Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Plant Biology

Wet scissors: How biomolecular condensates cut cellular membranes

Xiaofeng Fang[1], Alexander I. May[2,3], Katharina Sporbeck[2], Lukas Hauer[2,4] and Roland L. Knorr[2,4,5,6]

Membrane shape is a fundamental determinant of cellular organisation. Reshaping of membranes is crucial for dynamic processes including organelle and cell division, endocytosis and membrane trafficking. Membrane fission (or scission) is a discontinuous, topological shape change that is central in many such processes. Specialised remodelling proteins, such as dynamins and ESCRT proteins, are capable of forming oligomeric spirals that drive membrane fission in cells. In this review, we summarise evidence demonstrating that capillary forces generated by liquid-like biomolecular condensates can facilitate cellular membrane reshaping and drive fission events. We draw on our recent findings that condensates are implicated in multivesicular body formation to describe the molecular and physical principles that allow biomolecular condensates to cut membranes. We further discuss possible interactions between novel condensate-mediated fission processes and established reshaping processes. We propose that condensates make an important contribution to membrane remodelling events involved in the biogenesis of diverse cellular structures. The characterisation of condensate-mediated membrane reshaping promises to transform our understanding of intracellular organisation and dynamics.

Addresses
[1] School of Life Sciences, Tsinghua University, Beijing, 100084, China
[2] Institute of Biology, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany
[3] Institute for Integrated Research, Institute of Science Tokyo, Tokyo, Japan
[4] University of Cologne, Faculty of Medicine and University Hospital Cologne, Cologne, Germany
[5] Cologne Excellence Cluster on Cellular Stress Responses in Aging-Associated Diseases (CECAD), University of Cologne, Cologne, Germany
[6] Graduate School and Faculty of Medicine, The University of Tokyo, Tokyo, Japan

Corresponding authors: Fang, Xiaofeng (xffang@tsinghua.edu.cn); Knorr, Roland L. (roland.knorr@uni-koeln.de)

Current Opinion in Plant Biology 2025, **86**:102740

This review comes from a themed issue on **Cell biology and cell signalling 2025**

Edited by **Sharon A. Kessler** and **Cecilia Rodriguez-Furlan**

For complete overview of the section, please refer the article collection - Cell biology and cell signalling 2025

Available online 3 June 2025

https://doi.org/10.1016/j.pbi.2025.102740

Cellular membranes exist in diverse conformations that have important implications for their function, as observed in intricate organelle morphologies or the invaginations and protrusions of plasma membranes [1]. Membrane bending, which is the continuous morphological deformation of a membrane, can result in the formation of narrow membrane necks that are important for membrane fission (also called 'scission') [2]. This discontinuous topological change is critical for endocytosis, trafficking, the biogenesis and movement of organelles as well as cellular motility [3].

The mechanisms driving membrane fission have been the subject of intense investigation for many years. Current models contend that the combined action of proteins that exert mechanical forces (mechanoenzymes) and various physicochemical factors is responsible for deformation and eventual cutting of membranes [3–5]. However, preliminary evidence has suggested that biomolecular condensates can drive membrane fission without dedicated fission machineries [6]. Condensates, which form through liquid–liquid phase separation (LLPS), are dynamic intracellular compartments that form as proteins and other molecules demix from the cytosol while retaining liquid-like material properties [7,8]. Condensate component proteins often contain an intrinsically disordered region (IDR) that is responsible for both extensive low-affinity intra-condensate interactions and structural plasticity that together cause the dynamic molecular network characteristic of these transient structures. The molecular bases underlying biomolecular condensation and their functional complexity, which is comparable to conventional membrane-bound organelles, are extensively reviewed elsewhere [9–11].

While often defined as membrane-less compartments, condensates are able to associate with membranes in a process known as 'wetting'. Wetting can result in deformation of both the membrane and the condensate [12–14] with important functional implications. In this

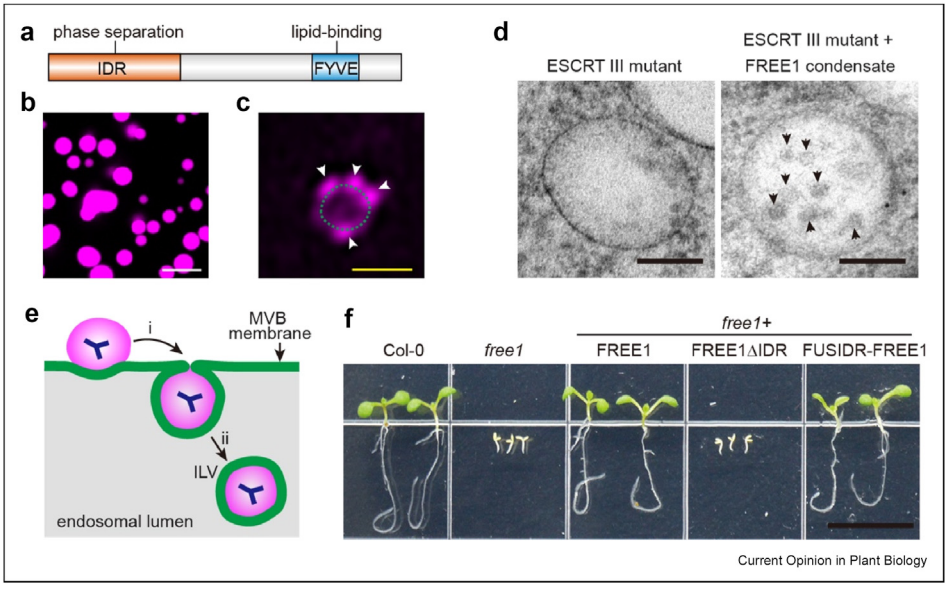
review, we discuss the role of condensate-membrane interactions in membrane fission. It is known that membrane-bound liquid condensates are involved in membrane trafficking processes including intraluminal vesicle formation within multivesicular bodies (MVBs) [15], plasma membrane-localised endocytic condensates [16,17], internalisation and degradation of cytosolic condensates via the lysosome [18,19], and the biogenesis of condensate-containing secretory granules and protein storage vacuoles [20,21]. All these processes require a fission event to complete, suggesting that condensate wetting may contribute to membrane neck formation, neck cutting and, thereby, cellular trafficking processes.

Remodelling and fission of membranes by a membrane-binding condensate, FREE1

MVBs are endosomal compartments that function in cellular quality control through the capture and degradation of membrane-bound cargo proteins within intraluminal vesicles (ILVs) [22]. ILVs form through invagination and fission of the MVB membrane, which requires the endosomal sorting complexes required for transport (ESCRT), an evolutionarily conserved protein machinery that governs diverse membrane remodelling events in eukaryotic cells. ESCRT plays a central role in membrane fission through four successive subcomplexes that are numbered 0-III [22,23]. During ILV biogenesis, the subcomplexes form ILVs in sequential steps: recognition of ubiquitinated membrane proteins, cargo sorting, invagination/neck formation and, finally, fission [24]. The fission step involves the ATP-dependent constriction of ESCRT-III filaments that localise to the luminal side of the neck, releasing discrete ILVs that are degraded once the MVB ultimately fuses with a lysosome or vacuole [5,25].

While ESCRT subcomplexes I-III are found in plants, they lack a canonical ESCRT-0 homologue that performs cargo sorting functions in other eukaryotes [26]. Instead, the plant-specific ESCRT-associated protein FREE1 (FYVE domain protein required for endosomal sorting 1) [27] binds the lipid phosphatidylinositol 3-phosphate (PI3P) via its FYVE domain (Figure 1a) to mediate endosomal cargo sorting. The loss of FREE1 prevents ILV formation and results in seedling lethality, underscoring its critical role in cargo sorting [27]. Recently, we showed [15] that FREE1 forms condensates (Figure 1b) in a manner that depends on its extended IDR (Fig. 1A). We also found that FREE1 condensates localise to MVBs (Figure 1c), mediate ILV formation (Figure 1d) and drive fission of membrane necks via a membrane-wetting mechanism (Figure 1e) [15]. The ability of FREE1 to form a condensate is critical for this function: mutant FREE1 lacking the IDR was unable to complement the lethal phenotype, but swapping of FREE1's IDR with heterologous IDRs

Figure 1



FREE1 condensates remodel and fission membranes. (**a**) Domain structure of the condensate-forming, plant-specific protein FREE1. (**b**) FREE1 condensate formation *in vitro*. Scale bar, 5 μm. (**c**) FREE1 condensates (arrowheads) localise to MVB membranes that contain PI3P. *Arabidopsis thaliana* root tip cells. Scale bar, 1 μm. Green dashed line indicates the MVB membrane. (**d**) FREE1 rescues ILV formation (arrows) in a knock-out of the essential ESCRT-III machinery component Vps2. Electron microscopy images of MVBs in early-stage *A. thaliana* embryos. Scale bars, 100 nm. (**e**) Model of condensate-mediated formation of intraluminal vesicles (ILV). (i) Condensates (magenta) bind and shape membranes (green), driving membrane neck formation. (ii) Line tension force contributes to neck fission. Blue Y, ubiquitinated cargo. (**f**) The ability to form condensates is necessary and sufficient for FREE1 function in plant development. Scale bar, 1 cm. (**b**, **c**), confocal imaging of GFP-FREE1. Figures modified from Wang et al., 2024 [15]. IDR, intrinsically disordered domain. FYVE, domain that binds PI3P.

from unrelated condensate-forming proteins both restored condensate formation and rescued seedling lethality (Figure 1f). Importantly, FREE1 chimeras with heterologous IDRs were unable to prevent lethality under osmotic stress conditions. However, seedling survivability under stress was restored by provision of an additional domain that binds downstream ESCRTs, suggesting that interplay between FREE1 condensation and the ESCRT machinery is important for FREE1 function. In line with this, FREE1 overexpression partially restored ILV formation and rescued seedling lethality observed upon deletion of the essential ESCRT-III machinery component Vps2 (Figure 1d). Together, these data demonstrate that FREE1 condensate interactions with the ESCRT machinery are essential for MVB function in plants and further suggest that ILV biogenesis can be mediated by condensate-dependent pathways alone.

Conservation of membrane shaping condensates

Originally, FREE1 was identified in eudicots [27]. However, a recent phylogenetic analysis [15] identified homologues in a broad range of land plants, all of which contain a lipid-binding domain (typically a FYVE or PH domain), coiled-coil regions, an extended IDR (Figure 2a) and a central yet uncharacterised conserved domain. Notably, the sequence variability within IDRs is significant (Figure 2b), which is consistent with our finding that FREE1 function is complemented by heterologous IDRs (Figure 1f).

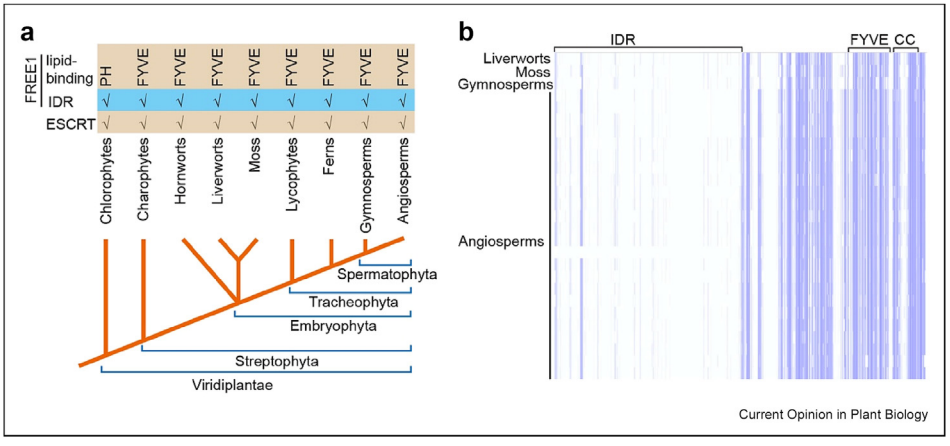
Intriguingly, although mammals and yeast lack a direct FREE1 homologue, ectopic expression of FREE1 in mammalian cells induces ILV formation in MVBs. In yeast, it has been shown that the ESCRT-0 components Hse1 and Vps27 condense with polyubiquitin on vacuolar membranes to facilitate cargo sorting [19]. Vps27 contains a FYVE domain and Hse1 harbours an IDR, further hinting at the critical combination of IDRs and lipid-binding domains. The conservation of this combination across eukaryotes and the functional interchangeability of IDRs in FREE1 suggest that the membrane reshaping and fission functions of membrane-binding condensates may represent a universal strategy for cellular organisation and trafficking across different kingdoms of life.

Physical forces that drive condensate-mediated membrane fission

Fission can be understood as a consequence of membrane neck instability. Spontaneous neck fission has been observed for neck constriction forces above approximately 25 pN [28], which is within the range that capillarity can generate during membrane wetting by liquid-like condensates [15]. Molecules at the condensate surface experience unevenly distributed force interactions (Figure 3a). This yields an excess energy known as surface tension. By driving liquids to reduce their surface area, surface tension is responsible for the characteristic spherical shape of membrane-less condensates.

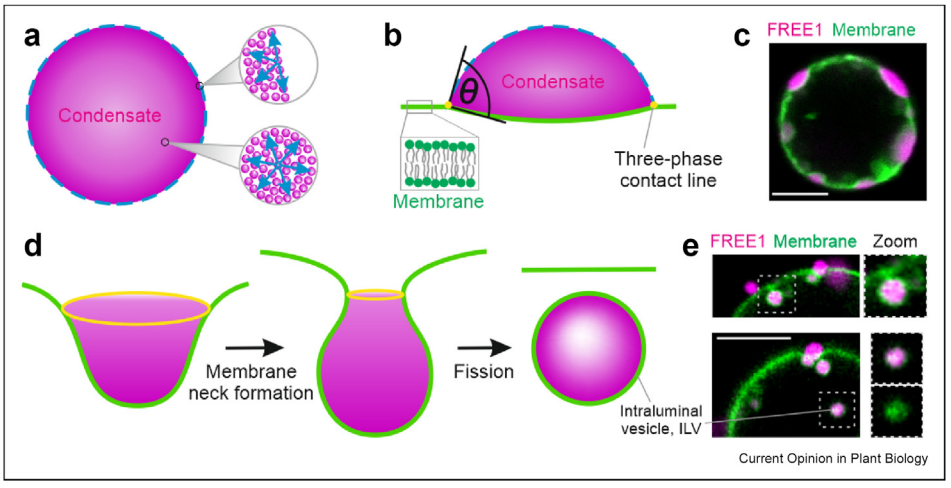
Adhesive forces between condensates and membranes can overcome surface tension. This causes condensates to wet membranes, resulting in three-phase contact lines (Figure 3b and c). Here, surface tension exerts capillary forces, which drive shape changes of membranes, condensates or both. Importantly, membrane deformation requires tension-free membranes with excess area that is available for reshaping. Both variables—the balance between surface tension and adhesion, as well as membrane availability—determine the degree of condensate-membrane shaping and, thereby, the morphology that arises during wetting (Figure 3b–e).

Figure 2



FREE1 is conserved in land plants. (**a**) FREE1 homologs are present in land plants. (**b**) Sequence alignment of FREE1 homologs. Several selected species from indicated phyla are shown. Line intensity indicates degree of conservation. The central conserved domain is not yet characterised. CC, coiled-coil domain. The alignment was performed according to Wang et al., 2024 [15].

Figure 3



Physical mechanisms underlie condensate-mediated membrane neck formation and membrane fission. (**a**) Force interactions are not equally distributed around molecules localised at the surface of condensates, leading to an interfacial excess energy termed 'surface tension'. Condensate surface tension (blue dotted line) forces liquid condensates to minimise their surface area by forming spherical shapes. (**b**) The balance between surface tensions and adhesion of the condensate to membranes is called wetting and can be quantified by measurements of the contact angle θ at the three-phase contact line (yellow dots in the cross section). The length scale over which membrane-deforming wetting phenomena are expected in cells and biomimetic systems is in the order of 0.1–10 μm. (**c**) Several large FREE1 condensates wet the membrane of a giant unilamellar vesicle under tension with a contact angle of about 70°. (**d**) Left, line tension is the 1D analogue of surface tension and is the excess energy of the three-phase contact line (yellow circle in 3D) per contact line length. Centre, shortening of the contact line facilitates membrane budding and neck formation. Right, contact line elimination driving fission of nanometre-sized membrane necks. (**e**) Wetting of small FREE1 condensates drives membrane neck formation of tension-free membranes in vitro (top). Membrane fission generates ILVs in vitro (bottom). Right, image magnifications of boxes in the left panels. Bottom right, membrane fluorescence of panel above. Scale bars, 5 μm. (**c**, **e**), confocal sections of GFP-FREE1 condensates and membranes labelled using a minor fraction of the membrane dye DiIC18. Modified from Wang et al., 2024 [15].

Wetting also causes a contact line to form between the two coexisting phases and the membrane (Figure 3b–d). This three-phase contact line has been extensively studied in a range of macroscopic, non-biological wetting scenarios, such as film, bubble and foam formation [29,30]. As observed in the simpler case of condensate surfaces, contact between three phases gives rise to an excess energy per unit length called the three-phase line tension. At the nanometre scale, this line tension drives minimisation of the contact line length. Our work [15] shows that capillary forces and three-phase line tension are responsible for the generation of nanometre-sized membrane necks when condensates contact membranes during ILV formation (Figure 3d and e). Mathematical modelling and computer simulations further showed that contact line elimination can generate the constriction forces required for membrane neck fission during MVB formation [15]. This finding indicates that intracellular capillarity alone can fission membranes subsequent to membrane neck formation, even without mechanoenzymes.

Highway to fission: diverse mechanisms can interact to cut membranes

Membrane fission is an essential process that is required for diverse membrane trafficking processes, such as protein transport, exosome formation and degradation pathways. Our findings raise the question of how condensate-driven fission is integrated with established cellular fission pathways that employ active protein machineries. Typically, these machineries assemble at membrane necks and trigger fission by hydrolysing ATP or GTP. One of the best-known classes of such machineries, the dynamins, polymerise to form a filament that constricts, leading to mechanical fission of membrane necks. Dynamins localise to the outside of the neck, which suggests that forces generated by wetting condensates within the neck may prime the system for fission to occur. This hints at independent yet potentially cooperative roles for both fission mechanisms.

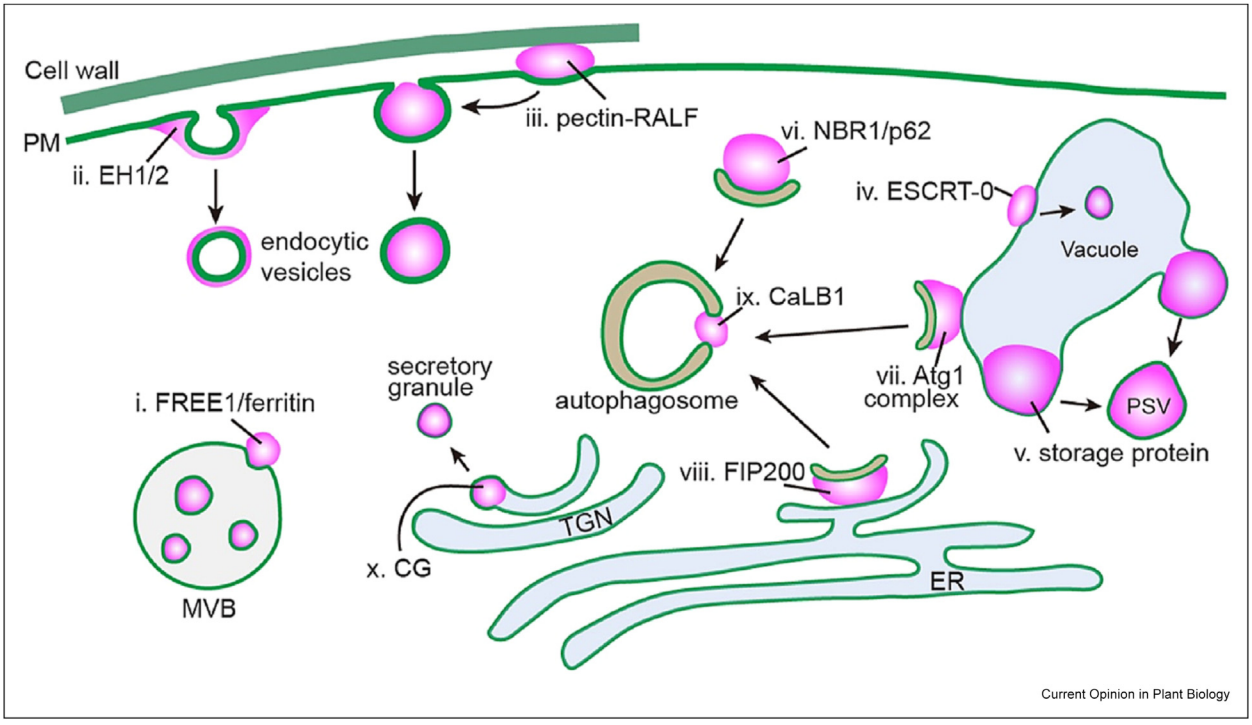
In contrast to dynamins, the filamentous ESCRT-III machinery assembles and cuts membrane necks from within [5]. Interestingly, FREE1 condensates recruit ESCRT machinery components sequentially [15] and likely also accumulate a range of additional client molecules by partitioning. Even if clients are not directly involved in active fission mechanisms, these molecules may modulate fission passively by altering surface tensions and adhesive forces, thereby tuning line tension and wetting geometries to favour fission. Further, condensate clients may facilitate membrane fission by inducing membrane asymmetries through phenomena

including molecular crowding [31], insertions of molecules into the membrane [32], lipid demixing [33–35] or actin recruitment [36]. Thus, membrane-bound condensates likely contribute to fission in indirect ways beyond the generation of line tension, such as interactions with active protein machineries and modulation of local membrane properties.

Condensates and membrane fission are involved in diverse physiological processes

Biomolecular condensates play critical roles in various cellular processes by facilitating membrane reshaping and contributing to membrane fission (Figure 4). During endocytosis in plants, condensates forming from TPLATE complex subunits or pectin-RALF assemblies drive plasma membrane vesiculation, including fission, by clustering receptors with endocytic components and condensate-membrane wetting [16,37]. Similarly, autophagosome biogenesis leverages condensates such as the mammalian scaffold protein FIP200 [38], the yeast Atg1 complex [39] or mammalian p62 and its plant homologue NBR1 [40,41]. Based on theoretical models and experimental evidence [40,42], wetting interactions have been shown to control the direction and form of isolation membrane growth. During this process, condensate surface tension enhances the shape stability of growing isolation membranes. Further, condensate-forming proteins (including CaLB1-ALIX, FREE1) may also facilitate isolation membrane fission in plants [43]. Further, condensates dictate membrane reshaping during morphogenic processes originating at plant vacuoles [21] and the mammalian Golgi-apparatus [20]. In these examples, wetting luminal condensates mediate sorting of storage proteins and proinsulin to form discrete vesicle-like structures that arise by fission events and are called protein storage vacuoles and secretory granules, respectively.

Figure 4



Cellular processes that involve membrane-bound liquid condensates, membrane reshaping and a membrane fission step. (i) Ferritin particles form condensates in an NCOA4-dependent manner in yeast, which are engulfed by endosomes similarly to FREE1 condensates. (ii). Clathrin-mediated endocytosis in plants requires the TPLATE complex formed by the subunits EH1/2. EH1/2 condensates form on the plasma membrane and facilitate endocytosis. (iii) In the apoplast of plant cells, pectin/RALF peptide condensates are important for receptor clustering and endocytosis. (iv) Yeast ESCRT-0/polyubiquitin condensates form on vacuole membranes and facilitate direct cargo uptake into vacuoles. (v) During seed maturation, vacuolar storage proteins form condensates within the vacuole lumen. Condensate wetting mediates vacuole shaping and biogenesis of individual protein storage vacuoles (PSVs). (vi-ix) Condensate surfaces facilitate autophagosome formation either as cargoes or assembly sites. (vi) Autophagy receptor condensates positive for e.g. p62 and NBR1 function as sites of autophagosome formation or are transported as autophagosomal cargoes. (vii) In yeast, Atg1 complex condensates are tethered to vacuole membranes and initiate autophagosome formation. (viii) In mammalian cells, elevated Ca^{2+} concentrations can induce condensed FIP200 autophagosome initiation complexes on the endoplasmic reticulum (ER). (ix) *A. thaliana* CaLB1/ALIX condensates are required for the maturation of autophagosomes, and FREE1 regulates autophagosome fission. (x) Golgi-luminal chromogranin (CG) protein condensates facilitate receptor-independent secretory granule formation. PM, plasma membrane. TGN, trans-Golgi network.

Collectively, these findings suggest that condensates can serve as versatile tools for membrane shaping and fission. While canonical GTP- or ATP-dependent machineries like dynamins or ESCRT-III are well-known to directly fission membranes, condensates may also act indirectly by priming membranes for fission via signalling, orchestration of spatio-temporal fission complex organisation, mechanical coordination with fission complexes, or by changing membrane properties locally. This complex interplay implies a continuum of passive and active fission mechanisms, where phase separation could adaptively regulate membrane dynamics in response to physicochemical cues, allowing for optimisation of membrane function in diverse physiological contexts.

Author contributions

Conceptualization, Visualization, Writing – original draft, review and editing: XF, RLK. Funding acquisition: XF, AIM, RLK. Writing – review and editing: AIM, KS, LH.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by grants from the Ministry of Science and Technology of China (2022YFA1303400) and National Natural Science Foundation of China (32450060, 32222015) to XF, Deutsche Forschungsgemeinschaft grants 460056461 and 506366351 to RLK and JSPS KAKENHI grant JP21K15083 and JP25K09574 to AIM.

Data availability

No data was used for the research described in the article.

References

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest
** of outstanding interest

1. McMahon HT, Gallop JL: **Membrane curvature and mechanisms of dynamic cell membrane remodelling**. *Nature* 2005, **438**:590–596.

2. Knorr RL, Lipowsky R, Dimova R: **Autophagosome closure requires membrane scission**. *Autophagy* 2015, **11**:2134–2137.

3. Renard HF, Johannes L, Morsomme P: **Increasing diversity of biological membrane fission mechanisms**. *Trends Cell Biol* 2018, **28**:274–286.

4. Antonny B, Burd C, De Camilli P, Chen E, Daumke O, Faelber K, Ford M, Frolov VA, Frost A, Hinshaw JE, *et al.*: **Membrane fission by dynamin: what we know and what we need to know**. *EMBO J* 2016, **35**:2270–2284.

5. Pfitzner AK, Moser von Filseck J, Roux A: **Principles of membrane remodeling by dynamic ESCRT-III polymers**. *Trends Cell Biol* 2021, **31**:856–868.

6. **Cell membranes shaped and cut by phase-separated liquid protein condensates**. *Nature* 2024, **634**:1204–1210.

7. Banani SF, Lee HO, Hyman AA, Rosen MK: **Biomolecular condensates: organizers of cellular biochemistry**. *Nat Rev Mol Cell Biol* 2017, **18**:285–298.

8. Shin Y, Brangwynne CP: **Liquid phase condensation in cell physiology and disease**. *Science* 2017, **357**, eaaf4382.

9. Emenecker RJ, Holehouse AS, Strader LC: **Emerging roles for phase separation in plants**. *Dev Cell* 2020, **55**:69–83.

10. Fang X, Li P: **SnapShot: condensates in plant biology**. *Cell* 2024, **187**:2894. 2894.

11. Peng J, Yu Y, Fang X: **Stress sensing and response through biomolecular condensates in plants**. *Plant Commun* 2024, **6**, 101225.

12. Kusumaatmaja H, May AI, Knorr RL: **Intracellular wetting mediates contacts between liquid compartments and membrane-bound organelles**. *J Cell Biol* 2021, **220**, e202103175.

13. Gouveia B, Kim Y, Shaevitz JW, Petry S, Stone HA, Brangwynne CP: **Capillary forces generated by biomolecular condensates**. *Nature* 2022, **609**:255–264.

14. Lalchand P, Ashley DD, Pan X: **Biomolecular condensates at the plasma membrane: insights into plant cell signaling**. *Curr Opin Plant Biol* 2025, **84**, 102697.

15. ** Wang Y, Li S, Mokbel M, May AI, Liang Z, Zeng Y, Wang W, Zhang H, Yu F, Sporbeck K, *et al.*: **Biomolecular condensates mediate bending and scission of endosome membranes**. *Nature* 2024, **634**:1204–1210.
This study provides a compelling set of in vivo, *in vitro* and theoretical data suggesting that wetting FREE1 condensates fission endosome membranes during biogenesis of MVBs. It demonstrates that tension of the three-phase contact line and surface tension together are sufficient to mediate ILV formation, including fission.

16. ** Dragwidge JM, Wang Y, Brocard L, De Meyer A, Hudecek R, Eeckhout D, Grones P, Buridan M, Chambaud C, Pejchar P, *et al.*: **Biomolecular condensation orchestrates clathrin-mediated endocytosis in plants**. *Nat Cell Biol* 2024, **26**:438–449.
Evidence is provided showing that the evolutionarily ancient TSET–TPLATE complex is a cytosolic condensate that wets plasma membranes and facilitates clathrin assembly and endocytosis.

17. Bergeron-Sandoval LP, Kumar S, Heris HK, Chang CLA, Cornell CE, Keller SL, Francois P, Hendricks AG, Ehrlicher AJ, Pappu RV, *et al.*: **Endocytic proteins with prion-like domains form viscoelastic condensates that enable membrane remodeling**. *Proc Natl Acad Sci U S A* 2021, **118**, e2113789118.

18. Ohshima T, Yamamoto H, Sakamaki Y, Saito C, Mizushima N: **NCOA4 drives ferritin phase separation to facilitate macroferritinophagy and microferritinophagy**. *J Cell Biol* 2022, **221**, e202203102.

19. Banjade S, Zhu L, Jorgensen JR, Suzuki SW, Emr SD: **Recruitment and organization of ESCRT-0 and ubiquitinated cargo via condensation**. *Sci Adv* 2022, **8**, eabm5149.

20. Parchure A, Tian M, Stalder D, Boyer CK, Bearrows SC, Rohli KE, Zhang J, Rivera-Molina F, Ramazanov BR, Mahata SK, *et al.*: **Liquid-liquid phase separation facilitates the biogenesis of secretory storage granules**. *J Cell Biol* 2022, **221**, e202206132.

21. Kusumaatmaja H, May AI, Feeney M, McKenna JF, Mizushima N, Frigerio L, Knorr RL: **Wetting of phase-separated droplets on plant vacuole membranes leads to a competition between tonoplast budding and nanotube formation**. *Proc Natl Acad Sci U S A* 2021, **118**, e2024109118.

22. Hanson PI, Cashikar A: **Multivesicular body morphogenesis**. *Annu Rev Cell Dev Biol* 2012, **28**:337–362.

23. Vietri M, Radulovic M, Stenmark H: **The many functions of ESCRTs**. *Nat Rev Mol Cell Biol* 2020, **21**:25–42.

24. Remec Pavlin M, Hurley JH: **The ESCRTs - converging on mechanism**. *J Cell Sci* 2020, **133**, jcs240333.

25. Alonso YAM, Migliano SM, Teis D: **ESCRT-III and Vps4: a dynamic multipurpose tool for membrane budding and scission**. *FEBS J* 2016, **283**:3288–3302.

26. Gao C, Zhuang X, Shen J, Jiang L: **Plant ESCRT complexes: moving beyond endosomal sorting**. *Trends Plant Sci* 2017, **22**: 986–998.

27. Gao C, Luo M, Zhao Q, Yang R, Cui Y, Zeng Y, Xia J, Jiang L: **A unique plant ESCRT component, FREE1, regulates multivesicular body protein sorting and plant growth**. *Curr Biol* 2014, **24**:2556–2563.

28. Steinkuhler J, Knorr RL, Zhao Z, Bhatia T, Bartelt SM, Wegner S, Dimova R, Lipowsky R: **Controlled division of cell-sized vesicles by low densities of membrane-bound proteins**. *Nat Commun* 2020, **11**:905.

29. Amirfazli A, Neumann AW: **Status of the three-phase line tension: a review**. *Adv Colloid Interface Sci* 2004, **110**:121–141.

30. Schimmele L, Napiorkowski M, Dietrich S: **Conceptual aspects of line tensions**. *J Chem Phys* 2007, **127**, 164715.

31. Snead WT, Hayden CC, Gadok AK, Zhao C, Lafer EM, Rangamani P, Stachowiak JC: **Membrane fission by protein crowding**. *Proc Natl Acad Sci U S A* 2017, **114**:E3258–E3267.

32. Lee MC, Orci L, Hamamoto S, Futai E, Ravazzola M, Schekman R: **Sar1p N-terminal helix initiates membrane curvature and completes the fission of a COPII vesicle**. *Cell* 2005, **122**:605–617.

33. Wang HY, Chan SH, Dey S, Castello-Serrano I, Rosen MK, Ditlev JA, Levental KR, Levental I: **Coupling of protein condensates to ordered lipid domains determines functional membrane organization**. *Sci Adv* 2023, **9**, eadf6205.

34. * Lee Y, Park S, Yuan F, Hayden CC, Wang L, Lafer EM, Choi SQ, Stachowiak JC: **Transmembrane coupling of liquid-like protein condensates**. *Nat Commun* 2023, **14**:8015.
This study employs reconstituted model membranes and model condensates to show that condensates can form two-dimensional condensates on membranes and that condensate locations at both membrane sides are coupled

35. Legrand A, D GC, Jolivet MD, Decossas M, Lambert O, Bayle V, Jaillais Y, Loquet A, Germain V, Boudsocq M, *et al.*: **Structural determinants of REMORIN nanodomain formation in anionic membranes**. *Biophys J* 2023, **122**:2192–2202.

36. ** Graham K, Chandrasekaran A, Wang L, Ladak A, Lafer EM, Rangamani P, Stachowiak JC: **Liquid-like VASP condensates drive actin polymerization and dynamic bundling**. *Nat Phys* 2023, **19**:574–585.
This study presents evidence that actin polymerises within liquid VASP condensates and that liquid-like condensate properties are critical for actin bundling as the droplet's surface tension balances the rigidity of actin filaments.

37. ** Liu M-CJ, Yeh F-LJ, Yvon R, Simpson K, Jordan S, Chambers J, Wu H-M, Cheung AY: **Extracellular pectin-RALF phase separation mediates FERONIA global signaling function**. *Cell* 2024, **187**:312–330.
This study demonstrates that extracellular condensates can also drive endocytosis. RALF condensation, a ligand of the FERONIA receptor kinase, triggers cell surface responses and endocytosis while remaining extracellular.

38. Zheng Q, Chen Y, Chen D, Zhao H, Feng Y, Meng Q, Zhao Y, Zhang H: **Calcium transients on the ER surface trigger liquid-liquid phase separation of FIP200 to specify autophagosome initiation sites**. *Cell* 2022, **185**:4082–4098.

39. Fujioka Y, Alam JM, Noshiro D, Mouri K, Ando T, Okada Y, May AI, Knorr RL, Suzuki K, Ohsumi Y, *et al.*: **Phase separation organizes the site of autophagosome formation**. *Nature* 2020, **578**: 301–305.

40. Agudo-Canalejo J, Schultz SW, Chino H, Migliano SM, Saito C, Koyama-Honda I, Stenmark H, Brech A, May AI, Mizushima N, *et al.*: **Wetting regulates autophagy of phase-separated compartments and the cytosol**. *Nature* 2021, **591**: 142–146.

41. Yan H, Qi A, Lu Z, You Z, Wang Z, Tang H, Li X, Xu Q, Weng X, Du X, *et al.*: **Dual roles of AtNBR1 in regulating selective autophagy via liquid-liquid phase separation and recognition of non-ubiquitinated substrates in Arabidopsis**. *Autophagy* 2024:1–12.

42. Schultz SW, Agudo-Canalejo J, Chino H, Migliano SM, Saito C, Koyama-Honda I, Stenmark H, Brech A, Mizushima N, Knorr RL, *et al.*: **Should I bend or should I grow: the mechanisms of droplet-mediated autophagosome formation**. *Autophagy* 2021, **17**:1046–1048.

43. ** Zeng Y, Li B, Huang S, Li H, Cao W, Chen Y, Liu G, Li Z, Yang C, Feng L, *et al.*: **The plant unique ESCRT component FREE1 regulates autophagosome closure**. *Nat Commun* 2023, **14**:1768.
This study shows that upon phosphorylation, FREE1 contributes to fission of autophagosomes by linking ATG conjugation to ESCRT-III complexes.