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Division Without a Device: The Dusk Shape, the Tethered Domains, and the Window of the Gain

Charles D. Schaper, Ph.D.
Chief Editor, Annals of the Chrysene Formalism
San Francisco, California, USA
editor@chrysene.com

Abstract. The preceding article asked what force divides a vessel at the closure scale and found the line tension of the anchored domain short of the bending cost of fission. That cost was mispriced. It charged the vessel the difference between one sphere and two, but the vessel at dusk is not a sphere: the cycle brings it to reduced volume 0.7071, which is exactly the limit shape of two touching spheres, of the same bending energy as the pair. The deformation has been paid for by growing flaccid. What remains is the single new closed surface, $4\pi\kappa_G$, which is negative: -101 to $-251\ k_BT$ over the moduli considered. At the dusk shape fission lowers the energy, and no curvature device is needed to make it possible.
The same geometry does not, however, bound the cycle from below. A vessel can form at most v^{-2} equal spheres, but availability is not preference: each further sphere costs 4.00 to $4.80\,\pi\kappa$ more, so three are never preferred to two, and two flaccid daughters are available at every reduced volume. The lower bound on the gain that counting seems to offer does not follow, and what selects binary fission is structural: a vessel carrying two strands carries two tethered footprints, and if those demix they are the two centres about which the daughters form. What the geometry does give is $g \leq 1$, the condition that the vessel is not too taut, and the observation that $g = 1$ is the point the cycle is built around.
The reduced volume does not fall of its own accord: on the orbit area and volume double together and v is constant. Division is approached only by incorporation biased toward the membrane, which moves the set point to $g_{\mathrm{eff}} = g_0(1 + F/\lambda)^{-3/2}$. A genome of 200 units, which the preceding article placed outside the viable band, is returned to the window by an environmental flux of 0.53 to $0.75\,\lambda$ per period. The tethers that insert as a strand is nucleated cover one to five per cent of the bilayer each: they fix the fission axis, assign one strand to each daughter, and select two as the number, but supply no drive, which under the corrected pricing they need not. Of three candidate devices the photochrome fails as a curvature switch by a factor of four, the strand fails as a constricting ring against its own overstretch force, and the free remnant, if it partitions outward, supplies more area excess than was ever required. Stimulated uptake is bounded below, at about a third of a doubling per period at the baseline considered, and above only by the stability of the set point.

Keywords: limit shape; Gaussian curvature modulus; binary fission; reduced volume; tethered domain; fission axis; area bias; environmental lipid; division device; Chrysene Formalism

1 Introduction

1.1 What the preceding articles left

Article 72 found that a lineage keeping one strand per vessel comes to consist of closure vesicles dividing symmetrically at dusk, on an orbit whose single parameter is the gain g, bounded above by one and unbounded below (its Target 11.7). Article 73 asked what divides such a vessel, took the bending cost of fission as $8\pi\kappa$, and found the line tension of the anchored domain short of it at the closure scale under every criterion it carried. It specified a curvature-active component to make good the deficit, and left the decisive question to a calculation at the molecular scale (its Target 11.9).

1.2 What this article finds

The deficit was an artefact of the comparison (Section 4). The counting argument that appears to bound g from below does not survive, and binary fission is selected by the strands rather than by the shape (Section 5). The reduced volume falls only under incorporation biased to the membrane, and that bias restores genome lengths the preceding article excluded (Section 6). The tethers place the daughters rather than driving them apart (Section 7). Three devices are assessed (Section 8) and the chain from the environment to the strand is bounded below (Section 9).

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1.3 What is established here, by kind

Proved here. The marginal cost of fission at the dusk shape (Theorem 4.3); the monotonicity of the multi-sphere energies and what it denies (Proposition 5.2); the direction condition and the shifted set point (Proposition 6.1, Theorem 6.2).
Computed here. The limit shapes and the marginal cost over the moduli; the flux that returns a lineage to the dividing range; the tether and guest coverage; the three devices; the floor on uptake. Appendix B.
Supposed. The seven hypotheses of Section 2.1.
Not claimed. Everything in Section 3.

2 Status and hypotheses

Convention 2.1 (Status labels)**.** [A] As in the coordinating paper. A statement marked *computed* is emitted by a block of Appendix B. Constants from outside the corpus are marked where used.

Notation 2.2 (Symbols)**.** [A] As in Articles 72 and 73: $\lambda = vL/2$, R_{62}, w_{62}, the gain g, the guest share ϕ, the bending modulus κ, the Gaussian modulus κ_G, the line tension γ. Here v is the reduced volume, n a number of equal daughters, F an environmental lipid flux per period, r an uptake proportional to the lipid count, t the number of tethers per base, and g_{eff} the gain measured at the enlarged set point.

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, with the guest area of Article 73. Registered as H1.

Hypothesis 2.4 (Bending energy)**.** [D] A closed bilayer carries the Helfrich bending energy [Hel73]; a sphere carries $8\pi\kappa$ whatever its radius, and each closed surface carries $4\pi\kappa_G$ by Gauss–Bonnet. κ lies in 10–20 k_BT [ROM+00] and κ_G/κ in -1.0 to -0.8 [HBD12]. External. Registered as H2.

Hypothesis 2.5 (Shape attainment)**.** [D] A vessel at reduced volume v adopts the shape of least bending energy at its area and volume, and the configuration of n equal spheres is available to it when $v \le n^{-1/2}$. At $v = 2^{-1/2}$ the least-energy shape is the limit shape of two equal spheres: the prolate branch of the bending model terminates there, and the prolate–oblate transition lies near $v = 0.65$, so the prolate branch is the relevant one [Sei97]. External for that identification. Registered as H3.

Hypothesis 2.6 (Tethers at nucleation)**.** [D] The nucleotide–chrysene tethers insert into the bilayer as the strand is nucleated and copied, so each strand carries its own membrane footprint of t tethers per base, t in 1 to 5; the corpus states $5L$ anchor units per period in its ledger and one tether per base in the enclosure, and the discrepancy is carried as a range (Target 10.6). Registered as H4.

Hypothesis 2.7 (Tethered demixing)**.** [D] The guests of a strand, its tethers and what they recruit, demix from the bulk lipid as Article 73, Proposition 10.1, estimates, and two strands' footprints demix from one another rather than merging. Registered as H5.

Hypothesis 2.8 (Environmental lipid)**.** [D] Lipid may be taken from the environment as in Article 73, Hypothesis H8, as a flux F or an uptake $r\Lambda$ proportional to the lipid count, and it carries no lumen solute. Registered as H6.

Hypothesis 2.9 (The input chain)**.** [D] Material entering through the pore reaches the strand, whose activity sets the rate at which chrysene-tethered units are incorporated into the bilayer; the rate scales with the number of tethers and hence with the membrane. Registered as H7.

3 Non-implications

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

(i) That fission is reached, or at what rate. *The marginal cost at the dusk shape is computed; the neck through which the vessel must pass is singular in continuum theory and is not priced (Article 73, Target 11.9).*

(ii) That the comparison extends below $g = 1$. *At $g = 1$ the dusk shape is exactly the two-sphere limit shape and the comparison is exact. Below it both parent and daughters are flaccid, and their shape energies are not computed here.*

(iii) That the vessel attains its minimal shape. *H3 supposes it; relaxation times are not estimated.*

(iv) That the remnant partitions outward. *The device of*

Section 8 is conditional on a leaflet assignment the corpus has not made.

(v) That the tethers demix as supposed. *H5 rests on an estimate, not a calculation.*

4 The shape at dusk

Proposition 4.1 (Limit shapes)**.** 🄳 *Under H2, a closed bilayer of area A folded into n equal spheres has reduced volume $n^{-1/2}$ and bending energy $8n\pi\kappa$, and carries $n-1$ closed surfaces beyond the first, each $4\pi\kappa_G$ (block U1):*

n	$v = n^{-1/2}$	*bending*	*extra Gaussian*
1	*1.0000*	$8\pi\kappa$	0
2	*0.7071*	$16\pi\kappa$	$4\pi\kappa_G$
3	*0.5774*	$24\pi\kappa$	$8\pi\kappa_G$
4	*0.5000*	$32\pi\kappa$	$12\pi\kappa_G$

Proof. n spheres of total area A have radius $(A/4\pi n)^{1/2}$ and volume $n \cdot \frac{4}{3}\pi(A/4\pi n)^{3/2}$, whence $v = n^{-1/2}$. The bending integral of a sphere is 8π whatever its radius, and Gauss–Bonnet gives $4\pi\kappa_G$ per closed surface. □

Remark 4.2 (Where the cycle delivers the vessel)**.** 🄰 On the orbit of Article 72 the vessel is born at $v = g$ and reaches dusk at $v = g/\sqrt{2}$, since lipids and osmolyte both double. At $g = 1$ the dusk reduced volume is 0.7071: exactly the limit shape of two touching spheres. The cycle delivers the vessel to the fission shape, and does so by construction rather than by design.

Theorem 4.3 (The marginal cost of fission)**.** 🄳 *Under H1–H3 at $g = 1$, the parent at dusk and the two daughters have the same bending energy, $16\pi\kappa$, and the marginal cost of fission is the one new closed surface,*

$$\Delta E = 4\pi\kappa_G < 0,$$

computed over the moduli as -101 to $-251\ k_BT$ (block U1). At the dusk shape the parent's limit shape is two spheres joined at a point, so the theorem compares that configuration with two separated spheres and ΔE is the cost of the topological cut. It prices the end states, not the passage: whatever opposes fission is confined to the neck, which continuum theory makes singular exactly there and which is not priced here (Target 10.3). The statement holds at $g = 1$, where the dusk reduced volume is exactly $2^{-1/2}$; below it both parent and daughters are flaccid and the comparison is not made (Target 10.5).

Proof. At $g = 1$ the vessel is born taut, $v = 1$, and reaches dusk at $v = 2^{-1/2}$ with twice its birth area. By Proposition 4.1 with $n = 2$ that is the limit shape of two equal spheres, whose bending energy is $16\pi\kappa$; by H3 the parent adopts it. Each daughter receives half the area and half the volume, so each is a sphere, of bending energy $8\pi\kappa$. The bending energies agree and only the Gauss–Bonnet term differs, by $4\pi\kappa_G$ for the one additional closed surface. □

Ruling 4.4 (Against Article 73)**. 73.1** 🄳 *The bending cost of fission was mispriced.* Article 73's criteria (A), (B) and (C) each charge the vessel $8\pi\kappa$, 251 to 503 k_BT, for the passage from one sphere to two. The vessel at dusk is not a sphere and has already paid that deformation by growing flaccid (Remark 4.2). At $g = 1$ the correct marginal cost is $4\pi\kappa_G$, which is negative (Theorem 4.3).

73.2 🄳 *Proposition 7.2 and Scholium 7.3 do not apply to whole-vessel fission.* Article 73 prices the budding of a domain from a membrane, and this article prices the fission of a vessel at its limit shape; they are different processes, and at the closure scale, where domain and vessel are comparable in size, which one the cycle performs is not obvious. The cycle divides a vessel in two at dusk (Article 72, Definition 5.1), so whole-vessel fission is what is modelled here, and Article 73's criteria do not govern it. What survives of that article's finding is that the closure scale is where the question is decided, and that the neck remains unpriced (its Target 11.9).

73.3 🄳 *Corollary 8.3 is conditional, not required.* A curvature-active component is not needed to make division possible. Where it would act is on the neck and on the promptness of fission, neither of which is computed here.

73.4 🄰 *Proposition 10.2 stands as domain budding.* Shedding a guest domain is domain budding and not vessel fission, so Article 73's criteria are the right ones there; what is reopened is only the choice among its three, which this article does not settle.

Scholium 4.5 (What was wrong, and what it cost)**.** The error is instructive. A vessel's bending energy depends on its shape alone, not on its size, so the whole question is which shapes the area and the volume permit. Article 73 compared the end state against a sphere because a sphere is the shape one pictures; the cycle, however, hands division a vessel that has been made flaccid on purpose. The lesson

is that a drive must be priced against the state the cycle actually produces, and the reduced volume is what records that state.

5 How many daughters

Proposition 5.1 (Availability)**.** [D] *Under H1–H3, a vessel at reduced volume v can form at most $\lfloor v^{-2} \rfloor$ equal spheres, since n equal spheres require $v = n^{-1/2}$ (Proposition 4.1). On the orbit, where $v = g/\sqrt{2}$ at dusk, three become available below $g = \sqrt{2/3} = 0.8165$ (block U2).*

Proposition 5.2 (Availability is not preference)**.** [D] *Under H2, each further sphere costs*

$$E(n+1) - E(n) = 8\pi\kappa + 4\pi\kappa_G = 4.00 \text{ to } 4.80\,\pi\kappa,$$

positive over the whole range of κ_G, so $E(n)$ rises monotonically with n and three equal spheres are never preferred to two (block U2). Moreover two daughters are available at every dusk reduced volume: by Article 72, Definition 5.1, a vessel below $2^{-1/2}$ divides symmetrically into two flaccid *daughters at $v_d = v\sqrt{2}$, which exists for any v. No lower bound on g follows from counting the configurations a vessel could adopt.*

Remark 5.3 (Where an energetic bound would lie)**.** [A] Three spheres cost 16.0 to 17.6 $\pi\kappa$ over the range of κ_G, against $16\,e(v_d) + 4\kappa_G/\kappa \cdot \pi\kappa$ for two flaccid daughters, where e is the reduced bending energy of a vesicle at reduced volume v_d, unity for a sphere. The crossing lies at $e(v_d)$ between 1.250 and 1.300 (block U2). The corpus supplies no $e(v)$, so the crossing cannot be located here (Target 10.4).

Proposition 5.4 (What the upper bound gives)**.** [D] *Under H1–H3 the gain satisfies $g \le 1$, since a vessel whose reduced volume at dusk exceeds $2^{-1/2}$ cannot form two spheres and one above unity does not divide at all (Article 72, Definition 5.1). This is the condition that the vessel is not too taut, and it is the only bound on g that the geometry of this section supplies.*

Scholium 5.5 (Why fission is binary, and what settles it)**.** Article 72 obtained one strand per vessel from division at every dusk, and that argument needs the division to be into two. The geometry does not supply it: two is available everywhere and preferred to three, but nothing here forbids a vessel from parting into unequal or multiple pieces, and the counting argument that might have bounded g from below does not survive Proposition 5.2. What does select two is structural, and it is the subject of Section 7: a vessel carrying two strands carries two tethered footprints, and if those demix they are two centres about which the daughters form. The selection rule for binary fission is the strand, not the shape. Article 72's Target 11.7, the flaccid limit, therefore remains open (Target 10.4).

Remark 5.6 ($g = 1$ is the designed point)**.** [A] Article 72 called $g = 1$ marginal, because a founder off the orbit there loses cells. Geometrically it is the point the cycle is built around: the vessel is born a sphere and arrives at dusk at the two-sphere limit shape, where the bending energies agree and the daughters are again spheres. Below it the daughters are born flaccid, at $v = g_{\text{eff}}$, and whether a lineage remains viable as it becomes more flaccid is not settled here.

6 Area-biased incorporation

Proposition 6.1 (The direction of the loop)**.** [A] *Since $v = (N/N_0)(\Lambda/\Lambda_0)^{-3/2}$,*

$$\frac{dv}{v} = \frac{dN}{N} - \frac{3}{2}\frac{d\Lambda}{\Lambda},$$

so the reduced volume falls, and division is approached, only when the lumen content grows more slowly than three halves of the relative lipid growth. Material entering the lumen raises v and postpones division; material entering the bilayer lowers it. On the orbit both double each period and, with the factor $\sqrt{2}$ that halving contributes, the net factor is one: the orbit holds its shape and does not drift toward division of its own accord (block U3).

Theorem 6.2 (The shifted set point)**.** [D] *Under H1 and H6, let a vessel receive an extra lipid flux F per period carrying no lumen solute, with the genome-tied osmolyte gain J unchanged. The birth size settles at $\Lambda^* = \lambda + F$ and the reduced volume at birth at*

$$g_{\text{eff}} = g_0\Big(1 + \frac{F}{\lambda}\Big)^{-3/2}, \qquad g_0 = \frac{J}{N_\lambda},$$

so a lineage too taut to divide is brought within Proposition 5.4's bound by environmental lipid alone.

Proof. The birth-size map is $\Lambda' = (\Lambda + \lambda + F)/2$ with fixed point $\lambda + F$ (Article 73, Theorem 9.1(i)), and the osmolyte at birth is J. The reduced volume at birth is $J/N_{\text{taut}}(\Lambda^*)$, and N_{taut} scales as the lipid count to the power $3/2$. □

Proposition 6.3 (A genome returned to the window)**.** 🄳 *At Article 71's baseline without condensation, $g_0 = 1.8829$ at $L = 200$, an extra flux of at least $0.525\,\lambda$ per period brings g_{eff} to one or below (block U3), so the vessel divides at dusk. Article 72 placed the lower edge of its band at 735 units and Article 73 at 118–169 on a packing floor; the length 200, excluded by the first on the gain, is recovered without changing the genome. By Proposition 5.4 the requirement is one-sided: a larger flux divides the vessel sooner in the period and leaves the daughters more flaccid, and nothing in this article bounds that from above.*

Scholium 6.4 (What the environment buys)**.** The environment does not supply the drive, which the dusk shape already provides. What it supplies is the bias: a flux of membrane that is not matched by lumen content, which is what carries the vessel from the spherical birth shape to the fission shape within one period. A lineage whose genome-tied gain is already inside the window needs none.

7 The tethered domains

Proposition 7.1 (The footprint of a strand)**.** 🄳 *Under H1 and H4, the tethers of one strand cover, of the dusk bilayer area, 0.010 at $t = 1$ and 0.048 at $t = 5$, at every genome length; all guests together cover 0.124 at $L = 200$ rising to 0.190 at 1000, as Article 73 found (block U4).*

Corollary 7.2 (The domains do not tile)**.** 🄳 *Under H4 and H5 two tethered domains occupy a tenth of the bilayer between them at most, so they are patches and not hemispheres, their mutual boundary is not a great circle, and the line energy available there is a small fraction of what a hemispherical domain would release.*

Scholium 7.3 (Axis, not drive)**.** This is where the strand's connection to the membrane earns its place, and it is not where Article 64 placed it. The tethers insert as the strand is nucleated and copied, so the daughter strand acquires its own footprint as it is made; two footprints that demix (H5) sit apart, and the vessel that divides between them sends one strand to each daughter. That is segregation, the choice of a fission axis, and the selection of two as the number of daughters, which Proposition 5.2 shows the geometry does not supply. It is not a drive, and by Theorem 4.3 it does not need to be: at the dusk shape the vessel is already past the bending cost. The replication schedule and the division schedule are then tied by geometry as well as by the clock, which is what Article 72's copy-number argument required and could not supply.

8 Three devices

Proposition 8.1 (The photochrome as a curvature switch)**.** 🄳 *An outer-leaflet area excess δ requires a mole fraction $x = \delta a/\Delta A$ of switching lipid. At a per-molecule area change of 0.10–0.25 nm^2 and the excesses Article 73 required, x runs from 0.17 to 2.18 (block U5), against the four per cent of Article 64, Proposition 9.6, and its leak above a few per cent (Theorem 9.7). Put the other way, the population the corpus admits, all in one leaflet and all switched, delivers δ of 0.012 to 0.031 against a requirement from 0.066: a shortfall of two to five. The mechanism is sound and its amplitude is too small for this office.*

Proposition 8.2 (The strand as a constricting ring)**.** 🄳 *One strand's contour Lh reaches round the neck at the equator of the dusk vessel, $2\pi R\sqrt{2}$, only from about 735 units; two strands reach at every length (block U6). Holding a neck of radius R_n needs a force of order $2\pi\kappa/R_n$: 52 to 260 pN at R_n of 5 and 2 nm, against a duplex that overstretches near 65 pN (external). The device is marginal, and under Theorem 4.3 it is not required.*

Proposition 8.3 (The remnant as a wedge)**.** 🄳 *The free remnant is the largest guest class and its leaflet is unassigned (Article 71, Target 12.10). If it partitions to the outer leaflet it supplies an area excess of 0.107 at $L = 200$, rising to 0.240 at 1000 (block U7), which reaches the lower part of the 0.066–0.335 Article 73 required and exceeds the connectors by three to eight times. The margin has two sources: a partitioned guest contributes its whole footprint, 0.41 nm^2, where a switched connector contributes only the change in its own area; and there are about twice as many remnants as the admissible connector population. It is already in the membrane and already paid for. Against it: the same partitioning removes the remnant from the inner face where condensation consumes it, and the loop of Article 71 would have to be rebuilt accordingly.*

Scholium 8.4 (Which device, and for what)**.** None of the three is needed to make division possible, and none of them causes division: by Theorem 4.3 the end states already favour it. Their office, if any, is the neck, to lower whatever the molecular passage costs and to make fission prompt on the dusk schedule rather than merely favourable. The three are therefore ranked by amplitude at a requirement that Article 73 set under its own pricing and that this article has removed; the ranking stands, but what amplitude is actually needed is not known until the neck is priced (Target 10.3). On that ranking the remnant is the cheapest by far, since it asks for a leaflet assignment rather than a new species. The photochrome is not refuted as a mechanism: it switches, it is in the membrane, and it already holds two offices in the cycle, the gate on expression and the timing of the tether. What it lacks is amplitude. A switch moves only the change in one molecule's area, 0.10–0.25 nm^2, where a partitioned guest moves its whole footprint, 0.41 nm^2; and the population that may switch without leaking is about half the remnant's. The two effects compound to the factor of three to eight between them.

9 The input chain and its ceiling

Proposition 9.1 (The two-sided ceiling)**.** [D] *Under H1, H6 and H7, uptake proportional to the lipid count, $G = \lambda + r\Lambda$, has the set point $\lambda/(1-r)$ and is stable for $r < 1$ (Article 73, Theorem 9.1(iii)); by Theorem 6.2 the gain at that set point is $g_{\mathrm{eff}} = g_0(1-r)^{3/2}$, which Proposition 5.4 requires not to exceed one. At $g_0 = 1.8829$ and $L = 200$ (block U8):*

r	Λ^*/λ	g_{eff}	*outcome*
0.00	*1.000*	*1.8829*	*too taut*
0.30	*1.429*	*1.1027*	*too taut*
0.35	*1.538*	*0.9867*	*divides*
0.40	*1.667*	*0.8751*	*divides*
0.45	*1.818*	*0.7680*	*divides*
0.60	*2.500*	*0.4763*	*divides*

The condition is one-sided: below about 0.34 *of a doubling per period the vessel is too taut to divide at this baseline, and above it division proceeds with the daughters born progressively more flaccid, bounded above only by $r < 1$.*

Scholium 9.2 (A strand that is more active when stimulated)**.** The chain from the environment through the pore and the tethers to the strand, and back through incorporation to the membrane, is a positive loop: more membrane carries more tethers, which carry more activity, which makes more membrane. What the geometry requires of it is a floor, not a ceiling: enough bias to carry the vessel from its spherical birth shape to a dividing one within the period. Whether the loop also needs a ceiling turns on how flaccid a vessel may be born and still be viable, which Article 72 left open (its Target 11.7) and which Proposition 5.2 shows the counting of daughters does not answer. That is now the question on which the regulation of the chain depends (Target 10.4).

10 Registers, precedence, targets, conclusion

10.1 Consolidated register

What does fission cost at the dusk shape?
One new closed surface, $4\pi\kappa_G$: -101 to $-251\,k_BT$. It lowers the energy.
Rests on: Thm. 4.3; block U1.
Standing: [D] on H2, H3, at $g = 1$.

How many daughters can a vessel make?
At most v^{-2} equal ones, but each further sphere costs 4.00–4.80 $\pi\kappa$ more and two flaccid daughters are available at every reduced volume, so counting gives no lower bound on g; only $g \le 1$ follows.
Rests on: Props. 5.1–5.4; block U2.
Standing: [D]; Article 72's Target 11.7 remains open.

Does the orbit drift toward division?
No: area and volume double together and v is constant. Only membrane-biased incorporation lowers it.
Rests on: Prop. 6.1; block U3.
Standing: [A].

Can environmental lipid place a lineage in the window?
Yes: $g_{\mathrm{eff}} = g_0(1+F/\lambda)^{-3/2}$; at $L = 200$ a flux of 0.525–0.745 λ suffices.
Rests on: Thm. 6.2, Prop. 6.3; block U3.
Standing: [D] on H6.

What do the tethers do?
Cover 1–5% of the bilayer each; they fix the fission axis, segregate the strands and select two as the number, and supply no drive.
Rests on: Prop. 7.1, Cor. 7.2; block U4.
Standing: [D] on H4, H5.

Which device is worth building?
The remnant as an outer-leaflet wedge, if its leaflet may be assigned; the photochrome fails in this role and the strand ring is marginal.
Rests on: Props. 8.1–8.3; blocks U5–U7.
Standing: [D]; none is required.

How active may a stimulated strand be?
At least about 0.34 of a doubling per period at the baseline considered; no upper bound beyond $r < 1$.

Rests on: Prop. 9.1; block U8.
Standing: [D] on H7.

10.2 Falsification register

Theorem 4.3
A vessel at $v = 2^{-1/2}$ whose minimal shape is not the two-sphere limit shape, or a positive Gaussian modulus.

Proposition 5.2
A Gaussian modulus below -2κ, which would make further spheres cheaper and could favour fragmentation.

Proposition 6.1
A vessel approaching division while its lumen content grows faster than three halves of its relative lipid growth.

Corollary 7.2
A tethered domain covering a hemisphere at the closure scale.

10.3 Precedence

Ruling 4.4, against Article 73, is stated in Section 4.

Ruling 10.1 (Against Article 72). **72.1** [A] *Target 11.7 remains open.* The flaccid limit is not supplied by counting the daughters a reduced volume admits, since further spheres are dearer and two are always available (Proposition 5.2). It awaits the shape energies (Target 10.4).

72.2 [D] $g = 1$ *is the designed point.* Its Remark 7.4 calls the taut orbit marginal on the evidence of founder losses; geometrically it is where the dusk shape is exactly the fission shape (Remark 5.6).

72.3 [D] *The lower edge of its band is not binding on the gain.* A genome of 200 units, excluded by its Proposition 10.1 through g, is admitted under Theorem 6.2 with environmental lipid (Proposition 6.3).

72.4 [D] *Its Definition 5.1 is load-bearing.* That a vessel below $2^{-1/2}$ divides into two flaccid daughters, rather than into more pieces, is what makes binary fission available at every reduced volume (Proposition 5.2); the definition should be read as a modelling choice that Section 7 supports structurally and the geometry does not force.

Ruling 10.2 (Against Article 64). [D] Consistent, and its drive is relieved of a burden. The line tension of Proposition 9.5 need not pay the bending cost of fission, which the dusk shape has already paid (Theorem 4.3); what remains for it, and for any device, is the neck.

10.4 Targets

Target 10.3 (The neck). Price the molecular passage through the neck at the closure scale, which continuum theory makes singular; this is the last unpaid cost of fission and inherits Article 73, Target 11.9.

Target 10.4 (The shape branches). Supply the reduced bending energy $e(v)$ of a vesicle on its stable branch, which would locate the crossing of Remark 5.3, settle how flaccid a vessel may be born, and close Article 72's Target 11.7.

Target 10.5 (Below $g = 1$). Compute the shape energies of parent and daughters for g inside the window but below one, where both are flaccid, and confirm that fission remains downhill there.

Target 10.6 (The tether count). Reconcile the $5L$ anchor units of the ledger with one tether per base in the enclosure; the footprint of a strand depends on it.

Target 10.7 (The remnant's leaflet). Decide whether the free remnant partitions to the outer leaflet, which would supply the curvature of Proposition 8.3 at no cost and would displace the condensation site.

Target 10.8 (What saturates the chain). Determine what bounds the incorporation rate from above, since the geometry admits only a tenth of a doubling per period (Scholium 9.2).

10.5 Conclusion

Proposition 10.9 (What is established). [A] *Subject to Appendix A:*

(i) At $g = 1$ the dusk shape is the two-sphere limit shape and fission costs only $4\pi\kappa_G < 0$; Article 73's deficit was an artefact of comparing against a sphere (Theorem 4.3, Ruling 4.4).

(ii) Counting the daughters a reduced volume admits gives no lower bound on the gain: further spheres are dearer and two flaccid daughters are available throughout, so only $g \le 1$ follows, and what selects binary fission is the pair of tethered footprints (Propositions 5.2, 5.4, Scholium 5.5).

(iii) The orbit does not drift toward division; membrane-biased incorporation carries it there, and restores a

genome length Article 72 excluded (Proposition 6.1, Theorem 6.2, Proposition 6.3).

(iv) The tethers fix the axis, segregate the strands and select two as the number; they supply no drive and need not (Corollary 7.2, Scholia 5.5, 7.3).

(v) Of three devices the remnant wedge is cheapest, the photochrome fails in this role, and none is required (Propositions 8.1–8.3).

(vi) Stimulated uptake is bounded below, at about a third of a doubling per period at the baseline considered (Proposition 9.1).

Remark 10.10 (What is not established)**.** [A] The neck is unpriced, the comparison is exact only at $g = 1$, the elastic constants are borrowed, the tether count is a range, the remnant's leaflet is undecided, and how flaccid a vessel may be born is not settled. The cycle now has a division whose end states are favourable at the shape the cycle produces, and a selection rule for binary fission that rests on the strands rather than on the geometry.

A Hypothesis register

B Verification

Every number in the body is emitted by `acf-74-blocks.py` (standard library only; a run takes under a second), or is quoted from the source named.

U1 [COMPUTED] **The dusk shape**

Limit shapes and their energies; where the orbit delivers the vessel; the marginal cost of fission over the moduli; the comparison with Article 73.

U2 [COMPUTED] **How many daughters**

Daughters available against the gain; the monotonicity of the multi-sphere energies; the daughters Article 72's reset produces below the limit shape; where an energetic bound would lie.

U3 [COMPUTED] **Area bias**

The direction identity; the net factor over a period; the flux that places a lineage in the window.

U4 [COMPUTED] **The tethered domains**

Tether and guest coverage at two tether counts and four genome lengths.

U5 [COMPUTED] **Device A**

Mole fraction of switching lipid needed against what the corpus admits.

U6 [COMPUTED] **Device B**

Strand contour against the neck; the force a ring must exert.

U7 [COMPUTED] **Device C**

The area excess the remnant would supply if it partitioned outward.

U8 [COMPUTED] **The chain**

Set point, gain and outcome against the uptake rate, with the one-sided condition.

C Sources and literature

C.1 The corpus, by use

Article 62 [Sch26d]: the closure geometry, the footprint of a chrysene unit, the rise per base. Article 64 [Sch26e]: division at dusk, the drive, the connectors and the leak. Article 71 [Sch26a]: the loop, the catalyst density, the remnant and its open fate. Article 72 [Sch26b]: the symmetric doubling orbit, the gain, the band, and the flaccid-limit target closed here. Article 73 [Sch26c]: the guest area, the line tension, the curvature requirement, the environmental-lipid theorem, and the mispriced cost corrected here.

C.2 Established literature

The bending energy and the Gauss–Bonnet term are Helfrich's [Hel73]; limit shapes and the reduced volume are standard [Sei97]. The bending modulus is from micropipette measurements [ROM+00] and the Gaussian modulus from simulation [HBD12]. The overstretch force of a nucleic acid duplex is from single-molecule measurement [SCB96]. None enters a proof beyond the constant named.

References

[HBD12] M. Hu, J. J. Briguglio, and M. Deserno. Determining the Gaussian Curvature Modulus of Lipid Membranes in Simulations. *Biophysical Journal*, 102(6):1403–1410, 2012.

[Hel73] W. Helfrich. Elastic Properties of Lipid Bilayers: Theory and Possible Experiments. *Zeitschrift für Naturforschung C*, 28:693–703, 1973.

[ROM+00] W. Rawicz, K. C. Olbrich, T. McIntosh, D. Needham, and E. Evans. Effect of Chain Length and Unsaturation on Elasticity of Lipid Bilayers. *Biophysical Journal*, 79(1):328–339, 2000.

Table 1: Hypotheses of this article.

	Premise	What rests on it	What survives its failure
H1	Article 72's orbit with Article 73's guest area	Every section	Prop. 4.1 and Prop. 5.2 as geometry
H2	Helfrich bending, κ and κ_G ranges (external)	Thm. 4.3; Prop. 5.2; the devices	Prop. 6.1
H3	The vessel adopts its minimal shape, identified at $2^{-1/2}$	Thm. 4.3; Props. 5.1, 5.4	The direction condition and the set point
H4	Tethers at nucleation, t in 1–5	Prop. 7.1	Everything outside Section 7
H5	Tethered footprints demix	Sch. 7.3	The cost and the window
H6	Environmental lipid, no lumen solute	Thm. 6.2; Prop. 6.3	Everything else
H7	Incorporation scales with the tethers	Prop. 9.1	The window itself

[SCB96] S. B. Smith, Y. Cui, and C. Bustamante. Overstretching B-DNA: The Elastic Response of Individual Double-Stranded and Single-Stranded DNA Molecules. *Science*, 271(5250):795–799, 1996.

[Sch26a] Charles D. Schaper. Addressing the Division Clock: Codon Gating at the Membrane, the Reusable X-A Catalyst, and the Set Point of the Lineage. *Annals of the Chrysene Formalism*, 1(3):1453–1471, 2026. Article 71. DOI: https://doi.org/10.68366/xq2xgj80.

[Sch26b] Charles D. Schaper. Cycle Integration: Copy Number, the Closure Vesicle, and the Band of the Genome. *Annals of the Chrysene Formalism*, 1(3):1472–1483, 2026. Article 72. DOI: https://doi.org/10.68366/7fdnjs23.

[Sch26c] Charles D. Schaper. Fission at the Closure Scale: Guest Area, the Curvature Floor, and Line-Tension Drive. *Annals of the Chrysene Formalism*, 1(3):1484–1492, 2026. Article 73. DOI: https://doi.org/10.68366/ptnxhv14.

[Sch26d] Charles D. Schaper. The Enclosure via the Encoded Chrysene Cluster: Integrated Synthesis of Nucleic Acids and Phospholipids, and the Orientational Encoding of the Membrane. *Annals of the Chrysene Formalism*, 1(3):1279–1320, 2026. Article 62. DOI: https://doi.org/10.68366/24m3wx88.

[Sch26e] Charles D. Schaper. The Photoentrained Cycle: Existence and Stability of a Periodic Orbit in a Forced Hybrid Protocell. *Annals of the Chrysene Formalism*, 1(3):1348–1370, 2026. Article 64. DOI: https://doi.org/10.68366/h9rzkd75.

[Sei97] U. Seifert. Configurations of Fluid Membranes and Vesicles. *Advances in Physics*, 46(1):13–137, 1997.

D Revision record

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

Item	Critique	Revision
R1	The window inferred preference from availability	Theorem withdrawn; Props. 5.1–5.4 and Sch. 5.5 replace it, binary fission selected by the tethered footprints; block U2 rebuilt; Article 72's Target 11.7 reopened
R2	Thm. 4.3 reads wider than it is	Stated as a comparison of end states at a single g, with the neck named as the unpriced remainder
R3	H3's minimal shape asserted	Identified and cited
R4	Ruling 73.2 overreached	Domain budding and vessel fission distinguished; Ruling 73.4 restored to the earlier article
R5	Two-sided bounds	Props. 6.3, 9.1 and Sch. 9.2 made one-sided; block U8 rebuilt

E Correction ledger

Art.	Location	As printed	Corrected
73	Thm. 7.1, cost of fission	$8\pi\kappa$	$4\pi\kappa_G$ at the dusk shape
73	Prop. 7.2, the shortfall	short in every case	not carried
73	Sch. 7.3	copy number cost the drive	the drive was mispriced
73	Cor. 8.3	a component is needed	conditional, for the neck
73	Prop. 10.2, shedding	cannot shed	reopened
72	Target 11.7	open	still open; counting does not close it
72	Rem. 7.4, $g = 1$	marginal	the designed point
72	Def. 5.1	a reset	load-bearing; supported structurally
72	Prop. 10.1 lower edge	735 on the gain	200 with environmental lipid