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Fission at the Closure Scale: Guest Area, the Curvature Floor, and Line-Tension Drive

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Abstract. The preceding article found that a lineage keeping one strand per vessel comes to consist of closure vesicles, the smallest enclosures of the anchored strand, of radius about 13 nm at 200 units. This article asks what the membrane of such a vessel is and whether it can divide.

The chrysene guests of the membrane take 12.4% of its area at 200 units, so the vessel is born a little larger than the closure vesicle, 13.82 nm, and the existence condition of the preceding article relaxes to $g \leq 1.192$. A packing floor of 10–12 nm, rather than the conventional 25, admits genomes from 118–169 units. The contact energy that an earlier article left open is supplied from the stacking energies of the corpus, giving a line tension of 1.03–2.27 k_BT per nanometre.

The central question is whether the line tension of the anchored domain divides such a vessel, and the answer turns on which division criterion is taken. Under the barrier-free threshold the line tension is short in every case considered, by factors of 1.3 to 5.6; under an energy balance it suffices in two cases of six, and with the Gaussian curvature modulus, which fission incurs once, in four, every case with the stronger stacking among them. The drive is comfortable at the 100-nm vessel for which it was proposed and marginal at 14 nm: keeping one strand per vessel brought the vessel to the scale at which the question arises. A shape-minimised calculation at this scale would settle it.

Two aids are examined. Spontaneous curvature would remove a barrier of 12 to 340 k_BT at an outer-leaflet area excess of 0.066 to 0.335; the anchors of the corpus push the other way and its photochrome connectors supply under 0.01, so a curvature-active component is specified rather than found. Lipid taken from the environment enlarges the vessel in three forms, a fixed flux, a diffusion-limited capture, or incorporation proportional to area at less than one doubling per period, the last with set point $\Lambda^* = \lambda/(1-r)$. The guests demix into domains, which a closure vessel can shed only under the laxer criteria. Corrections to earlier articles are recorded as precedence rulings.

Keywords: closure vesicle; guest area; curvature floor; line tension; domain budding; Gaussian curvature modulus; spontaneous curvature; environmental lipid; photochrome; Chrysene Formalism

1 Introduction

1.1 What the preceding articles left

Article 72 showed that replication once per period and division only at dusk keep one strand per vessel if and only if every vessel divides at every dusk, and that the population then comes to consist of closure vesicles dividing symmetrically. It counted only lipid area, took the curvature floor at Article 64's conventional 25 nm, and took the drive for division from Article 64 without asking whether that drive works at the closure scale. Article 64 drives division by the line tension at the boundary of the anchored domain, $\gamma = 0.59\,\varepsilon$ nm, and leaves the contact energy ε unsupplied.

1.2 What this article finds

Guest area is a correction (Section 4); the curvature floor does not bind (Section 5); the contact energy can be supplied from Article 68 (Section 6). Whether the drive divides the closure vesicle turns on the division criterion (Section 7). Of the two aids, spontaneous curvature is specified but not found in the corpus (Section 8), and environmental lipid works in three forms (Section 9). The guests form domains, which the vessel can shed only under the laxer criteria (Section 10).

1.3 What is established here, by kind

Proved here. The corrected closure identity (Corollary 4.2); the drive condition under the budding criterion (Theorem 7.1); the curvature needed (Proposition 8.1); the set point under environmental lipid (Theorem 9.1).

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Computed here. Guest inventories and shares; the floor; the contact energy and line tension; the shortfall; the curvature the corpus supplies; the uptake required; the demixing parameter and the shedding size. Appendix B.
Supposed. The nine hypotheses of Section 2.1, four of which are external constants or criteria stated as ranges.
Not claimed. Everything in Section 3.

1.4 Organization

Section 2 fixes status and hypotheses; Section 3 states the non-implications. Sections 4 to 10 carry the results in the order above. Section 11 carries the registers, rulings, targets and conclusion; the appendices carry the hypothesis register, the verification, the sources and the correction ledger.

2 Status and hypotheses

Convention 2.1 (Status labels)**.** [A] As in the coordinating paper: [A] finite or axiom-free; [D] derived under named hypotheses; [C] imported, with the source named; [E] molecular reading, entering no proof. A statement marked *computed* is emitted by a block of Appendix B. Constants from outside the corpus are marked as such where used.

Notation 2.2 (Symbols)**.** [A] As in Article 72: $\lambda = \nu L/2$ lipids per period, R_{62} the closure radius, w_{62} its osmolyte per lipid, g the gain of Article 72, Theorem 7.1. Here $f = 0.41$ nm^2 is the footprint of a chrysene unit (Article 62, Corollary 7.7), ϕ the guest share of the bilayer area, κ the bending modulus, γ the line tension of a domain boundary, C_0 the spontaneous total curvature, $d = 4.0$ nm the bilayer thickness, R a vessel's radius at birth.

2.1 The hypothesis register

Hypothesis 2.3 (The orbit)**.** [D] Vessels run the symmetric doubling orbit of Article 72, Theorem 7.1, under its Hypotheses H1–H9. Registered as H1.

Hypothesis 2.4 (Guest area)**.** [D] Each chrysene guest in the bilayer occupies a footprint f in one leaflet. Lipid flip-flop is slow against the period, so leaflet areas are counted separately; the bilayer area is that of the larger leaflet, and where guests are shared between the leaflets a guest adds $f/2$ as a lipid adds $a/2$. The share ϕ of Section 4 is computed on that convention, and the leaflet difference the inner-leaflet anchors create is kept, not relaxed (Proposition 8.2). Registered as H2.

Hypothesis 2.5 (Bending modulus)**.** [D] The bending modulus of the route-A bilayer lies in 10–20 k_BT, the upper value being that of an unsaturated C18 phosphatidylcholine bilayer [ROM+00]. External. Registered as H3.

Hypothesis 2.6 (Domain budding)**.** [D] The bending energy of a sphere of radius R is $8\pi\kappa(1 - C_0R/2)^2$ with spontaneous total curvature C_0 [Hel73], and a flat domain of disc-equivalent radius l and boundary line tension γ carries line energy $2\pi l\gamma$. Three criteria for when the domain buds are carried, in decreasing severity: (A) *barrier-free*, $\gamma l \geq 8\kappa$, the size at which the flat domain ceases to be a minimum [Lip92]; (B) *energy balance*, $2\pi l\gamma \geq 8\pi\kappa$, the budded state lower in energy with a barrier remaining; (C) balance with the Gaussian term of Hypothesis 2.7. External. Registered as H4.

Hypothesis 2.7 (Gaussian modulus)**.** [D] Fission creates one additional closed surface and so incurs the Gaussian bending energy once, $4\pi\kappa_G$, with κ_G/κ in -1.0 to -0.8, near -0.9 in simulation estimates [HBD12]. External. Registered as H5; the packing floor becomes H6, the contact energy H7, environmental lipid H8 and the bilayer couple H9.

Hypothesis 2.8 (Packing floor)**.** [D] No bilayer vesicle of this lipid is stable below an outer radius R_c in 10–12 nm, the smallest phospholipid vesicles having an outer radius near 10.5 nm [HM78]. External. Registered as H6.

Hypothesis 2.9 (Contact energy)**.** [D] The contact free energy per unit stacking face is the stacking energy per contact of Article 68, 3.8–8.4 kJ mol^{-1}, over the chrysene face of 12.5×7.0 Å. Registered as H7.

Hypothesis 2.10 (Environmental lipid)**.** [D] Lipid may be taken from the environment in addition to the genome-tied supply λ, in one of three forms: a fixed flux F per vessel per period; a capture limited by diffusion to the vessel, kR; or incorporation proportional to the vessel's lipid count, $r\Lambda$. Registered as H8.

Hypothesis 2.11 (Bilayer couple)**.** [D] A preferred fractional area difference δ between outer and inner leaflet corresponds to a spontaneous total curvature $C_0 = \delta/d$, $d = 4.0$ nm. Registered as H9.

3 Non-implications

Proposition 3.1 (Non-implications)**.** [A] *None of the following is asserted below.*

(i) That the route-A bilayer's elastic constants are known. *κ and the packing floor are taken as ranges from bilayers of other lipids.*

(ii) That any of the three budding criteria is exact for this geometry. *They are continuum estimates applied at radii of a few times the bilayer thickness, where continuum elasticity is at its edge, and the paper does not choose between them.*

(iii) That the barrier is surmounted or not. *The height below criterion (A) is computed; no rate is estimated and no attempt frequency is supplied.*

(iv) That a curvature-active component exists. *Its required properties are specified; none is exhibited.*

(v) That environmental lipid is available, or in which form. *H7 is an allowance, examined for its consequences.*

(vi) That the guests' domains are their equilibrium state. *The demixing estimate is a regular-solution argument.*

4 Guest area

Proposition 4.1 (The guests at dusk)**.** [D] *Under H1 and H2, with the free remnant at $g w_{62}$ per lipid ($g = 1$), the anchors of two strands, the catalyst at Article 71's baseline density* 0.08 *per lipid as an illustration, and two pores of nine units, the guest share of the bilayer area at dusk is (block Z1):*

L	remnant	anchors	catalyst	pores	ϕ	R_{62}	R
200	1117	400	1052	18	0.124	13.04	13.82
500	4416	1000	2629	18	0.155	20.62	22.15
735	7870	1470	3865	18	0.173	24.99	27.07
1000	12490	2000	5259	18	0.190	29.15	31.80

Radii in nanometres; R is the radius at birth. Every guest is given the footprint $f = 0.41$ nm^2 of Article 62's tethered unit; the free remnant is a spent arm and may be smaller, and it is the largest class at the longer genomes, so ϕ is an upper estimate there.

Corollary 4.2 (The closure identity becomes an inequality)**.** [D] *Under H1 and H2, symmetric division halves lipids and guests alike, so a vessel is born with one period's lipid area enlarged by the factor $1 + \phi$, and radius $R_{62}\sqrt{1+\phi}$. The existence condition $g \le 1$ of Article 72, Theorem 7.1, measured in units of the taut osmolyte of a λ-lipid vesicle, becomes $g \le (1+\phi)^{3/2}$: 1.192 at $L = 200$ and 1.270 at $L = 735$ (block Z1).*

> *Proof.* The dusk vessel carries 2λ lipids and G guests; with H2 its area is $(2\lambda a + G f)/2$, and each daughter has half. Its taut osmolyte scales as the area to the power $3/2$. □

Proposition 4.3 (Counting at the head-group surfaces)**.** [D] *Counting lipids at the head-group surfaces, $R \pm d/2$, gives $8\pi(R^2 + d^2/4)/a$ against Article 62's $8\pi R^2/a$: a correction of* 1.0235 *at* 13.04 *nm and* 1.0064 *at* 25 *nm. The inner leaflet holds* 0.350 *of the lipids at* 13.04 *nm (block Z6).*

5 The curvature floor

Proposition 5.1 (A packing floor)**.** [D] *Under H5 the strand-fit condition $R_{62}(L) \ge R_c$ bounds the genome below by $L \ge 2E^* R_c^2/(L_p h)$: 118 at $R_c = 10$ nm, 130 at* 10.5 *and* 169 *at* 12*, against* 735 *at Article 64's conventional* 25 *nm (block Z2). The closure vesicle at $L = 200$, of radius* 13.04 *nm, lies above the floor.*

Remark 5.2 (What replaces the convention)**.** [A] Article 72 placed the lower edge of the genome band at 735, resting entirely on the convention. On a packing floor the edge falls to 118–169, and Section 7 shows that the edge which actually binds is set by the drive for division.

6 The contact energy and the line tension

Proposition 6.1 (Supplying ε)**.** [D] *Under H6 the contact energy and Article 64's line tension $\gamma = 0.59\,\varepsilon$ nm are (block Z3):*

E	E/k_BT	ε	γ	γ (pN)
3.8	1.52	1.74	1.03	4.3
8.4	3.37	3.85	2.27	9.4

E in kJ mol^{-1}, ε in k_BT/nm^2, γ in k_BT/nm. This discharges Article 64, Target 16.5, as an estimate.

7 The drive for division

Theorem 7.1 (The drive condition)**.** 🄳 *Under H1, H4 and H5, and with each daughter's territory taken as half the dusk vessel's area and treated as a flat disc, line tension divides a vessel of birth radius R when*

$$\gamma R \geq 4\kappa \ (A), \quad \gamma R \geq 2\kappa \ (B), \quad \gamma R \geq 2\kappa + \kappa_G \ (C),$$

according to which criterion of H4 is taken; (C) is $1.1\kappa/R$ at $\kappa_G = -0.9\kappa$. Criteria (B) and (C) say the divided state is favoured, not that it is reached: below (A) a barrier stands, of height at most $8\pi\kappa(1-\gamma R/4\kappa)^2$.

Proof. At dusk the vessel has twice its birth area, $8\pi R^2$; half of it, $4\pi R^2$, is a disc of radius $l = 2R$. Substituting in the three criteria of H4 gives the three conditions, the third carrying the single Gaussian term of H5. □

Proposition 7.2 (The drive at the closure scale)**.** 🄳 *At $L = 200$, birth radius 13.82 nm with guests, the line tension against the three criteria, and the barrier below (A) (block Z4):*

κ	E	γ	(A)	(B)	(C)	barrier
10	3.8	1.03	2.89*	1.45*	0.80	105
10	8.4	2.27	2.89*	1.45	0.80	12
15	3.8	1.03	4.34*	2.17*	1.19*	220
15	8.4	2.27	4.34*	2.17	1.19	86
20	3.8	1.03	5.79*	2.89*	1.59*	340
20	8.4	2.27	5.79*	2.89*	1.59	186

κ in k_BT, E in kJ mol^{-1}, γ and the three requirements in k_BT/nm, the barrier in k_BT; an asterisk marks a line tension short of that criterion. Under (A) the line tension is short in every case, by factors of 1.3 to 5.6. Under (B) it suffices in two cases and under (C) in four, every case with the stronger stacking among them. The genome length at which the closure vessel first meets each criterion ranges from 1587 down to 25 (block Z4).

Scholium 7.3 (What copy number cost)**.** At Article 64's 100-nm vessel the requirement under the severest criterion is $4\kappa/100$ nm, 0.40–0.80 k_BT per nanometre, which the line tension met under all three. Article 72 showed that keeping one strand per vessel brings the vessel to the closure scale, and the drive's requirement grows as $1/R$. The same step that secured copy number therefore took the vessel to the scale at which the question arises at all: the drive is comfortable at 100 nm and marginal at 14. Whether it suffices there is not settled by the criteria carried here, and Target 11.9 names the calculation that would settle it.

8 Spontaneous curvature

Proposition 8.1 (The curvature needed)**.** 🄳 *Under H4, H9 and criterion (A), the drive condition with spontaneous curvature is $2\gamma R \geq 8\kappa(1-C_0R/2)^2$, so the curvature needed is $C_0 = (2/R)\left(1-\sqrt{\gamma R/(4\kappa)}\right)$, and the outer-leaflet area excess $\delta = C_0 d$. At $L = 200$ (block Z5):*

κ	E	C_0 (nm^{-1})	δ
10	3.8	0.0585	0.234
10	8.4	0.0165	0.066
15	3.8	0.0743	0.297
15	8.4	0.0400	0.160
20	3.8	0.0837	0.335
20	8.4	0.0541	0.216

Under (B) and (C) the requirement is smaller and in four of the six cases nil (Proposition 7.2).

Proof. Replace the bending energy $8\pi\kappa$ of a bud in H4 by $8\pi\kappa(1-C_0R/2)^2$, set $l = 2R$, and solve for C_0. □

Proposition 8.2 (What the corpus supplies)**.** 🄳 *The anchors sit in the inner leaflet only (Article 62, Section 8), and under H2 that asymmetry persists over a period; at dusk at $L = 200$ they enlarge the inner leaflet by $\delta = -0.038$, the wrong sign for outward division. The azo connectors of Article 64 modulate the area by under one per cent (its Proposition 9.6), so $|\delta| < 0.01$ even if all sit in one leaflet and switch together. They fall short of the needed excess by a factor of 6.6 to 33.5 (block Z5).*

Corollary 8.3 (A curvature-active component, specified)**.** 🄳 *Under H1–H9, a vessel at the closure scale divides without a barrier only with an outer-leaflet area excess of 0.066 to 0.335 beyond what its anchors oppose; where the line tension meets criterion (B) or (C) but not (A), the excess is what removes a barrier of 12 to 340 k_BT rather than what makes division possible (Proposition 7.2). No component of the corpus supplies it. A component that does must sit in the outer leaflet, or switch to a larger area there at dusk, and must not open the leak that Article 64, Theorem 9.7, found for azo-bearing lipids at the mole fractions needed to change the area.*

Scholium 8.4 (The photochrome)**.** The programme's aim is to shape the vessel by the photochrome. This section says what that shaping must achieve at the closure scale: a leaflet asymmetry of tens of per cent, switched or held, without leakage. Article 64's connectors gate the moment

of division and were never asked to shape the vessel; they cannot. The component specified in Corollary 8.3 is the first membrane device the programme needs, ahead of any pore or rotor. Its office is to make division prompt and barrier-free at a scale where the line tension alone leaves it marginal, and to do so on the dusk schedule the clock sets.

9 Lipid from the environment

Theorem 9.1 (The set point under environmental lipid)**.** [D] *Under H1 and H7 let a vessel gain $G(\Lambda)$ lipids per period. On the symmetric doubling orbit the birth size obeys $\Lambda' = (\Lambda + G(\Lambda))/2$, whose fixed points satisfy $\Lambda^* = G(\Lambda^*)$ and are stable if and only if $G'(\Lambda^*) < 1$. In particular:*

(i) a fixed flux, $G = \lambda + F$, has the stable set point $\lambda + F$;

(ii) a diffusion-limited capture, $G = \lambda + kR$, is sublinear in Λ and has a stable set point;

(iii) incorporation proportional to area, $G = \lambda + r\Lambda$, has the set point $\Lambda^* = \lambda/(1-r)$, stable if and only if $r < 1$, with contraction factor $(1 + r)/2$ per period.

Pure surface-catalysed growth, $G = r\Lambda$ without the genome-tied term, has no set point for $r \neq 1$. The theorem is about the symmetric doubling orbit, which exists only where the vessel divides at dusk; it presupposes a drive, and says which supplies keep a set point once there is one.

Proof. Each vessel gains G and divides symmetrically, so $\Lambda' = (\Lambda + G)/2$. The derivative of the map is $(1 + G')/2$, below one if and only if $G' < 1$. For (i) $G' = 0$; for (ii) $G' = k\, dR/d\Lambda$, which vanishes as Λ grows; for (iii) $G' = r$. Without λ the map is $\Lambda' = \Lambda(1 + r)/2$, which has no fixed point other than zero unless $r = 1$. □

Proposition 9.2 (Computed)**.** [D] *Iterating the birth-size map sixty times at $L = 200$ from 2λ and 10λ (block Z8): a fixed flux of 6λ settles at 34.50 nm from both; a diffusion-limited capture at $k = 2000$ per nm at 54.83 nm from both; incorporation at $r = 0.8$ at 29.14 and 29.18 nm, still converging; at $r = 1.2$ the vessel grows to 601.23 and 880.67 nm and does not settle.*

Proposition 9.3 (The uptake the drive needs)**.** [D] *Under H1, H3, H4, H7 and H8, a birth radius $R_d = 4\kappa/\gamma$, the radius at which criterion (A) is met, needs a per-period gain of $8\pi R_d^2/a$ lipids (block Z8). Under (B) the radius is half and the gain a quarter; under (C) less again, and where the line tension already meets (C) no uptake is needed on that count.*

κ	E	R_d	gain/λ	r	contraction
10	3.8	38.9	8.9	0.888	0.944
10	8.4	17.6	1.8	0.452	0.726
20	3.8	77.9	35.7	0.972	0.986
20	8.4	35.2	7.3	0.863	0.932

The last two columns are for incorporation proportional to area.

Remark 9.4 (The cost, and a consequence for flaccidity)**.** [A] Where the drive is weak, incorporation proportional to area must come close to one doubling per period, and a perturbed vessel returns slowly, by a factor 0.986 per period at the weakest. And if the tethering of environmental lipid triggers codon expression, as Article 71's gate implies, the osmolyte gain grows with uptake but more slowly than the vessel's taut capacity, so g falls and the vessel is born more flaccid. Article 72 sets no lower bound on the reduced volume (its Target 11.7); with environmental lipid that target becomes binding.

10 The guests: domains and shedding

Proposition 10.1 (The guests demix)**.** [D] *In a regular-solution estimate with z lateral face-to-face contacts per guest, the demixing parameter is $\chi = zE/k_BT$, with demixing for $\chi > 2$. With $z = 1$ the guests stay dispersed at the weaker stacking ($\chi = 1.52$) and demix at the stronger (3.37); with $z = 2$ they demix at both (3.05, 6.74) (block Z7). This is the unfavourable prior that Article 62, Remark 7.16, recorded against its dispersal hypothesis.*

Proposition 10.2 (Shedding turns on the criterion)**.** [D] *Under H2–H5 a guest domain of n units sheds when its disc-equivalent radius exceeds the criterion radius: $8\kappa/\gamma$ under (A), $4\kappa/\gamma$ under (B), $(4\kappa + 2\kappa_G)/\gamma$ under (C). Against 2,587 guests in a vessel at $L = 200$, the smallest shed domain is 9,511 to 185,892 units under (A), 2,378 to 46,473 under (B) and 719 to 14,058 under (C) (block Z7). No vessel can shed under (A); one of the four cases can under (B) and two under (C), both at the stronger stacking. Whether the co-aggregate can leave turns on the same criterion as division itself.*

11 Registers, precedence, targets, conclusion

11.1 Consolidated register

How much of the membrane do the guests take?
12.4% of the area at 200 units, 19.0% at 1000; the vessel is born at 13.82 nm instead of 13.04.
Rests on: Prop. 4.1, Cor. 4.2; block Z1.
Standing: [D] on H2; the catalyst density is illustrative.

Does curvature bound the genome?
Not at the corpus length: a packing floor of 10–12 nm admits L from 118–169.
Rests on: Prop. 5.1; block Z2.
Standing: [D] on H5, external.

What is the line tension?
1.03–2.27 k_BT per nm, from the corpus stacking energies.
Rests on: Prop. 6.1; block Z3.
Standing: [D] on H6.

Can the line tension divide the closure vesicle?
It depends on the criterion: short in every case under the barrier-free threshold, sufficient in two cases of six under an energy balance and in four with the Gaussian term.
Rests on: Thm. 7.1, Prop. 7.2; block Z4.
Standing: [D] on H3–H5, H7; open.

Could spontaneous curvature help?
It would remove a barrier of 12–340 k_BT at an outer-leaflet excess of 0.066–0.335; the corpus supplies under 0.01 and its anchors oppose.
Rests on: Props. 8.1, 8.2, Cor. 8.3; block Z5.
Standing: [D]; the component is specified, not found.

Could environmental lipid close the gap?
Yes, as a fixed flux, a diffusion-limited capture, or incorporation proportional to area at $r < 1$, with set point $\lambda/(1-r)$.
Rests on: Thm. 9.1, Props. 9.2, 9.3; block Z8.
Standing: [D] on H7, an allowance.

Where do the guests go?
Into domains in three cases of four; a closure vessel sheds them only under the laxer criteria.
Rests on: Props. 10.1, 10.2; block Z7.
Standing: [D]; a regular-solution estimate.

11.2 Falsification register

Theorem 7.1
A shape-minimised calculation at this scale giving a threshold outside the range spanned by criteria (A) to (C), or a daughter territory not well modelled by a disc of radius $2R$.

Proposition 7.2
A bending modulus below $10\,k_BT$ or a contact energy above 8.4 kJ mol^{-1}, either of which would narrow or close the shortfall.

Corollary 8.3
A component of the corpus that supplies an outer-leaflet excess above 0.066 without leakage.

Theorem 9.1
A lineage with incorporation proportional to area at $r \geq 1$ that nonetheless settles, or one at $r < 1$ that does not.

Proposition 10.2
A closure vessel shedding a domain under criterion (A), or failing to shed one under (C) at the stronger stacking.

11.3 Precedence

Ruling 11.1 (Against Article 64). **64.1** [D] *The drive* of Proposition 9.5 carries a scale condition it does not state: γR against 4κ, 2κ or $2\kappa + \kappa_G$ by criterion (Theorem 7.1). It holds under all three at the 100-nm vessel for which it was proposed, and at the closure scale holds under none, two of six or four of six (Proposition 7.2).

64.2 [D] *Target 16.5 is discharged as an estimate.* The contact energy is 1.74–3.85 k_BT per nm^2 and the line tension 1.03–2.27 k_BT per nm (Proposition 6.1).

64.3 [A] *Theorem 10.15 is qualified.* Surface-catalysed growth has no stable area when it is the only supply; with a genome-tied flux beside it, growth proportional to area has a stable set point for $r < 1$ (Theorem 9.1).

64.4 [D] *The floor of Remark C.5* is replaced by a packing floor of 10–12 nm (Proposition 5.1).

Ruling 11.2 (Against Article 72). **72.1** [D] *Proposition 4.1 becomes an inequality.* One period's area exceeds the minimal enclosure by the guest share, and the existence condition of Theorem 7.1 relaxes to $g \leq (1+\phi)^{3/2}$ (Corollary 4.2).

72.2 [D] *The lower edge of the band* in Proposition 10.1 rests on a packing floor of 118–169 units rather than the convention's 735; the edge that binds is set by the drive (Proposition 7.2).

72.3 [D] *Theorem 7.1 needs the drive.* The symmetric doubling orbit is an orbit of the cycle only where the vessel can divide at dusk, which at the closure scale is not settled (Proposition 7.2). Where it fails, a curvature-active component or environmental lipid would supply it (Sections 8 and 9).

Ruling 11.3 (Against Article 62)**.** [D] Hypothesis 7.15, that tethered units disperse, is not supported at the closure scale in three of the four cases of Proposition 10.1; it survives only at one contact per guest with the weaker stacking. The estimate agrees with the unfavourable prior of its Remark 7.16.

Ruling 11.4 (Against Article 68)**.** [A] Consistent; one use added. Its stacking energies supply the contact energy of Article 64's line tension (Proposition 6.1).

11.4 Targets

Target 11.5 (The curvature-active component)**.** Design, from chrysene derivatives, an outer-leaflet component supplying the area excess of Corollary 8.3, switched at dusk or held, without the leak of Article 64, Theorem 9.7.

Target 11.6 (The elastic constants)**.** Determine κ, κ_G and the packing floor for the route-A bilayer with its chrysene guests; the verdict on the drive and the floor rest on ranges from other lipids.

Target 11.7 (The form of environmental uptake)**.** Decide which form of H7 applies, and at what rate; Theorem 9.1 says which forms keep a set point.

Target 11.8 (The flaccid limit)**.** Determine the smallest reduced volume at which a vessel divides; with environmental lipid it binds (Remark 9.4).

Target 11.9 (Division at the nanoscale)**.** Replace the three continuum criteria at radii of a few bilayer thicknesses by a shape-minimised or coarse-grained calculation, with the Gaussian modulus carried explicitly, and so settle whether the closure vesicle divides by line tension. This is the decisive open question of this article.

11.5 Conclusion

Proposition 11.10 (What is established)**.** [A] *Subject to Appendix A:*

(i) The guests take 12–19% *of the area; the closure identity becomes an inequality and the existence condition relaxes (Corollary 4.2).*

(ii) A packing floor admits the corpus genome (Proposition 5.1).

(iii) The line tension is 1.03–2.27 k_BT *per nm, and whether it divides the closure vesicle turns on the criterion: not under (A), in two cases of six under (B), in four under (C) (Theorem 7.1, Proposition 7.2).*

(iv) Spontaneous curvature would remove the barrier at an outer-leaflet excess the corpus does not supply; the component is specified (Corollary 8.3).

(v) Environmental lipid enlarges the vessel in three forms, each with a stable set point (Theorem 9.1).

(vi) The guests demix, and shed only under the laxer criteria (Proposition 10.2).

Remark 11.11 (What is not established)**.** [A] The elastic constants are borrowed, the three budding criteria are continuum estimates at the edge of their scale, the curvature-active component is a specification, and the environmental lipid is an allowance. The article does not settle whether the closure vesicle divides by line tension; it establishes that the question is decided at that scale and names the calculation that would answer it (Target 11.9).

A Hypothesis register

B Verification

Every number in the body is emitted by `acf-73-blocks.py` (standard library only; a run takes under a second), or is quoted from the source named.

Z1 [COMPUTED] **Guest area**

Inventories and shares at four genome lengths; the corrected radius and existence condition.

Z2 [COMPUTED] **The curvature floor**

The genome length admitted at four floors.

Z3 [COMPUTED] **Contact energy and line tension**

From the stacking energies of Article 68.

Z4 [COMPUTED] **The drive**

The three criteria, the line tension against each, the barrier below the barrier-free threshold, and the smallest radius and genome length at which each is met.

Z5 [COMPUTED] **Spontaneous curvature**

The curvature and area excess needed; what the anchors and connectors supply.

Z6 [COMPUTED] **Leaflet counting**

The head-group correction and the inner share.

Z7 [COMPUTED] **Guests**

The demixing parameter; the smallest shed domain under each of the

Table 1: Hypotheses of this article.

	Premise	What rests on it	What survives its failure
H1	Article 72's orbit	Every section	Theorem 7.1 as a statement about any vessel
H2	Guest footprint and lipid redistribution	Section 4	Sections 5–9 at the uncorrected radius
H3	κ in 10–20 k_BT (external)	The verdict on the drive	The form of the drive condition
H4	Three budding criteria and the sphere's bending energy (external)	Thm. 7.1; Prop. 8.1	Sections 4, 5, 9
H5	κ_G/κ in -1.0–-0.8 (external)	Criterion (C)	Criteria (A) and (B)
H6	Packing floor 10–12 nm (external)	Prop. 5.1	Everything else
H7	Contact energy from Article 68	The line tension	The form of the drive condition
H8	Environmental lipid in three forms	Section 9	Everything else
H9	Bilayer couple, $d = 4.0$ nm	The area excess in Prop. 8.1	The curvature C_0 itself

three criteria.

Z8 [COMPUTED] **Environmental lipid**

The three forms iterated from two starts; the uptake the drive needs.

C Sources and literature

C.1 The corpus, by use

Article 62 [Sch26c]: the footprint and face of a chrysene unit (Corollary 7.7, Proposition 7.3), the anchors in the inner leaflet (Section 8), the dispersal hypothesis and its prior (Hypothesis 7.15, Remark 7.16), and the closure geometry. Article 64 [Sch26e]: the drive (Proposition 9.5), the connectors (Proposition 9.6), the leak (Theorem 9.7), the growth laws (Theorems 10.14–10.15), the floor (Remark C.5), the caps, and Target 16.5. Article 68 [Sch26d]: the stacking energies, through Article 71's block P1i [Sch26a]. Article 72 [Sch26b]: the orbit, the closure identity, the existence condition and the band.

C.2 Established literature

The bending energy and its spontaneous curvature are Helfrich's [Hel73]; the reduced volume and the bilayer couple are standard [Sei97]. The barrier-free budding criterion is Lipowsky's [Lip92]; the Gaussian curvature modulus of lipid bilayers is taken from simulation [HBD12]. The bending modulus of an unsaturated C18 bilayer is from micropipette measurements [ROM+00], and the smallest phospholipid vesicles from packing [HM78]. Protocell membranes grow by taking up amphiphile from their surroundings [CRS04, ZS09], which is the setting of H7. None of these is used beyond the constant or criterion named.

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D Revision record

The referee's items and their dispositions. Every item was accepted.

Item	Critique	Revision
R1	The negative result is the verdict of one criterion; the Gaussian modulus omitted	κ_G registered as H5; three criteria carried in H4 and Thm. 7.1; blocks Z4 and Z7 emit all three; abstract, Sch. 7.3, Cor. 8.3, Prop. 10.2, conclusion, rulings and Target 11.9 restated
R2	H2 contradicted Prop. 8.2	H2 now counts leaflets separately, flip-flop being slow; the anchors' asymmetry stands
R3	Thm. 7.1's "if and only if"	Criteria and disc geometry stated; the biconditional dropped
R4	The ruling on dispersal overstated	"three of the four cases"
R5	One footprint for every guest	Noted at Prop. 4.1; ϕ an upper estimate at longer genomes
R6	Thm. 9.1 presupposes the drive	Stated in the theorem and in Prop. 9.3

The referee's recomputation of the shedding sizes under criterion (C) differs from block Z7, which halves the criterion radius for a domain whose line energy is released once; the block's values are the ones carried.

E Correction ledger

Art.	Location	As printed	Corrected
64	Prop. 9.5, drive	divides	scale condition, 4κ, 2κ or $2\kappa + \kappa_G$ by criterion
64	Target 16.5, ε	open	1.74–3.85 $k_B T$/nm^2
64	Thm. 10.15	no stable area	stable for $r < 1$ with a fixed supply
64	Rem. C.5 floor	25 nm	10–12 nm
72	Prop. 4.1	identity	inequality, factor $1 + \phi$
72	Prop. 10.1 lower edge	735	118–169; the drive binds
62	Hyp. 7.15	dispersal	domains in three cases of four