

BIOGRAPHICAL SKETCH

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NAME: Kirchhausen, Tomas

eRA COMMONS USER NAME: kirchhausen

POSITION TITLE: Professor of Cell Biology and Professor of Pediatrics, Harvard Medical School, Senior Investigator, Boston Children's Hospital; Springer Family Chair, Boston Children's Hospital

EDUCATION/TRAINING

| INSTITUTION AND LOCATION | DEGREE | Completion Date | FIELD OF STUDY |
|--|------------|-----------------|---------------------------|
| Universidad Peruana Cayetano Heredia, Peru | B.S. | 04/72 | Biology |
| Instituto Venezolano de Investigaciones Cientificas, Venezuela | M.S. | 06/75 | Biophysics |
| Universidad Peruana Cayetano Heredia, Peru | M.S. | 06/75 | Biophysics |
| Instituto Venezolano de Investigaciones Cientificas, Venezuela | Ph.D. | 06/77 | Biophysics and Physiology |
| Harvard University | M.A. (HON) | 12/99 | Cell Biology |

A. Personal Statement

Successful and productive research projects in structural biology, cell biology, chemical genetics, live cell and single-molecule fluorescence microscopy imaging, have enabled strong track record in advising predoctoral and postdoctoral trainees. Experience in teaching and organizing international, graduate-level courses in different countries. Principal participant since 1997 in biennial membrane-biology EMBO course (Cargese). Chair/co-chair of two Gordon Research Conferences. Leader (and co-founder) for 7 years of the Harvard-Portugal program, the longest lasting international collaborative educational and research program at Harvard Medical School.

B. Positions and Honors

Positions and Employment

- 1980- Tutor in Biochemical Sciences, Harvard University
1981-1982 Postdoctoral, Harvard University, Department of Biochemistry and Molecular Biology
1982-1985 Research Associate in Biochemistry, Harvard University
1984-1985 Assistant Head Tutor, Biochemical Sciences, Harvard University
1986-1991 Assistant Professor of Anatomy and Cellular Biology, Harvard Medical School
1991-1993 Associate Professor of Anatomy and Cellular Biology, Harvard Medical School
1992-1999 Investigator, The Center for Blood Research, Inc.
1993-1999 Associate Professor, Department of Cell Biology, Harvard Medical School
1999- Professor, Department of Cell Biology, Harvard Medical School
1999-2012 Senior Investigator, Immune Disease Institute, (formerly CBR Inst. for Biomedical Research)
2006-2012 Chair IT Committee, Immune Disease Institute.
2007-2012 Executive Faculty Committee, Immune Disease Institute.
2009-2015 HMS Director, Harvard-Portugal Program in Translational Research and Medical Education
2012- Senior Investigator, Program in Cellular and Molecular Medicine (PCMM) at Boston Children's Hospital
2012- Professor, Department of Pediatrics, Harvard Medical School
2013- Springer Family Professor of Pediatrics, Harvard Medical School
2016-2018 Visiting Scientist at Janelia Research Campus, HHMI

Honors

| | |
|-----------|---|
| 1982-1984 | Research Fellow, Charles A. King Trust |
| 1986-1991 | Established Investigator Award, American Heart Association |
| 2002- | Honorary Professor, Universidad Peruana Cayetano Heredia, Peru |
| 2008- | AAAS Fellow |
| 2012 | John Cebra Endowed Lecture, Dynamics and Endocytosis. Marine Biological Laboratory, Woods Hole |
| 2013- | Springer Family Professor of Pediatrics, Harvard Medical School |
| 2013- | Doctor Honoris Causa, Universidad Ricardo Palma, Peru |
| 2014- | Associated Member EMBO |
| 2014- | SMB Jose Laguna Lecture for Outstanding Basic Research in Dynamics of Endocytosis |
| 2015- | Netherlands Society for Biochemistry and Molecular Biology: Speaker of the year |
| 2015 | EMBO Keynote Lecture, Systems Biology of Infection |
| 2016- | Academia Nacional de Ciencias (Peru), Academico Correspondiente |
| 2016- | Honorary Professor, University of Hong Kong |
| 2017 | EMBO Keynote Lecture, FEBS – EMBO Advance Lecture Course in Molecular Architecture, Dynamics and Function of Biomembranes |
| 2017- | Honorary Member, Associazione di Biologia Cellulare e del Differenziamento, Italy |
| 2018 | EMBO Global Lecturer, India |
| 2019 | Carl Friedrich von Siemens Stiftung, Lecture |

Other Experience and Professional Memberships

| | |
|-----------|--|
| 1996-1999 | Ad-hoc member of NIH Study Section, CB-1 |
| 1999-2003 | Member, NIH Study Section, CDF-2 |
| 2001- | Member, Advisory Committee, Imaging Facility, Dept. of Cell Biology, Harvard Med. School |
| 2004-2012 | Ad-hoc member of NIH Study Sections CD-4 and ZRG1 |

C. Contribution to Science

1. Molecular architecture of clathrin coats and mechanism of uncoating (1981-)

Through studies extending over three decades, we defined the structure and interactions of clathrin and many of its associated proteins and the assembly and uncoating mechanisms for clathrin coats¹. Highlights: clathrin heavy-chain sequence²—at the time, the longest protein sequence derived by cDNA cloning; high-resolution crystal structures of a large N-terminal fragment of clathrin³ and its complex with a "clathrin box" peptide⁴, of the core of the AP-1 adaptor complex⁵, and of a complex between Dishevelled and the μ 2 subunit of the AP-2 adaptor complex⁶; subnanometer structure of a clathrin coat (22MDa) by electron cryomicroscopy (cryoEM), yielding a complete molecular model for clathrin at 8 Å resolution⁷; cryoEM structure of a clathrin coat with bound auxilin and Hsc70^{8,9} and subsequent *in vitro* single-molecule total internal reflection fluorescence (TIRF) microscopy studies of uncoating¹⁰.

1. Kirchhausen, T., Owen, D. & Harrison, S. C. Molecular structure, function, and dynamics of clathrin-mediated membrane traffic. *Cold Spring Harb Perspect Biol* **6**, a016725 (2014). PMCID: PMC3996469.
2. Kirchhausen, T., Harrison, S. C., Chow, E. P., Mattaliano, R. J., Ramachandran, K. L., Smart, J. & Brosius, J. Clathrin heavy chain: molecular cloning and complete primary structure. *Proc Natl Acad Sci USA* **84**, 8805–8809 (1987).
3. Haar, ter, E., Musacchio, A., Harrison, S. C. & Kirchhausen, T. Atomic structure of clathrin: a beta propeller terminal domain joins an alpha zigzag linker. *Cell* **95**, 563–573 (1998).
4. Haar, ter, E., Harrison, S. C. & Kirchhausen, T. Peptide-in-groove interactions link target proteins to the beta-propeller of clathrin. *Proc Natl Acad Sci USA* **97**, 1096–1100 (2000).
5. Heldwein, E. E., Macia, E., Wang, J., Yin, H. L., Kirchhausen, T. & Harrison, S. C. Crystal structure of the clathrin adaptor protein 1 core. *Proc Natl Acad Sci USA* **101**, 14108–14113 (2004).
6. Yu, A., Xing, Y., Harrison, S. C. & Kirchhausen, T. Structural Analysis of the Interaction between Dishevelled2 and Clathrin AP-2 Adaptor, A Critical Step in Noncanonical Wnt Signaling. *Structure* **18**, 1311–1320 (2010). PMCID: PMC2992793.

7. Fotin, A., Cheng, Y., Sliz, P., Grigorieff, N., Harrison, S. C., Kirchhausen, T. & Walz, T. Molecular model for a complete clathrin lattice from electron cryomicroscopy. *Nature* **432**, 573–579 (2004).
8. Fotin, A., Cheng, Y., Grigorieff, N., Walz, T., Harrison, S. C. & Kirchhausen, T. Structure of an auxilin-bound clathrin coat and its implications for the mechanism of uncoating. *Nature* **432**, 649–653 (2004).
9. Xing, Y., Böcking, T., Wolf, M., Grigorieff, N., Kirchhausen, T. & Harrison, S. C. Structure of clathrin coat with bound Hsc70 and auxilin: mechanism of Hsc70-facilitated disassembly. *EMBO J* **29**, 655–665 (2010). PMCID: PMC2830701.
10. Böcking, T., Aguet, F., Harrison, S. C. & Kirchhausen, T. Single-molecule analysis of a molecular disassemblase reveals the mechanism of Hsc70-driven clathrin uncoating. *Nat Struct Mol Biol* **18**, 295–301 (2011). PMCID: PMC3056279.
11. Ehrlich, M., Boll, W., van Oijen, A., Hariharan, R., Chandran, K., Nibert, M. L. & Kirchhausen, T. Endocytosis by random initiation and stabilization of clathrin-coated pits. *Cell* **118**, 591–605 (2004).

2. Live-cell imaging (2004-)

Building on the biochemical and structural discoveries outlined above, we analyzed mechanisms of coated-vesicle formation in living cells, applying emerging technologies in fluorescence microscopy and live-cell imaging. Our use of spinning disc confocal microscopy led to the following description of molecular events in clathrin-mediated endocytosis: coated pits nucleate at the plasma membrane and grow by steady addition of clathrin triskelions¹¹; Hsc70-mediated uncoating follows promptly upon dynamin-induced membrane scission¹²; arrival of auxilin, the clathrin specific, J-domain co-chaperone for Hsc70, determines the timing of this event^{12,13}; clathrin assembly ordinarily provides the principal driving force for membrane invagination, but at high membrane tension¹⁴ or with very elongated cargo¹⁵, actin polymerization is also required. When our TIRF microscopy technology had reached the level of single-molecule counting, we showed that coated-pit initiation proceeds by coordinated arrival of clathrin and the AP2 adaptor complex¹⁶, the latter recruited by interaction with PtdIns (3,4)P₂, and that accessory proteins are then essential for sustained growth, and that a single rung of a dynamin tube is sufficient for coated pit neck scission¹⁷.

12. Massol, R. H., Boll, W., Griffin, A. M. & Kirchhausen, T. A burst of auxilin recruitment determines the onset of clathrin-coated vesicle uncoating. *Proc Natl Acad Sci USA* **103**, 10265–10270 (2006).
13. He, K., Marsland Iii, R., Upadhyayula, S., Song, E., Dang, S., Capraro, B. R., Wang, W., Skillern, W., Gaudin, R., Ma, M. & Kirchhausen, T. Dynamics of phosphoinositide conversion in clathrin-mediated endocytic traffic. *Nature* **552**, 410–414 (2017). PMID:29236694 [Pubmed in process].
14. Boulant, S., Kural, C., Zeeh, J.-C., Ubelmann, F. & Kirchhausen, T. Actin dynamics counteract membrane tension during clathrin-mediated endocytosis. *Nat Cell Biol* **13**, 1124–1131 (2011). PMCID: PMC3167020.
15. Cureton, D. K., Massol, R. H., Whelan, S. P. J. & Kirchhausen, T. The length of vesicular stomatitis virus particles dictates a need for actin assembly during clathrin-dependent endocytosis. *PLoS Pathog* **6**, e1001127 (2010). PMCID: PMC2947997.
16. Cocucci, E., Aguet, F., Boulant, S. & Kirchhausen, T. The first five seconds in the life of a clathrin-coated pit. *Cell* **150**, 495–507 (2012). PMCID: PMC3413093.
17. Cocucci, E., Gaudin, R. & Kirchhausen, T. Dynamin recruitment and membrane scission at the neck of a clathrin-coated pit. *Mol Biol Cell* **25**, 3595–3609 (2014). PMCID: PMC4230619.

A subset of earlier studies directly linked to the MIRA grant proposal include papers showing: regulation of ligand-independent Notch signal by intracellular trafficking¹⁸; generation of a ligand-independent Notch signal through synergy of the ESCRT-III complex and Deltex¹⁹; requirement that AMSH be targeted to endosomes for epidermal growth factor receptor degradation²⁰.

18. Hori, K., Sen, A., Kirchhausen, T. & Artavanis-Tsakonas, S. Regulation of ligand-independent Notch signal through intracellular trafficking. *Commun Integr Biol* **5**, 374–376 (2012). PMCID: PMC3460843.
19. Hori, K., Sen, A., Kirchhausen, T. & Artavanis-Tsakonas, S. Synergy between the ESCRT-III complex and Deltex defines a ligand-independent Notch signal. *J Cell Biol* **195**, 1005–1015 (2011). PMCID: PMC3241730.
20. Ma, Y. M., Boucrot, E., Villén, J., Affar, E. B., Gygi, S. P., Göttlinger, H. G. & Kirchhausen, T. Targeting of AMSH to endosomes is required for epidermal growth factor receptor degradation. *J Biol Chem* **282**, 9805–9812 (2007).

3. Frontier optical-imaging modalities using LLSM (2015-2017)

After initial use at Janelia Research Campus of LLSM to resolve the dorsal from the ventral surfaces of thin lamellipodial protrusions²¹, we built a second generation LLSM with guidance from Betzig and team at Janelia

Research Campus; it has been in continuous use since July, 2014. Our published work with this instrument has included: reexamination of the clathrin-coat assembly dynamics over the entire surfaces of 45 cells and ~250,000 AP-2 traces that required MATLAB software development resulting in the generation of 3D cmeAnalysis (clathrin-mediated endocytosis analysis (with Francois Aguet and Gaudenz Danuser)²²; full-cell imaging measurements of cell surface area and volume throughout the cell cycle, both for single cells in culture and for cells in the eye of a developing zebrafish embryo²²; studies of lipid-droplet maturation (with Walter and Farese)²³; studies of assembly mechanisms in the ESCRT pathway in yeast (with Teis)²⁴. We provide direct evidence (with Janet Shaw) that the intracellular location of mitochondria shapes subcellular energy gradients²⁵. Finally, we developed a new generation of phosphoinositide sensors and showed that a cascade of molecular conversions, made possible by the separation of a clathrin coated vesicle from its parent membrane, can label membrane-traffic intermediates and determine their destinations¹³. In this work, we used LLSM to visualize the sensors across the entire cellular volume, showing that a cascade of molecular signals, one of which is accumulation of PtdIns (3,4)P2 during uncoating, may bring about arrival of Rab5GTPases¹³.

21. Kural, C., Akatay, A. A., Gaudin, R., Chen, B.-C., Legant, W. R., Betzig, E. & Kirchhausen, T. Asymmetric formation of coated pits on dorsal and ventral surfaces at the leading edges of motile cells and on protrusions of immobile cells. *Mol Biol Cell* **26**, 2044–2053 (2015). PMCID: PMC4472015.
22. Aguet, F., Upadhyayula, S., Gaudin, R., Chou, Y.-Y., Cocucci, E., He, K., Chen, B.-C., Mosaliganti, K., Pasham, M., Skillern, W., Legant, W. R., Liu, T.-L., Findlay, G., Marino, E., Danuser, G., Megason, S., Betzig, E. & Kirchhausen, T. Membrane dynamics of dividing cells imaged by lattice light-sheet microscopy. *Mol Biol Cell* (2016). doi:10.1091/mbc.E16-03-0164. PMCID: PMC5221578.
23. Wang, H., Becuwe, M., Housden, B. E., Chitraj, C., Porras, A. J., Graham, M. M., Liu, X. N., Thiam, A. R., Savage, D. B., Agarwal, A. K., Garg, A., Olarte, M.-J., Lin, Q., Fröhlich, F., Hannibal-Bach, H. K., Upadhyayula, S., Perrimon, N., Kirchhausen, T., Ejsing, C. S., Walther, T. C. & Farese, R. V. Seipin is required for converting nascent to mature lipid droplets. *Elife* **5**, (2016). PMCID: PMC5035145.
24. Adell, M. A. Y., Migliano, S. M., Upadhyayula, S., Bykov, Y. S., Sprenger, S., Pakdel, M., Vogel, G. F., Jih, G., Skillern, W., Behrouzi, R., Babst, M., Schmidt, O., Hess, M. W., Briggs, J. A., Kirchhausen, T. & Teis, D. Recruitment dynamics of ESCRT-III and Vps4 to endosomes and implications for reverse membrane budding. *Elife* **6**, e31652 (2017). PMCID: PMC5665648.

4. Frontier optical-imaging modalities using AO-LLSM (2016-)

Since August 2016, we have collaborated closely with Eric Betzig in developing AO-LLSM and using it to visualize live, multicellular structures (organoids, worms, plants and most extensively, zebrafish embryos). A collaborative study with Sean Megason led to the unexpected discovery of a physical relief valve in the endolymphatic sac, a dead-end epithelial tube connected to the inner ear: Megason²⁶. The most recent study (currently under revision in Science)²⁷ is a comprehensive collaboration with Betzig to test AO-LLSM, particularly focused on visualizing developmental processes in zebrafish embryos. Examples include: quantitative tracking of all endocytic coated pits and vesicles in muscle and brain cells (the dynamics are faster in brain, and the coats are smaller); visualization and quantification of migrating lymphocytes and human cancer cells; measurements of cell area and volume and organelle distribution during cell division; tracing of axonal growth in the hindbrain.

These applications demonstrate the advantage of LLSM and AO-LLSM and how they set a new standard for imaging membrane dynamics in single cells and multicellular assemblies.

25. Schuler, M.-H., Lewandowska, A., Di Caprio, G., Skillern, W., Upadhyayula, S., Kirchhausen, T., Shaw, J. M. & Cunniff, B. Miro1-mediated mitochondrial positioning shapes intracellular energy gradients required for cell migration. *Mol Biol Cell* mbc.E16–10–0741 (2017). doi:10.1091/mbc.E16-10-0741. PMCID: PMC5531732.
26. Swinburne, I. A., Mosaliganti, K. R., Upadhyayula, S., Liu, T.-L., Hildebrand, D. G. C., Tsai, T., Chen, A., Al-Obeidi, E., Fass, A., Malhotra, S., Engert, F., Lichtman, J. W., Kirchhausen, T., Betzig, E. & Megason, S. G. Lamellar Junctions In The Endolymphatic Sac Act As A Relief Valve To Regulate Inner Ear Pressure. *bioRxiv* 143826 (2017). doi:10.1101/143826. [Preprint].
27. Liu, T.-L., Upadhyayula, S., Milkie, D. E., Singh, V., Wang, K., Swinburne, I. A., Mosaliganti, K. R., Collin, Z. M., Hiscock, T. W., Shea, J., Kohrman, A. Q., Medwig, T. N., Dambourne, D., Forster, R., Cunniff, B., Ruan, Y., Yashiro, H., Scholpp, S., Meyerowitz, E. M., Hockemeyer, D., Drubin, D. G., Martin, B. L., Matus, D. Q., Koyama, M., Megason, S. G., Kirchhausen, T. & Betzig, E. Observing the Cell in Its Native State: Imaging Subcellular Dynamics in Multicellular Organisms. *Science*, *in press* (2018).

Complete List of Published Work in MyBibliography:

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Selected peer-reviewed publications (204 in chronological order).

1. Mateu, L., Kirchhausen, T. and Camejo, G. 1977. A low temperature structural transition in human serum low density lipoproteins. *Biochim Biophys Acta.* 487. 1. 243-245.
2. Mateu, L., Kirchhausen, T., Padron, R. and Camejo, G. 1977. Small-angle x-ray scattering study of human serum low-density lipoproteins with differential reactivity for an arterial proteoglycan. *J Supramol Struct.* 7. 3-4. 435-442.
3. Mateu, L., Kirchhausen, T. and Camejo, G. 1978. Small-angle X-ray scattering and differential scanning calorimetry studies on reversibly modified human-serum low density lipoproteins. *Biochemistry.* 17. 8. 1436-1440.
4. Kirchhausen, T., Untracht, S. H., Fless, G. M. and Scanu, A. M. 1979. Atherogenic diets and neutral-lipid organization in plasma low density lipoproteins. *Atherosclerosis.* 33. 1. 59-70.
5. Mateu, L. and Kirchhausen, T. 1979. Kinetics of thermal transitions in human serum low density lipoproteins (LDL) and neutral lipids. A dynamic small-angle X-ray scattering study. *Acta Cient Venez.* 30. 5. 478-483.
6. Kirchhausen, T., Fless, G. and Scanu, A. M. 1980. The structure of plasma low density lipoproteins: experimental facts and interpretations--a minireview. *Lipids.* 15. 6. 464-467.
7. Kirchhausen, T. and Harrison, S. C. 1981. Protein organization in clathrin trimers. *Cell.* 23. 3. 755-761.
8. Fless, G. M., Kirchhausen, T., Fischer-Dzoga, K., Wissler, R. W. and Scanu, A. M. 1982. Serum low density lipoproteins with mitogenic effect on cultured aortic smooth muscle cells. *Atherosclerosis.* 41. 2-3. 171-183.
9. Harrison, S. C. and Kirchhausen, T. 1983. Clathrin, cages, and coated vesicles. *Cell.* 33. 3. 650-652.
10. Hogle, J., Kirchhausen, T. and Harrison, S. C. 1983. Divalent cation sites in tomato bushy stunt virus. Difference maps at 2-9 Å resolution. *J Mol Biol.* 171. 1. 95-100.
11. Kirchhausen, T., Harrison, S. C., Parham, P. and Brodsky, F. M. 1983. Location and distribution of the light chains in clathrin trimers. *Proc Natl Acad Sci U S A.* 80. 9. 2481-2485.
12. Leon, V., Kirchhausen, T., Avila, E. M. and Mateu, L. 1983. Thermal effects in human plasma high density lipoproteins (HDL)3: a 13C-FT-NMR study. *Acta Cient Venez.* 34. 3-4. 209-215.
13. Kirchhausen, T. and Harrison, S. C. 1984. Structural domains of clathrin heavy chains. *J Cell Biol.* 99. 5. 1725-1734.
14. Heuser, J. and Kirchhausen, T. 1985. Deep-etch views of clathrin assemblies. *J Ultrastruct Res.* 92. 1-2. 1-27.
15. Kirchhausen, T., Wang, J. C. and Harrison, S. C. 1985. DNA gyrase and its complexes with DNA: direct observation by electron microscopy. *Cell.* 41. 3. 933-943.
16. Kirchhausen, T., Harrison, S. C. and Heuser, J. 1986. Configuration of clathrin trimers: evidence from electron microscopy. *J Ultrastruct Mol Struct Res.* 94. 3. 199-208.
17. Kirchhausen, T., Harrison, S. C., Chow, E. P., Mattaliano, R. J., Ramachandran, K. L., Smart, J. and Brosius, J. 1987. Clathrin heavy chain: molecular cloning and complete primary structure. *Proc Natl Acad Sci U S A.* 84. 24. 8805-8809.
18. Kirchhausen, T., Scarmato, P., Harrison, S. C., Monroe, J. J., Chow, E. P., Mattaliano, R. J., Ramachandran, K. L., Smart, J. E., Ahn, A. H. and Brosius, J. 1987. Clathrin light chains LCA and LCB are similar, polymorphic, and share repeated heptad motifs. *Science.* 236. 4799. 320-324.
19. Thurieau, C., Brosius, J., Burne, C., Jolles, P., Keen, J. H., Mattaliano, R. J., Chow, E. P., Ramachandran, K. L. and Kirchhausen, T. 1988. Molecular cloning and complete amino acid sequence of AP50, an assembly protein associated with clathrin-coated vesicles. *DNA.* 7. 10. 663-669.
20. Kirchhausen, T., Nathanson, K. L., Matsui, W., Vaisberg, A., Chow, E. P., Burne, C., Keen, J. H. and Davis, A. E. 1989. Structural and functional division into two domains of the large (100- to 115-kDa) chains of the clathrin-associated protein complex AP-2. *Proc Natl Acad Sci U S A.* 86. 8. 2612-2616.
21. Kirchhausen, T. 1990. Identification of a putative yeast homolog of the mammalian beta chains of the clathrin-associated protein complexes. *Mol Cell Biol.* 10. 11. 6089-6090.

22. Matsui, W. and Kirchhausen, T. 1990. Stabilization of clathrin coats by the core of the clathrin-associated protein complex AP-2. *Biochemistry*. 29. 48. 10791-10798.
23. Scarmato, P. and Kirchhausen, T. 1990. Analysis of clathrin light chain-heavy chain interactions using truncated mutants of rat liver light chain LCB3. *J Biol Chem*. 265. 7. 3661-3668.
24. Tucker, K. L., Nathanson, K. and Kirchhausen, T. 1990. Sequence of the rat alpha c large chain of the clathrin associated protein complex AP-2. *Nucleic Acids Res*. 18. 17. 5306.
25. Keen, J. H., Beck, K. A., Kirchhausen, T. and Jarrett, T. 1991. Clathrin domains involved in recognition by assembly protein AP-2. *J Biol Chem*. 266. 12. 7950-7956.
26. Kirchhausen, T., Davis, A. C., Frucht, S., Greco, B. O., Payne, G. S. and Tubb, B. 1991. AP17 and AP19, the mammalian small chains of the clathrin-associated protein complexes show homology to Yap17p, their putative homolog in yeast. *J Biol Chem*. 266. 17. 11153-11157.
27. Nakayama, Y., Goebi, M., O'Brine Greco, B., Lemmon, S., Pingchang Chow, E. and Kirchhausen, T. 1991. The medium chains of the mammalian clathrin-associated proteins have a homolog in yeast. *Eur J Biochem*. 202. 2. 569-574.
28. Gallusser, A. and Kirchhausen, T. 1993. The beta 1 and beta 2 subunits of the AP complexes are the clathrin coat assembly components. *Embo J*. 12. 13. 5237-5244.
29. Kirchhausen, T. 1993. Coated pits and coated vesicles - sorting it all out. *Current Opinion in Structural Biology*. 3. 182-188.
30. Kirchhausen, T., Staunton, D. E. and Springer, T. A. 1993. Location of the domains of ICAM-1 by immunolabeling and single-molecule electron microscopy. *J Leukoc Biol*. 53. 3. 342-346.
31. Kirchhausen, T. and Toyoda, T. 1993. Immunoelectron microscopic evidence for the extended conformation of light chains in clathrin trimers. *J Biol Chem*. 268. 14. 10268-10273.
32. Osborn, L., Vassallo, C., Browning, B. G., Tizard, R., Haskard, D. O., Benjamin, C. D., Dougas, I. and Kirchhausen, T. 1994. Arrangement of domains, and amino acid residues required for binding of vascular cell adhesion molecule-1 to its counter-receptor VLA-4 (alpha 4 beta 1). *J Cell Biol*. 124. 4. 601-608.
33. Phan, H. L., Finlay, J. A., Chu, D. S., Tan, P. K., Kirchhausen, T. and Payne, G. S. 1994. The *Saccharomyces cerevisiae* APS1 gene encodes a homolog of the small subunit of the mammalian clathrin AP-1 complex: evidence for functional interaction with clathrin at the Golgi complex. *Embo J*. 13. 7. 1706-1717.
34. Sogaard, M., Tani, K., Ye, R. R., Geromanos, S., Tempst, P., Kirchhausen, T., Rothman, J. E. and Sollner, T. 1994. A rab protein is required for the assembly of SNARE complexes in the docking of transport vesicles. *Cell*. 78. 6. 937-948.
35. Boll, W., Gallusser, A. and Kirchhausen, T. 1995. Role of the regulatory domain of the EGF-receptor cytoplasmic tail in selective binding of the clathrin-associated complex AP-2. *Curr Biol*. 5. 10. 1168-1178.
36. Ohno, H., Stewart, J., Fournier, M. C., Bosshart, H., Rhee, I., Miyatake, S., Saito, T., Gallusser, A., Kirchhausen, T. and Bonifacino, J. S. 1995. Interaction of tyrosine-based sorting signals with clathrin-associated proteins. *Science*. 269. 5232. 1872-1875.
37. Rad, M. R., Phan, H. L., Kirchrath, L., Tan, P. K., Kirchhausen, T., Hollenberg, C. P. and Payne, G. S. 1995. *Saccharomyces cerevisiae* Apl2p, a homologue of the mammalian clathrin AP beta subunit, plays a role in clathrin-dependent Golgi functions. *J Cell Sci*. 108 (Pt 4). 1605-1615.
38. Shih, W., Gallusser, A. and Kirchhausen, T. 1995. A clathrin-binding site in the hinge of the beta 2 chain of mammalian AP-2 complexes. *J Biol Chem*. 270. 52. 31083-31090.
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40. Speelman, B. A., Allen, K., Grounds, T. L., Neutra, M. R., Kirchhausen, T. and Wilson, J. M. 1995. Molecular characterization of an apical early endosomal glycoprotein from developing rat intestinal epithelial cells. *J Biol Chem*. 270. 4. 1583-1588.
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