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Theorem of inevitable death: calibration of the universal dissipative metabolism model on human ATP synthase

Pavel A. Polyukov ✉

Moscow, Russia
ORCID: 0009-0003-3370-1348
E-mail: ✉polyukov.pavel@yandex.ru

Abstract. This work presents an experimental calibration of a universal dissipative metabolism model describing the dynamics of three fundamental state parameters — resource m, variability g, and consolidation k. The model is based on the concept of a metabolic power quantum P as an atomic portion of negentropy flow and includes theorems on inevitable death, survival criterion, and fluctuation spectral density isomorphic to Planck's formula. Based on structural data of human ATP synthase (EMDB ID EMD-34572, PDB ID 8H9L) and modern biophysical studies, empirical calibration of key parameters was performed: reinvestment efficiency $\alpha_{\text{total}} = 0.17 - 0.25$, variability constant $\gamma_g = (2.8 \pm 0.5) \times 10^{16}$ m^{-2}, quantum energy $\varepsilon_0 = 3.2 \times 10^{-20}$ J. The characteristic frequency of the fluctuation spectrum was obtained as $\nu_{\text{char}} \approx 1.01 \times 10^{13}$ Hz (337 cm^{-1}), corresponding to the mid-IR range. E. Schrödinger's principle (1944) on the suppression of quantum fluctuations in large molecular aggregates is quantitatively confirmed: it is shown that the isolated c-ring reaches the theoretical quantum rotation limit ($\sim 43,000$ rps), but within the whole enzyme, rotation slows down by 1–3 orders of magnitude due to collective effects. The obtained values can be directly substituted into the model's dynamic equations for quantitative modeling of evolutionary, biological, and social processes.

Keywords: dissipative systems, reinvestment, death theorem, power quantum, ATP synthase, Planck's formula, Schrödinger's principle, model calibration, quantum rotation limit.

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1. Introduction

In [1], a universal mathematical model of dissipative systems capable of maintaining their structure by reinvesting part of the dissipated energy was proposed. The model is based on an isomorphism between a stick-slip oscillator (a mechanical system with dry friction), non-equilibrium thermodynamics, and quantum statistics. Three state parameters were introduced:

- m — accumulated resource (ATP/ADP pool, mass, capital);
- g — variability (conformational mobility, ability to reconfigure, mutational potential);
- k — consolidation (structural rigidity, institutional rigidity, logical strictness).

The key result of [1] is the system of dynamic equations:

$$\begin{cases} \dot{m} = \alpha_m P - \beta_m m \\ \dot{g} = \alpha_g P - \beta_g g \\ \dot{k} = \alpha_k P - \beta_k k \end{cases} \tag{1}$$

where $P = 2\mu_k v_0 g m$ is the metabolic power quantum, $\alpha_m + \alpha_g + \alpha_k = \alpha_{\text{total}}$ is the reinvestment efficiency, and β_i are degradation coefficients.

In [1], the following theorems were proven:

- **Theorem 1 (on inevitable death):** for fixed $\alpha_m, \alpha_g, \alpha_k$, the system degrades irreversibly;
- **Theorem 2 (survival criterion):** the system remains viable if and only if α_g and α_k are functions of the state, providing negative feedback;
- **Theorem 3 (on the irreversibility threshold):** for an ensemble of systems, there is a critical fraction of damaged elements θ_{crit}, after which collapse is inevitable;
- **Theorem 4 (on the necessity of phase transitions):** viability requires switching between fermionic (variability) and bosonic (consolidation) regimes;
- **Theorem 5 (on the cascade of evolutionary explosions):** each evolutionary leap creates conditions for the next with exponential acceleration $\tau_{n+1} \approx \tau_n/2$;
- **Theorem 6 (on spectral density):** the fluctuation spectrum of the system is isomorphic to Planck's formula:

$$p(\nu) = \frac{D(\nu) \cdot \varepsilon(\nu)}{e^{\alpha_{\text{total}} \varepsilon(\nu)/(h\nu)} - 1} \tag{2}$$

However, all these theorems operate with abstract parameters α_{total}, ε_0, γ_g, β_T, which require empirical calibration. **The aim of this work** is to determine the numerical values of these parameters based on independent experimental data for ATP synthase — a molecular machine that precisely implements the "accumulation-release-reinvestment"cycle underlying the model [1].

2. Connection to the Universal Model

2.1. Parameter Correspondence ATP synthase is an ideal object for calibration because:

1. Its operation follows stick-slip mechanics: an accumulation phase (protons create elastic stress in the stator) and a release phase (threshold rotation of the rotor upon reaching a membrane potential of ~ 200 mV);
2. In one revolution (360°), 3 ATP molecules are synthesized — a strictly defined cycle;
3. Extensive experimental data [4, 8] and high-quality structural data [2, 10] are available.

2.2. Role of Calibration Substituting the numerical values of α_{total}, ε_0, γ_g, β_T obtained in this work into equations (1) and the formulas of theorems 1–6 from [1] transforms the abstract model into a **quantitative tool** capable of:

- calculating irreversibility thresholds θ_{crit} for specific tissues;
- predicting the spectral density of fluctuations $p(\nu)$;
- estimating the rates of evolutionary explosions τ_n;
- numerically verifying Schrödinger's principle.

Таблица 1Correspondence between parameters of the model [1] and measurable quantities for ATP synthase

Model Parameter [1]	**Notation**	**Interpretation for ATP Synthase**	**Measurement Method**
Resource	m	ATP/ADP pool in the mitochondrial matrix	Biochemical analysis
Variability	g	Conformational rearrangement capability, modulated by protonmotive force	Indirectly via fluorescent probes and rotation speed
Consolidation	k	Rotor stiffness, activation energy for rotation	Molecular dynamics, normal modes
Power quantum	P	Dissipation power per enzyme	$P = \nu_{\text{rot}} \cdot 3 \cdot \Delta G_{\text{ATP}}$
Reinvestment efficiency	α_{total}	Fraction of energy used for structure maintenance	$\alpha_{\text{total}} = 1 - \eta$, where η is thermodynamic efficiency [4, 8]
Quantum energy	ε_0	Energy dissipated per proton transfer	$\varepsilon_0 = q \cdot \Delta\psi$
Variability constant	γ_g	$1/L_0^2$, where L_0 is a characteristic size	From homologous structures: $\gamma_g = 1/(\text{rotor diameter})^2$

3. Materials and Methods

3.1. Structural Data The cryo-EM structure of human mitochondrial ATP synthase, deposited in the Electron Microscopy Data Bank under the identifier **EMDB ID EMD-34572** (corresponding coordinate model in the Protein Data Bank — **PDB ID 8H9L**) [2, 10], was used. The structure was obtained by cryo-electron microscopy at a resolution of 2.61 Å [10]. The deposition date is October 25, 2022 [10]. The last revision of the coordinate model dates to July 3, 2024 (changes in the Data collection section) [2, 10].

Important note on the structure: The provided PDB coordinate model 8H9L describes exclusively the F1-domain and associated small subunits (inhibitor IF1, subunit O). The membrane Fo-domain, including the c-ring, is absent in this structure [2, 10]. According to EMDB metadata, the full map includes regions corresponding to the Fo-domain, but a coordinate model has not been built for it. Therefore, for the analysis of c-ring geometric parameters, homologous structures and literature data were used, as indicated in the relevant sections.

Imaging parameters (from EMDB metadata):

- Microscope: FEI Titan Krios at 300 kV
- Detector: FEI Falcon IV (4k × 4k)
- Energy filter: TFS Selectris X (10 eV slit)
- Total electron dose: 50 $e^-/Å^2$
- Nominal defocus: 1200–2400 nm
- Number of particles in reconstruction: 45,418
- Buffer: pH 7.4
- Initial model for reconstruction: AlphaFold
- Software: cryoSPARC (classification, CTF correction, angle assignment), PHENIX (model refinement)

Analysis methods:

- Atomic coordinates were downloaded from the PDB and processed using UCSF Chimera.
- Subunit composition was verified by chains: α-subunits (chains A, B, C, length 510 aa), β-subunits (chains E, F, D, length 482 aa), γ-subunit (chain G, length 273 aa), inhibitor IF1 (chain J, length 81 aa), subunit O (chain O, length 190 aa) [2].
- The volume of the F1-complex was calculated by approximating an ellipsoid based on three principal semi-axes obtained from the atomic coordinates.
- Due to the absence of c-ring coordinates in PDB 8H9L, calculating the density of vibrational states $D(\nu)$ for the complete complex is not possible. Section 6 presents a conceptual approach to such a calculation.

4. Dimensions of Quantities

To ensure physical consistency and direct substitution into the model equations [1], all quantities are assigned dimensions in the SI system.

Таблица 2Dimensions of the main model quantities

Quantity	**Notation**	**Dimension**	**Physical Meaning**
Resource	m	[M]	Accumulated mass/energy (ATP/ADP pool)
Variability	g	$[\mathrm{LT}^{-2}]$	Conformational mobility (analogous to acceleration)
Consolidation	k	$[\mathrm{MT}^{-2}]$	Bond stiffness (of the stator)
External flow	v_0	$[\mathrm{LT}^{-1}]$	Proton inflow rate
Friction coefficients	μ_s, μ_k	[1]	Dimensionless
Dissipation power	P	$[\mathrm{ML}^2\mathrm{T}^{-3}]$	Quantum of metabolic power
Reinvestment coefficients	$\alpha_m, \alpha_g, \alpha_k$	[1]	Dimensionless
Total reinvestment efficiency	α_{total}	[1]	
Degradation coefficients	$\beta_m, \beta_g, \beta_k$	$[\mathrm{T}^{-1}]$	Decay rates
Thermodynamic temperature	Θ	[Θ] (K)	
Coupling constant	κ	[Θ]	$\alpha_{\text{total}} = \kappa/\Theta$
Transformation coefficients	$\gamma_m, \gamma_g, \gamma_k$	$[\mathrm{T}^2\mathrm{L}^{-2}]$, $[\mathrm{L}^{-2}]$, $[\mathrm{L}^{-2}]$	Relate P to the rate of change
Planck's constant	h	$[\mathrm{ML}^2\mathrm{T}^{-1}]$	Fundamental quantum of action
Quantum energy	ε_0	$[\mathrm{ML}^2\mathrm{T}^{-2}]$	Energy of one proton
Density of states	$D(\nu)$	[T]	Number of modes per unit frequency
Spectral density	$\tilde{p}(\nu)$	$[\mathrm{ML}^2\mathrm{T}^{-2}]$	Power per unit frequency

5. Empirical Calibration Using ATP Synthase

5.1. Experimental Data

Таблица 3Experimental parameters of ATP synthase

Parameter	Value	Dimension	Source
H^+/ATP ratio (mitochondria)	3.3–4.7 (up to 5.8 in engineered constructs)	[1]	[4, 5, 8, 9]
Proton energy (membrane potential)	~ 0.2 eV	$[ML^2T^{-2}]$	[4, 8]
Quantum of action per ion transfer act	$(6.70 \pm 0.15) \times 10^{-34}$ J·s	$[ML^2T^{-1}]$	[5]
Standard free energy of ATP synthesis	30–34 kJ/mol	$[ML^2T^{-2}]$	[4]
Rotor rotation speed (intact mitochondria)	100–650 rps	$[T^{-1}]$	[4, 8]
Rotation speed of isolated c-rings	up to 43,000 rps	$[T^{-1}]$	[4, 8]
Thermodynamic energy conversion efficiency	75–83%	[1]	[4, 8]

5.2. Structural Parameters from PDB 8H9L / EMDB EMD-34572 Based on the analysis of the human ATP synthase structure, the following parameters were obtained (verified by EMDB and PDB metadata [2, 10]):

Таблица 4Structural parameters of ATP synthase from PDB 8H9L / EMDB EMD-34572

Parameter	Value	Source
Structure resolution	2.61 Å	EMDB metadata [2]
Molecular mass of F1-complex with inhibitor	~ 370 kDa	EMDB metadata [2]
Deposition date	2022-10-25	PDB [10], EMDB [2]
Last revision	2024-07-03 (Data collection)	PDB [10]
Total amino acid residues in the model	~ 3520	PDB sequence [2]
Total atoms in the model	$\sim 52,800$	Estimate based on composition
Presence of Fo-domain (c-ring)	Absent in coordinate model	PDB 8H9L
c-ring diameter (based on homologous structures, PDB 6TQJ)	5–7 nm	[4, 8]
Map unit cell dimensions	$373.76 \times 373.76 \times 373.76$ Å^3	EMDB metadata [2]
Map pixel spacing	0.73 Å	EMDB metadata [2]
Grid dimensions	$512 \times 512 \times 512$ voxels	EMDB metadata [2]
F1-complex dimensions	height ~ 8 nm, width ~ 10 nm	Estimate
Software used	cryoSPARC, PHENIX	EMDB metadata [2]
Initial model	AlphaFold	EMDB metadata [2]

5.3. Calibration of Key Model Parameters [1]

5.3.1. Reinvestment Efficiency α_{total} According to modern data [4, 8], the thermodynamic energy conversion efficiency of ATP synthase is:

$$\eta = 75 - 83\% \tag{3}$$

Therefore, the fraction of energy dissipated (reinvested in maintaining structure, overcoming friction, leaks, etc.) is:

$$\boxed{\alpha_{\text{total}} = 1 - \eta = 0.17 - 0.25} \tag{4}$$

In [4, 8], it was shown that the main dissipation channel is internal friction in the F1-motor, with contributions from viscous drag, proton leaks, electroviscous effects, elastic deformations, and information-theoretic costs. For further calculations, we will use the average value $\alpha_{\text{total}} = 0.21$ with the indicated range. This value is directly substituted into equations (1) of the model [1] and into the spectral density formula (2).

5.3.2. Coupling Constant κ From the relation $\alpha_{\text{total}} = \kappa/\Theta$ [1] at physiological temperature $\Theta = 310$ K (37°C for mammals):

$$\boxed{\kappa = \alpha_{\text{total}} \cdot \Theta = 0.21 \cdot 310 \approx 65 \text{ K}} \tag{5}$$

Considering the range of α_{total}: $\kappa = 52.7\tilde{}77.5$ K.

5.3.3. Quantum Energy ε_0 For mitochondria, the energy delivered by one proton is $\Delta\mu_{H+} \approx 0.2$ eV [4, 8]. Since the exact H^+/ATP ratio is a subject of debate and varies from 3.3 to 4.7, it is advisable to use the efficiency and the free energy of ATP synthesis directly to estimate the total energy per ATP synthesis. The energy dissipated per proton transfer act can be estimated as:

$$\boxed{\varepsilon_0 = \Delta\mu_{H+} = 0.2 \text{ eV} = 3.2 \times 10^{-20} \text{ J}} \tag{6}$$

The total energy expended for the synthesis of one ATP is $\Delta G_{\text{ATP}}/\eta \approx 32/0.79 = 40.5$ kJ/mol, which corresponds to ~ 0.42 eV per ATP molecule.

5.3.4. Effective Planck's Constant According to theoretical estimates [5], the process of ion transfer across a membrane can be quantized with a step close to the fundamental Planck's constant. The theoretically obtained value is:

$$\boxed{h_{\text{eff}} \approx (6.70 \pm 0.15) \times 10^{-34} \text{ J·s}} \tag{7}$$

This value is close to the fundamental Planck's constant $h = 6.626 \times 10^{-34}$ J·s (discrepancy $\sim 1\%$). As shown in [5], this indicates a possible fundamental nature of the ion transfer process and confirms the assumptions of the model [1] regarding the nature of the power quantum.

5.3.5. Variability Constant γ_g According to the model [1], the dissipation power P is related to the variability g by $P \sim \gamma_g g^2$, where $\gamma_g = 1/L_0^2$, and L_0 is the characteristic size of the system. Since the c-ring coordinates are absent in PDB 8H9L, we use literature data on the rotor diameter (PDB 6TQJ). According to [4, 8], for c-rings with 8 to 17 subunits, the diameter varies, and a characteristic value is $L_0 \approx 6$ nm $= 6 \times 10^{-9}$ m. Therefore:

$$\boxed{\gamma_g = \frac{1}{L_0^2} = \frac{1}{(6 \times 10^{-9})^2} = \frac{1}{3.6 \times 10^{-17}} = 2.78 \times 10^{16} \text{ m}^{-2}} \tag{8}$$

Considering the variability in c-ring size:

$$\boxed{\gamma_g = (2.8 \pm 0.5) \times 10^{16} \text{ m}^{-2}} \tag{9}$$

6. Density of Vibrational States $D(\nu)$: A Conceptual Approach

To verify Theorem 6 from [1] (spectral power density), knowledge of the density of states $D(\nu)$ for the complete ATP synthase is necessary. Due to the absence of Fo-domain coordinates in PDB 8H9L, a full calculation is not performed in this work. However, based on literature data on the structure and dynamics of ATP synthases from various species [4, 8], a conceptual three-component model can be proposed:

$$\boxed{D(\nu) = D_{\text{rot}}(\nu) + D_{\text{ac}}(\nu) + D_{\text{loc}}(\nu)} \tag{10}$$

6.1. Rotational Mode (Discrete)

$$D_{\text{rot}}(\nu) = A_{\text{rot}}\,\delta(\nu - \nu_{\text{rot}}) \tag{11}$$

with amplitude $A_{\text{rot}} = 1$ (one collective rotational mode). Rotation frequency for intact mitochondria: $\nu_{\text{rot}} \approx 100\tilde{}650$ Hz [4, 8].

6.2. Acoustic Modes (Phonons in the Protein Globule) In the Debye approximation for a three-dimensional elastic continuum:

$$D_{\text{ac}}(\nu) = \frac{12\pi V}{v_s^3}\,\nu^2 \cdot \Theta(\nu_D - \nu) \tag{12}$$

Estimated parameters for the F1-complex:

- $V_{\text{eff}} \approx 5.5 \times 10^{-25}$ m^3 — effective volume of the F1 protein globule
- $v_s \approx 1500$ m/s — speed of sound in a protein globule
- $\nu_D \approx 5 \times 10^{12}$ Hz — Debye frequency

6.3. Local Vibrations (Optical Modes) Local modes are approximated by a sum of Lorentzians with parameters characteristic of protein IR spectroscopy.

6.4. Characteristic Frequency of the Spectrum From Planck's formula (2), the characteristic frequency at which the exponent's argument is of order unity is:

$$\nu_{\text{char}} = \frac{\alpha_{\text{total}}\varepsilon_0}{h} = \frac{0.21 \cdot 3.2 \times 10^{-20}}{6.626 \times 10^{-34}} \approx 1.01 \times 10^{13}\ \text{Hz} \tag{13}$$

In wavenumbers:

$$\tilde{\nu}_{\text{char}} = \frac{\nu_{\text{char}}}{c} = \frac{1.01 \times 10^{13}}{3 \times 10^{10}} \approx 337\ \text{cm}^{-1} \tag{14}$$

which corresponds to the mid-IR range — the region where many collective vibrations of protein globules are manifested.

This prediction of the model [1] can be tested experimentally by IR spectroscopy of mitochondria.

7. Quantum Rotation Limit and Schrödinger's Principle

In [7] (Schrödinger, 1944), it was suggested that in large molecular aggregates, quantum effects should be suppressed by the collective interaction of many atoms. Modern research [4, 8] allows for a quantitative test of this principle using ATP synthase as an example.

7.1. Quantum Rotation Limit of the c-ring The maximum angular velocity of a quantum rotor with moment of inertia I is limited by the discreteness of the angular momentum levels. According to the derivation in [4, 8], for the smallest non-zero angular momentum ($l = 1$):

$$\omega_{\min} = \frac{\sqrt{2}\hbar}{I} \tag{15}$$

The moment of inertia of the ATP synthase c-ring depends on the number of subunits and, consequently, the ring size. According to [4, 8], for rings with 8–17 subunits, the moment of inertia varies, and the quantum rotation limit is:

$$\boxed{\nu_{\text{quantum}} = 13,000 - 62,000 \text{ rps}} \tag{16}$$

where the lower bound corresponds to the larger ring (17 subunits), and the upper bound to the smaller ring (8 subunits).

7.2. Experimental Values

- Rotation speed of intact ATP synthase in mitochondria: **100–650 rps** [4, 8]
- Rotation speed of isolated c-rings: **up to 43,000 rps** [4, 8]

Quote from the original work [4, 8]: *"Nevertheless, experimental estimates of the rotation rates in isolated c-rings suggest rates in the vicinity of 43,000 rps, right within our theoretical quantum estimates. However, ATP synthase as a whole operates firmly within the classical regime, despite its nanoscale dimensions, which highlights its evolutionary optimization for robust and efficient energy conversion at the quantum–classical boundary. This is the result of the rotatory coupling between the Fo and the much slower F1 unit."*

7.3. Suppression Factor and Its Interpretation For intact ATP synthase, the suppression factor relative to the quantum limit is:

$$\boxed{\frac{\nu_{\text{intact}}}{\nu_{\text{quantum}}} = \frac{100\text{–}650}{13,000\text{–}62,000} \approx 1.6 \times 10^{-3} - 5.0 \times 10^{-2}} \tag{17}$$

For the isolated c-ring:

$$\boxed{\frac{\nu_{\text{isolated}}}{\nu_{\text{quantum}}} = \frac{43,000}{13,000\text{–}62,000} \approx 0.69 - 3.3} \tag{18}$$

Values in the range and above 1 for the isolated ring indicate that the experimentally measured speed is within or may slightly exceed the theoretical quantum limit for an ideal quantum rotor. This may be related to the approximate nature of the moment of inertia estimate, as well as the fact that the rotation of the isolated c-ring is not a purely quantum process.

Key observation: the isolated c-ring reaches speeds on the order of the quantum limit, but within the whole enzyme, rotation slows down by 1–3 orders of magnitude. As shown in [4, 8], this is due to the rotational coupling between the fast Fo and the significantly slower F1, creating an effective negative feedback that slows the system to the classical regime.

7.4. Confirmation of Schrödinger's Principle The authors of [4, 8] directly link their results to Schrödinger's prediction: *"As Schrödinger stated in What is Life? (1944): 'The submicroscopic world is full of fluctuations. But in large aggregates of atoms, the law of large numbers ensures that these fluctuations become negligible' — a prediction directly confirmed here in the context of the rotational stability of the Fo unit."*

This directly confirms Schrödinger's principle: in an isolated nanoscale structure (c-ring), quantum effects are significant (the theoretical quantum limit is reached), but within a large molecular aggregate (whole ATP synthase), collective interaction suppresses these effects, ensuring classical behavior [4, 8].

8. New Universal Constants

From the analysis of experimental data and literature sources, new universal constants have been obtained that can be used in the model [1] for quantitative calculations.

Таблица 5New constants

Constant	Meaning	Value	Dimension	Status
γ_g	Variability constant	$(2.8 \pm 0.5) \times 10^{16}$	m^{-2}	Estimate based on homology
α_{total}	Reinvestment efficiency	0.17–0.25	[1]	Empirically confirmed
ν_Q	Characteristic frequency of quantum limit	1.3×10^4 – 6.2×10^4	Hz	Theoretically calculated, experimentally confirmed
ν_{char}	Characteristic frequency of spectrum	1.01×10^{13}	Hz	Theoretical prediction
κ	Coupling constant	52.7–77.5	K	Calculated

9. Comparison of Model Predictions with Experimental Confirmations

10. Discussion

10.1. Agreement with Model Predictions [1] The numerical values of the parameters obtained in this work agree with the theoretical predictions of [1]:

10.2. Novelty of the Obtained Results In this work, for the first time:

1. A calibration of the parameters of the universal dissipative metabolism model [1] was performed using modern data on human ATP synthase and verified literature sources from 2023–2025.
2. Schrödinger's principle was quantitatively confirmed on a molecular machine using modern data [4, 8], showing that the isolated c-ring reaches the quantum limit, while the whole enzyme does not.
3. Universal constants γ_g, α_{total} were obtained for calibrating the model [1], with ranges of values and degrees of certainty indicated.
4. The interpretation of the quantum rotation limit and suppression factors was refined considering current structural and biophysical data.

10.3. Limitations

1. **Absence of Fo-domain coordinates in PDB 8H9L:** a full calculation of the density of vibrational states for human ATP synthase was not performed in this work. Only a conceptual approach is presented.

Таблица 6Verification of theorems from the model [1]

Theorem from [1]	**Prediction**	**Experimental Confirmation**
Theorem 2 (survival criterion)	The system remains viable in the presence of negative feedback through state parameters	The rotational coupling between the fast Fo and slow F1 provides a feedback mechanism: an increase in Fo rotation speed leads to increased load from F1, which limits further acceleration and stabilizes the system in the classical regime [4, 8]. This corresponds to the negative feedback predicted by the model.
Theorem 5 (on the cascade of evolutionary explosions)	Suppression of quantum fluctuations occurs in large aggregates	The isolated c-ring reaches the theoretical quantum rotation limit ($\sim$ 43,000 rps) [4, 8], while the whole ATP synthase does not. The suppression factor is 10^{-3}–10^{-2}, which quantitatively confirms the principle of collective suppression of quantum effects predicted by Schrödinger [4, 7, 8].
Theorem 6 (on spectral density)	The fluctuation spectrum $p(\nu)$ has a form isomorphic to Planck's formula	A conceptual three-component model for the density of vibrational states $D(\nu)$ is proposed. The calculated characteristic frequency $\nu_{\text{char}} \approx 1.01 \times 10^{13}$ Hz (337 cm^{-1}) falls in the mid-IR range, where collective vibrations of protein globules are expected. Experimental verification is required.

Таблица 7Comparison with model predictions

Parameter	**Prediction [1]**	**Measured/Estimated Value**	**Discrepancy**
α_{total}	$0 < \alpha_{\text{total}} < 1$	0.17–0.25	—
ε_0	On the order of 10^{-20}–10^{-19} J	3.2×10^{-20} J	—
γ_g	$1/L_0^2$	2.8×10^{16} m^{-2}	—
ν_{char}	$\sim 10^{13}$ Hz	1.01×10^{13} Hz	—

2. **Stationarity approximation:** estimates are based on the assumption of a steady state.
3. **Variability of the H^+/ATP ratio:** different sources give values from 3.3 to 4.7, introducing uncertainty into the energy estimates.
4. **Estimation of the protein globule volume:** performed approximately and could be refined if a complete structure were available.

11. Experimental Predictions

Based on the obtained parameters, the model [1] makes the following testable predictions:

1. **Characteristic frequency** in the fluctuation spectrum of ATP synthase: $\nu_{\text{char}} \approx 1.01 \times 10^{13}$ Hz ($\tilde{\nu}_{\text{char}} \approx 337$ cm^{-1}, mid-IR) — could be detected by high-resolution IR spectroscopy of mitochondria in the 200–500 cm^{-1} range.
2. The **suppression factor** of 10^{-3}–10^{-2} for whole ATP synthase is specific to this enzyme and may differ for other molecular machines depending on their structure and size. Verification requires measuring the rotation speed of other rotary molecular motors in isolation and within

the complex.

3. The **quadratic frequency dependence** of the density of vibrational states in the acoustic branch: $D_{\text{ac}}(\nu) \sim \nu^2$ — could be verified by inelastic neutron or X-ray scattering methods.

Conclusion

This work presents an **experimental calibration of the universal dissipative metabolism model** developed in [1]. The main results are:

1. **Numerical values of the model's key parameters** for human ATP synthase were determined based on current literature data:
   - Reinvestment efficiency $\alpha_{\text{total}} = 0.17^{\smile}0.25$
   - Quantum energy (per proton) $\varepsilon_0 = 3.2 \times 10^{-20}$ J
   - Variability constant $\gamma_g = (2.8 \pm 0.5) \times 10^{16}$ m^{-2}
   - Characteristic spectrum frequency $\nu_{\text{char}} \approx 1.01 \times 10^{13}$ Hz (337 cm^{-1})
2. **Structural data** PDB 8H9L / EMDB EMD-34572 [2, 10] were **verified**, establishing the absence of Fo-domain coordinates in the model, which defines directions for future research.
3. **Schrödinger's principle (Theorem 5) was quantitatively confirmed**: it was shown that the isolated c-ring reaches the theoretical quantum rotation limit ($\sim 43,000$ rps) [4, 8], but within the whole enzyme, rotation slows down by 1–3 orders of magnitude due to collective effects, directly confirming Schrödinger's prediction about the suppression of quantum fluctuations in large molecular aggregates [4, 7, 8].
4. **Experimentally testable predictions** were proposed, including a characteristic frequency in the mid-IR range (337 cm^{-1}).

The obtained values can be directly substituted into the dynamic equations (1) of the model [1] and used for quantitative modeling of evolutionary, economic, and social processes, where ATP synthase serves as a reference example of a dissipative system with reinvestment.

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Pavel A. Polyukov — author of the theorem of inevitable death. Research interests: thermodynamics of complex systems, synergetics, mathematical modeling of biological and social processes, theory of dissipative structures, bioenergetics, molecular machines. Born 26.10.1972 in Moscow.
E-mail: polyukov.pavel@yandex.ru
ORCID: 0009-0003-3370-1348