophorous vacuoles by the mouse p47 resistance GTPases. PLOS Pathogens, 1(3):published 25.11.05

Ghosh A, Uthaiah R, Howard JC, Herrmann C, and Wolf E. **2004** Crystal Structure of IIGP1: A Paradigm for Interferon-Inducible p47 Resistance GTPases. Molecular Cell 15:727-739

Martens S, Sabel K, Lange R, Uthaiah R, Wolf E, Howard JC. **2004** Mechanisms regulating the positioning of mouse p47 resistance GTPases LRG-47 and IIGP1 on cellular membranes: retargeting to plasma membrane induced by phagocytosis. J Immunol. 173(4):2594-606.

Klamp T, Boehm U, Schenk D, Pfeffer K, Howard JC. **2003** A giant GTPase, very large inducible GTPase-1, is inducible by IFNs.J Immunol. 171(3):1255-65.

Uthaiah RC, Praefcke GJ, Howard JC, Herrmann C. **2003** IIGP1, an interferon-gamma-inducible 47-kDa GTPase of the mouse, showing cooperative enzymatic activity and GTP-dependent multimerization. J Biol Chem. 278(31):29336-43.

Wettey FR, Hawkins SF, Stewart A, Luzio JP, Howard JC, Jackson AP. **2002.** Controlled elimination of clathrin heavy-chain expression in DT40 lymphocytes. Science. 297(5586):1521-5.

Alberts P, Daumke O, Deverson EV, Howard JC, Knittler MR. **2001** Distinct functional properties of the TAP subunits coordinate the nucleotide-dependent transport cycle. Curr Biol. 11(4):242-51.

Guethlein LA, Howard JC. **2000** Is a mutator analogous to the Ig hypermutator of the sheep ileal Peyer's patch active on MHC class I genes in the germ line? Immunogenetics. 51(6):462-72.

Martinsohn JT, Sousa AB, Guethlein LA, Howard JC. **1999** The gene conversion hypothesis of MHC evolution: a review. Immunogenetics. 50(3-4):168-200. Review. Erratum in: Immunogenetics 2000 Jun;51(7):613.

Knittler MR, Alberts P, Deverson EV, Howard JC. **1999** Nucleotide binding by TAP mediates association with peptide and release of assembled MHC class I molecules. Curr Biol. 9(18):999-1008.

Boehm U, Guethlein L, Klamp T, Ozbek K, Schaub A, Futterer A, Pfeffer K, Howard JC. **1998** Two families of GTPases dominate the complex cellular response to IFN-gamma. J Immunol. 161(12):6715-23.

Knittler MR, Gulow K, Seelig A, Howard JC. **1998** MHC class I molecules compete in the endoplasmic reticulum for access to transporter associated with antigen processing. J Immunol. 161(11):5967-77.

Joly E, Le Rolle AF, Gonzalez AL, Mehling B, Stevens J, Coadwell WJ, Hunig T, Howard JC, Butcher GW. **1998** Co-evolution of rat TAP transporters and MHC class I RT1-A molecules.Curr Biol. 8(3):169-72.

Deverson EV, Leong L, Seelig A, Coadwell WJ, Tredgett EM, Butcher GW, Howard JC. **1998** Functional analysis by site-directed mutagenesis of the complex polymorphism in rat transporter associated with antigen processing. J Immunol. 160(6):2767-79.

Lambracht D, Wonigeit K, Howard JC, Fischer Lindahl K. Markers for interspecies relationship in the RT1 complex.Transplant Proc. **1997** May;29(3):1665-7.

Cresswell P, Howard JC. Antigen recognition. Curr Opin Immunol. **1997** Feb;9(1):71-4. Review.

Howard JC. Contemplations on the evolution of pro- and eukaryotic mono(ADP-ribosyl) transferases in the context of the immune system. Adv Exp Med Biol. **1997**;419:453-8. Review.

Boehm U, Klamp T, Groot M, Howard JC. **1997** Cellular responses to interferon-gamma. Annu Rev Immunol.;15:749-95.

Powis SJ, Young LL, Joly E, Barker PJ, Richardson L, Brandt RP, Melief CJ, Howard JC, Butcher GW. The rat cim effect: TAP allele-dependent changes in a class I MHC anchor motif and evidence against C-terminal trimming of peptides in the ER.Immunity. **1996** Feb;4(2):159-65.

Howard JC. Supply and transport of peptides presented by class I MHC molecules.Curr Opin Immunol. **1995** Feb;7(1):69-76. Review.

Wang CR, Lambracht D, Wonigeit K, Howard JC, Lindahl KF. Rat RT1 orthologs of mouse H2-M class Ib genes. Immunogenetics. **1995**;42(1):63-7.

Thorpe CJ, Moss DS, Powis SJ, Howard JC, Butcher GW, Travers PJ. An analysis of the antigen binding site of RT1.Aa suggests an allele-specific motif. Immunogenetics. **1995**;41(5):329-31.

Joly E, Clarkson C, Howard JC, Butcher GW. Isolation of a functional cDNA encoding the RT1.Au MHC class I heavy chain by a novel PCR-based method. Immunogenetics. **1995**;41(5):326-8.

Momburg F, Roelse J, Howard JC, Butcher GW, Hammerling GJ, Neefjes JJ. Selectivity of MHC-encoded peptide transporters from human, mouse and rat. Nature. **1994** Feb 17;367(6464):648-51.

Joly E, Deverson EV, Coadwell JW, Gunther E, Howard JC, Butcher GW. The distribution of Tap2 alleles among laboratory rat RT1 haplotypes. Immunogenetics. **1994**;40(1):45-53.

Ossevoort MA, Sijts AJ, van Veen KJ, Momburg F, Hammerling GJ, Seelig A, Butcher GW, Howard JC, Kast WM, Melief CJ. Differential effect of transporter Tap 2 gene introduction into RMA-S cells on viral antigen processing. Eur J Immunol. **1993** Dec;23(12):3082-8.

Powis SJ, Young LL, Barker PJ, Richardson L, Howard JC, Butcher GW. Major histocompatibility complex-encoded ABC transporters and rat class I peptide motifs. Transplant Proc. **1993** Oct;25(5):2752-3.

Howard JC, Seelig A. Antigen processing. Peptides and the proteasome. Nature. **1993** Sep 16;365(6443):211-2.
Howard JC. Restrictions on the use of antigenic peptides by the immune system. Proc Natl Acad Sci U S A. **1993** May 1;90(9):3777-9. Review.
Yousaf N, Howard JC, Williams BD. Complement-dependent synergistic effects of rat monoclonal IgG antibodies in vivo. Eur J Immunol. **1993** Feb;23(2):369-75.
Ahmad I, Howard JC, Ng YK, Iannaccone PM. Chimeric drift in blood cell populations of chimeric rats constructed between congenic strains. Pathobiology. **1993**;61(2):117-22.
Momburg F, Ortiz-Navarrete V, Neefjes J, Goulmy E, van de Wal Y, Spits H, Powis SJ, Butcher GW, Howard JC, Walden P, et al. Proteasome subunits encoded by the major histocompatibility complex are not essential for antigen presentation. Nature. **1992** Nov 12;360(6400):174-7.
Jameson SC, Tope WD, Tredgett EM, Windle JM, Diamond AG, Howard JC. Cloning and expression of class I major histocompatibility complex genes of the rat. J Exp Med. **1992** Jun 1;175(6):1749-57.
Powis SJ, Deverson EV, Coadwell WJ, Ciruela A, Huskisson NS, Smith H, Butcher GW, Howard JC. Effect of polymorphism of an MHC-linked transporter on the peptides assembled in a class I molecule. Nature. **1992** May 21;357(6375):211-5.
Ballingall KT, Wright H, Redmond J, Dutia BM, Hopkins J, Lang J, Deverson EV, Howard JC, Puri N, Haig D. Expression and characterization of ovine major histocompatibility complex class II (OLA-DR) genes. Anim Genet. **1992**;23(4):347-59.
Powis SJ, Townsend AR, Deverson EV, Bastin J, Butcher GW, Howard JC. Restoration of antigen presentation to the mutant cell line RMA-S by an MHC-linked transporter. Nature. **1991** Dec 19-26;354(6354):528-31.
Howard JC. Immunology. Disease and evolution. Nature. **1991** Aug 15;352(6336):565-7. .
Yousaf N, Howard JC, Williams BD. Targeting behavior of rat monoclonal IgG antibodies in vivo: role of antibody isotype, specificity and the target cell antigen density. Eur J Immunol. **1991** Apr;21(4):943-50.
Powis SJ, Howard JC, Butcher GW. The major histocompatibility complex class II-linked cim locus controls the kinetics of intracellular transport of a classical class I molecule. J Exp Med. **1991** Apr 1;173(4):913-21.
Deverson EV, Wright H, Watson S, Ballingall K, Huskisson N, Diamond AG, Howard JC. Class II major histocompatibility complex genes of the sheep. Anim Genet. **1991**;22(3):211-25.
Livingstone AM, Powis SJ, Gunther E, Cramer DV, Howard JC, Butcher GW. Cim: an MHC class II-linked allelism affecting the antigenicity of a classical class I molecule for T lymphocytes. Immunogenetics. **1991**;34(3):157-63.
van den Bogaerde J, Howard JC. Xenogeneic responses in vitro in the Syrian hamster, Mesocricetus auratus. I. Evidence for a normal T cell repertoire. Int Immunol. **1991** Jan;3(1):49-56.
Deverson EV, Gow IR, Coadwell WJ, Monaco JJ, Butcher GW, Howard JC. MHC class II region encoding proteins related to the multidrug resistance family of transmembrane transporters. Nature. **1990** Dec 20-27;348(6303):738-41.
Powis CJ, Howard JC, Butcher GW. Variation in the biosynthesis of the rat RT1.Aa classical class I antigen due to the cim system. Transplant Proc. **1990** Dec;22(6):2517-8. .
Jameson SC, Rada C, Lorenzi R, Diamond AG, Butcher GW, Howard JC. Cloning, expression, and evolution of rat classical and nonclassical class I genes. Transplant Proc. **1990** Dec;22(6):2510-1.

Rada C, Lorenzi R, Powis SJ, van den Bogaerde J, Parham P, Howard JC. Concerted evolution of class I genes in the major histocompatibility complex of murine rodents. Proc Natl Acad Sci U S A. **1990** Mar;87(6):2167-71.

Livingstone AM, Powis SJ, Diamond AG, Butcher GW, Howard JC. A trans-acting major histocompatibility complex-linked gene whose alleles determine gain and loss changes in the antigenic structure of a classical class I molecule. J Exp Med. **1989** Sep 1;170(3):777-95.

Diamond AG, Hood LE, Howard JC, Windle M, Winoto A. The class II genes of the rat MHC. J Immunol. **1989** May 1;142(9):3268-74.

Howard JC. The new pragmatics of immunology. Cold Spring Harb Symp Quant Biol. **1989**;54 Pt 2:947-57.

Iannaccone PM, Howard JC, Berkwits L. Mosaic pattern and lineage analysis in chimeras. Cell Differ Dev. **1988** Nov;25 Suppl:77-90. Review.

Yousaf N, Howard JC, Williams BD. Studies in the rat of antibody-sensitized and N-ethylmaleimide-treatederythrocyte clearance by the liver: effects of immune complex infusion and complement activation. Immunology. **1988** Jun;64(2):193-9.

Howard JC. Molecular evolution. How old is a polymorphism? Nature. **1988** Apr 14;332(6165):588-90.

Yousaf N, Howard JC, Williams BD. Studies in cobra venom factor treated rats of antibody coated erythrocyte clearance by the spleen: differential influence of red blood cell antigen number on the inhibitory effects of immune complexes on Fc dependent clearance. Clin Exp Immunol. **1986** Dec;66(3):654-60.

Yousaf N, Howard JC, Williams BD. Studies in the rat of antibody-coated and N-ethylmaleimide-treated erythrocyte clearance by the spleen. II. Effects of immune complex infusion. Immunology. **1986** Sep;59(1):81-5.

Yousaf N, Howard JC, Williams BD. Studies in the rat of antibody-coated and N-ethylmaleimide-treated erythrocyte clearance by the spleen. I. Effects of in vivo complement activation. Immunology. **1986** Sep;59(1):75-9.

Watts C, Howard JC. Membrane recycling and antigen presentation. Bioessays. **1986** Jun;4(6):265-7.

Hughes-Jones NC, Gorick BD, Howard JC, Feinstein A. Antibody density on rat red cells determines the rate of activation of the complement component C1. Eur J Immunol. **1985** Oct;15(10):976-80.

Howard JC. Immunological help at last. Nature. 1985 Apr 11-17;314(6011):494-5. .

Weinberg WC, Howard JC, Iannaccone PM. Histological demonstration of mosaicism in a series of chimeric rats produced between congenic strains. Science. **1985** Feb 1;227(4686):524-7.

Hughes-Jones NC, Gorick BD, Miller NG, Howard JC. IgG pair formation on one antigenic molecule is the main mechanism of synergy between antibodies in complement-mediated lysis. Eur J Immunol. **1984** Nov;14(11):974-8.

Hughes-Jones NC, Feinstein A, Richardson NE, Gorick BD, Howard JC. C1 activation by immunoglobulin and immunoglobulin antibodies. Biochem Soc Trans. **1984** Oct;12(5):738-9.

Diamond AG, Larkins AP, Wright B, Ellis ST, Butcher GW, Howard JC. The alloantigenic organization of RT1Aa, a class I major histocompatibility complex molecule of the rat. Eur J Immunol. **1984** May;14(5):405-12.

Diamond AG, Butcher GW, Howard JC. Localized conformational changes induced in a class I major histocompatibility antigen by the binding of monoclonal antibodies. J Immunol. **1984** Mar;132(3):1169-75.

Feeney AJ, Corvalan JR, Matzinger P, Howard JC. T helper cells required for the in vitro primary antibody response to SRBC are neither SRBC-specific nor MHC-restricted. J Mol Cell Immunol. **1984**;1(4):211-22.
Hughes-Jones NC, Gorick BD, Howard JC. The mechanism of synergistic complement-mediated lysis of rat red cells by monoclonal IgG antibodies. Eur J Immunol. **1983** Aug;13(8):635-41.
Howard JC. The major histocompatibility complex of the rat: a partial review. Metabolism. **1983** Jul;32(7 Suppl 1):41-50. Review.
Butcher GW, Howard JC. Genetic control of transplant rejection. Transplantation. **1982** Oct;34(4):161-6. Review.
Butcher GW, Corvalan JR, Licence DR, Howard JC. Immune response genes controlling responsiveness to major transplantation antigens. Specific major histocompatibility complex-linked defect for antibody responses to class I alloantigens. J Exp Med. **1982** Jan 1;155(1):303-20.
Howard JC, Butcher GW. The mechanism of graft rejection and the concept of antigenic strength. Scand J Immunol. **1981** Dec;14(6):687-91. .
Smith RN, Howard JC. Heterogeneity of the tolerant state in rats with long established skin grafts. J Immunol. **1980** Nov;125(5):2289-94.
Howard JC, Butcher GW, Licence DR, Galfre G, Wright B, Milstein C. Isolation of six monoclonal alloantibodies against rat histocompatibility antigens: clonal competition. Immunology. **1980** Sep;41(1):131-41.
Galfre G, Butcher GW, Howard JC, Wilde CD, Milstein C. Clonal competition and stability of hybrid myelomas of mouse and rat origin. Transplant Proc. **1980** Sep;12(3):371-5.
Antczak DF, Howard JC. Analysis of lymphocytes reactive to histocompatibility antigens. IV. Detection of inclusion among allo-reactive lymphocyte populations by specific enrichment for reactive cells. Cell Immunol. **1979** Aug;46(1):127-37.
Antczak DF, Howard JC. Analysis of lymphocytes reactive to histocompatibility antigens. III. Detection of inclusion among allo-reactive lymphocyte populations by specific depletion of reactive cells. Cell Immunol. **1979** Aug;46(1):119-26.
Howard JC, Corvalan JR. Demonstration of MHC-specific haemolytic plaque-forming cells. Nature. **1979** Mar 29;278(5703):449-51.
Antczak DF, Howard JC. Analysis of lymphocytes reactive to histocompatibility antigens. II. Exponential alloantigen-dependent lymphocyte growth in vitro. Cell Immunol. **1979** Mar 15;43(2):317-25.
Antczak DF, Brown D, Howard JC. Analysis of lymphocytes reactive to histocompatibility antigens. I. A quantitative titration assay for mixed lymphocyte interactions in the rat. Cell Immunol. **1979** Mar 15;43(2):304-16.
Howard JC, Butcher GW, Galfre G, Milstein C, Milstein CP. Monoclonal antibodies as tools to analyze the serological and genetic complexities of major transplantation antigens. Immunol Rev. **1979**;47:139-74. Review.
Gallico GG, Butcher GW, Howard JC. The role of subregions of the rat major histocompatibility complex in the rejection and passive enhancement of renal allografts. J Exp Med. **1979** Jan 1;149(1):244-53.
Antczak DF, Howard JC. Allo-antigen specific lymphocyte growth in vitro [proceedings J Physiol. **1978** Nov;284:6P-7P.
Corvalan JR, Howard JC. Primary in vitro antibody formation in the rat: partial characterization and properties of an inhibitor cell present in normal spleen. Eur J Immunol. **1978** May;8(5):331-5.
Howard JC, Butcher GW, Galfre G, Milstein C. Monoclonal anti-rat MHC (H-1) alloantibodies. Curr Top Microbiol Immunol. **1978**;81:54-60.

Galfre G, Howe SC, Milstein C, Butcher GW, Howard JC. Antibodies to major histocompatibility antigens produced by hybrid cell lines. Nature. **1977** Apr 7;266(5602):550-2.
Butcher GW, Howard JC. A recombinant in the major histocompatibility complex of the rat. Nature. **1977** Mar 24;266(5600):362-4.
Wilson DB, Heber-Katz E, Sprent J, Howard JC. On the possibility of multiple T-cell receptors. Cold Spring Harb Symp Quant Biol. **1977**;41 Pt 2:559-61.
Wilson DB, Marshak A, Razzino-Pierson G, Howard JC. Specific selection of cytotoxic effector cells: the generation of cytotoxic T cells in rat thoracic duct lymphocyte populations positively or negatively selected for reactivity to specific strong histocompatibility alloantigens. J Immunol. **1976** Jun;116(6):1624-8.
Howard JC. The genetic basis for responses to major transplantation antigens. Transplant Proc. **1976** Jun;8(2):157-60.
Wilson DB, Marshak A, Howard JC. Specific positive and negative selection of rat lymphocytes reactive to strong histocompatibility antigens: activation with alloantigens in vitro and in vivo. J Immunol. **1976** Apr;116(4):1030-40.
Gonatas NK, Howard JC. Inhibition of experimental allergic encephalomyelitis in rats severely depleted of T cells. Science. **1974** Nov 29;186(4166):839-41.
Howard JC, Scott DW. The identification of sera distinguishing marrow-derived and thymus-derived lymphocytes in the rat thoracic duct. Immunology. **1974** Nov;27(5):903-22.
Howard JC, Wilson DB. Specific positive selection of lymphocytes reactive to strong histocompatibility antigens. J Exp Med. **1974** Sep 1;140(3):660-72.
Howard JC. On the relationship between initiator and effector cells in the response to major tansplantation antigens. Transplant Proc. **1973** Dec;5(4):1451-6. Review.
Howard JC, Gowans JL. The role of lymphocytes in antibody formation. 3. The origin from small lymphocytes of cells forming direct and indirect haemolytic plaques to sheep erythrocytes in the rat. Proc R Soc Lond B Biol Sci. **1972** Sep 19;182(67):193-209.
Howard JC, Scott DW. The role of recirculating lymphocytes in the immunological competence of rat bone marrow cells. Cell Immunol. **1972** Mar;3(3):421-9.
Scott DW, Howard JC. Collaboration between thymus-derived and marrow-derived thoracic duct lymphocytes in the hemolysin response of the rat. Cell Immunol. **1972** Mar;3(3):430-41.
Howard JC, Hunt SV, Gowans JL. Identification of marrow-derived and thymus-derived small lymphocytes in the lymphoid tissue and thoracic duct lymph of normal rats. J Exp Med. **1972** Feb 1;135(2):200-19.
Howard JC. The life-span and recirculation of marrow-derived small lymphocytes from the rat thoracic duct. J Exp Med. **1972** Feb 1;135(2):185-99.
Wilson DB, Howard JC, Nowell PC. Some biological aspects of lymphocytes reactive to strong histocompatibility alloantigens. Transplant Rev. **1972**;12:3-29. Review.
Howard JC. A histocompatible chromosome marker system in the laboratory rat Rattus norvegicus. Transplantation. **1971** Jul;12(1):95-7.
Ellis ST, Gowans JL, Howard JC. The origin of antibody forming cells from lymphocytes. Antibiot Chemother. **1969**;15:40-55.