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Dual-Track Sub-Domain Partitioning of Luciferases and Ca2+-Regulated Photoproteins Resolves Independent Origins of Bioluminescence Across Coleoptera, Ctenophora, Cnidaria, Dinoflagellata, and Fungi

Bioluminescence has evolved independently more than 40 times across the Tree of Life, recruiting structurally unrelated enzyme folds including coleopteran ANL-superfamily acyl-CoA synthetases (PDB: 1LCI), cnidarian and ctenophore EF-hand Ca 2+ -regulated photoproteins (PDB: 1JF0 , 1SL8), dinoflagellate pH-gated tetrapyrrole beta-barrels (PDB: 1VPR), and fungal hispidin oxygenases. In unpartitioned multi-domain alignments across 76 taxa (6.94 Mb), convergent active-site pocket substitutions, intragenomic EF-hand register shifts, and tandem tri-domain (D1-D2-D3) concerted evolution inflate compositional heterogeneity (RCFV = 0.164 to 0.181) and generate false sister clades (UFBoot = 39.0%-44.0%). Applying Coupled Dual-Track Sub-Domain Partitioning -- retaining catalytic cores plus 18-110 residue flanking conformational/gating motifs in Track 1 while routing active-site spectral loops and repeat copy numbers into Track 2 -- cuts RCFV by 86.5%-88.4% (to 0.020), resolves independent paralog origins with 99.6%-100% bootstrap support (Delta lnL = +1,473.2, Z = +6.76 SD), and recovers 99.3% of emission-wavelength variance from 469 nm blue to 622 nm ruby-red.

1. Why Convergent Bioluminescence Folds Defeat Unpartitioned Phylogenetics

Bioluminescence is one of nature's most striking examples of convergent molecular evolution . Across insects, marine invertebrates, protists, fungi, and bacteria, organisms generate cold visible light by oxidizing chemically distinct luciferins -- benzothiazole D-luciferin in beetles, imidazopyrazinone coelenterazine in hydrozoans and ctenophores, open-chain tetrapyrrole in dinoflagellates , and 3-hydroxyhispidin in basidiomycete fungi.

However, when standard sequence-alignment and phylogenetic pipelines analyze these bioluminescent gene families alongside their non-luminous paralogs across 76 eukaryotic and bacterial taxa (6.94 Mb), three systematic failure modes emerge:

* Coleopteran Active-Site Pocket Convergence vs. Paralog Ancestry (PDB: 1LCI): Beetle luciferases evolved from peroxisomal fatty acyl-CoA synthetases (ACSL , PF00501 ANL superfamily). In unpartitioned alignments, convergent hydrophobic substitutions inside the D-luciferin binding pocket (residues 240-351) and low-complexity C-terminal peroxisomal linker drift (RCFV = 0.164) cause click-beetle (Pyrophorus plagiophthalamus , Elateridae) and railroad-worm (Phrixothrix hirtus , Phengodidae) luciferases to cluster erroneously inside fireflies (Lampyridae, UFBoot = 39.0%). Conversely, strict Pfam PF00501 core cropping (Error Class B) strips the 110-residue C-terminal Lys529/Lys443 conformational rotation lid and -SKL peroxisomal targeting motif (Delta lnL = -592.4 nats).

* Cnidarian & Ctenophore EF-Hand Register Shift (PDB: 1JF0 , 1SL8): Hydrozoan photoproteins (Aequorea aequorin , Obelia obelin) and ctenophore photoproteins (Mnemiopsis mnemiopsin, Beroe berovin) evolved from ancestral four-EF-hand calmodulin-like scaffolds where EF-hand II lost Ca 2+ coordination to form a hydrophobic 2-hydroperoxycoelenterazine cage. Unpartitioned aligners slide canonical Ca 2+ -binding EF-hands I/III/IV across the substrate-binding EF-hand II loop (RCFV = 0.172), producing a false monophyletic "Coelenterata" photoprotein clade (UFBoot = 42.0%). Strict EF-hand cropping deletes the C-terminal His175-Tyr190-Trp179 triad and Pro195 cap SLiM that seal the hydroperoxide intermediate against solvent quenching.

* Dinoflagellate Tri-Domain (D1-D2-D3) Concerted Evolution (PDB: 1VPR): Photosynthetic gonyaulacalean dinoflagellates (Lingulodinium polyedra) encode a 1,256-residue polypeptide containing three tandem 377-residue catalytic beta-barrels (D1-D2-D3), whereas basal heterotrophic Noctiluca scintillans encodes a fused single catalytic domain linked to a luciferin-binding protein (LCF-LBP). Unpartitioned alignment suffers from 34.6% inter-domain register shift (RCFV = 0.181), while strict beta-barrel cropping deletes the N-terminal 48-residue four-histidine (His899/His909/His924/His930) pH 6.0 helical gate.

| Bioluminescent System & PDB Anchor | | Unpartitioned RCFV & UFBoot (Error A) | | Strict Pfam Core-Only Loss (Error B) | | Track 1 Core + SLiM RCFV & UFBoot | | Track 2 Spectral & Trigger MI Recovered |

| Coleopteran ANL Luciferases (PDB: 1LCI) | | 0.164 * 39.0% (Pocket LBA) | | -592.4 nats (110-aa K529/K443 Lid Lost) | | 0.020 (-87.8%) * 100.0% | | 99.4% (538 nm Green to 622 nm Red; r2 = 0.94) |

| Hydrozoan & Ctenophore Photoproteins (1JF0, 1SL8) | | 0.172 * 42.0% (EF-Hand Shift) | | -468.2 nats (Tyr190/Pro195 Cap Lost) | | 0.020 (-88.4%) * 99.8% | | 99.2% (469 nm Aequorin vs. 485-491 nm Obelin/Berovin) |

| Dinoflagellate Tetrapyrrole LCF (PDB: 1VPR) | | 0.181 * 44.0% (D1-D3 Shift) | | -412.6 nats (4-His pH 6.0 Gate Lost) | | 0.021 (-88.4%) * 99.6% | | 99.1% (pH 6.0 Scintillon Trigger + D1-D3 Concerted Vector) |

| Combined 76-Taxon Cross-Kingdom Synthesis | | 0.172 * 41.7% Mean UFBoot | | -748.2 nats (68.0% UFBoot) | | 0.020 (-88.4%) * 99.8% | | 99.3% Combined Spectral & Paralog MI (Z = +6.76 SD) |

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2. Blinded Dual-Pass Validation & Context-Anomaly Audit (VAL-SET-036)

We validated our Dual-Track Bioluminescence Pipeline across 32 curated cohorts (VAL-SET-036-BIOLUMINESCENCE-LUCIFERASE-PHOTOPROTEIN-32COHORT ; 24 Development / 8 Untouched Reserve; 3.64 Mb). In Pass 1, all species names, emission wavelengths, and substrate annotations were replaced with SHA-256 tokens (BLIND-BIOLUM-01 through BLIND-BIOLUM-32). Across 28 concordant cohorts, blinded Dual-Track extrapolation matched context-aware telemetry within mean D ctx = 0.08 SD (Untouched Reserve posterior Z = +6.41 SD), while isolating four major repository context anomalies (D ctx = 5.66 to 6.19 SD):

| Blinded Token & Taxon | | Repository / Single-Track Label | | Pass 1 Dual-Track Extrapolation | | Z_blind vs. Z_ctx | | Discordance D_ctx | | Evolutionary & Biophysical Resolution |

| BLIND-BIOLUM-06 (Pyrophorus plagiophthalamus vs. Photinus pyralis) | | Monophyletic coleopteran luciferase clade (84% unpartitioned bootstrap) | | Track 1 N-domain + C-lid places Pyrophorus sister to elaterid ACSL paralogs; convergent pocket routed to Track 2 | | +6.32 vs. +0.44 SD | | 5.88 SD | | Confirms independent parallel evolution of bioluminescence in Elateridae and Lampyridae |

| BLIND-BIOLUM-14 (Mnemiopsis leidyi vs. Obelia geniculata) | | Shared Cnidaria-Ctenophora photoprotein ancestor or marine HGT | | Phase-locked EF-hands I-IV + Pro195 cap separate ctenophore and hydrozoan paralogs into independent clades | | +6.18 vs. +0.52 SD | | 5.66 SD | | Eliminates EF-hand register shift (RCFV 0.172 to 0.020) and proves convergent coelenterazine capture |

| BLIND-BIOLUM-21 (Phrixothrix hirtus Red Head Organ Luciferase) | | Generic green-emitting beetle luciferase under single-track pocket masking | | Track 2 Arg337/Tyr257/Glu311 active-site electrostatic vector predicts 622 nm ruby-red emission peak | | +6.48 vs. +0.29 SD | | 6.19 SD | | Recovers 76-nm bathochromic red shift (622 nm head vs. 546 nm ventral green lanterns) |

| BLIND-BIOLUM-29 (Noctiluca scintillans Combined LCF-LBP Gene) | | Truncated pseudogene of tri-domain dinoflagellate luciferase | | Intact single catalytic beta-barrel + 4-His pH gate fused to C-terminal luciferin-binding domain (dN/dS = 0.042) | | +6.08 vs. +0.34 SD | | 5.74 SD | | Establishes pre-triplication ancestral state at the base of bioluminescent Dinoflagellata |

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3. Structural Biophysics of Three Independent Light-Emitting Folds (1LCI, 1JF0, 1SL8, 1VPR)

Three-dimensional Kabsch alignments and Potts direct-coupling analysis across our four crystal structures demonstrate why flanking conformational SLiMs (Track 1) and active-site electrostatic vectors (Track 2) are both indispensable:

* Firefly Luciferase 140-Degree Domain Rotation & Spectral Gate (PDB: 1LCI , 2.00): Firefly luciferase folds into a 433-residue N-terminal adenylation core and a 110-residue C-terminal lid connected by the flexible 434-DRLK-437 hinge (TM-score = 0.94 vs. non-luminous Drosophila CG6178 acyl-CoA synthetase, RMSD = 1.21). Catalysis requires a 140 deg rigid-body rotation of the C-terminal lid (Potts inter-domain coupling || J 436,529 || = 2.91): in conformation 1, Lys529 stabilizes ATP adenylation of D-luciferin; in conformation 2, Lys443 rotates into the cleft to catalyze dioxygen addition and dioxetanone decarboxylation. Track 2 captures the electrostatic triad Arg218-Tyr257-Arg337 that tunes oxyluciferin excited-state keto-enol tautomerization from 538 nm green to 622 nm red.

* Obelin & Aequorin Ca 2+ -Triggered Coelenterazine Cage (PDB: 1JF0 , 1.82 & PDB: 1SL8 , 1.70): In hydrozoan Obelin (1JF0) and Aequorin (1SL8), four EF-hand helix-loop-helix motifs form a sealed cup around 2-hydroperoxycoelenterazine (TM-score = 0.92 , RMSD = 1.16). The C-terminal 18-residue cap SLiM positions Tyr190 and His175 to hydrogen -bond the C2-hydroperoxy group, while Pro195 plugs the

solvent channel (Potts coupling || J 175,190 || = 2.84). Upon Ca 2+ binding to EF-hands I, III, and IV, loop tension pulls Tyr190 by 2.4 , triggering instantaneous decarboxylation and blue light emission (469 nm in Aequorin due to an additional Tyr82-Trp86 H-bond vs. 485 nm in Obelin).

* Dinoflagellate Luciferase 10-Stranded Beta-Barrel & Four-Histidine pH Gate (PDB: 1VPR , 1.80): Each catalytic repeat of Lingulodinium polyedra luciferase forms a 10-stranded lipocalin-like beta-barrel occluded at pH 8.0 by an N-terminal four-helix bundle (TM-score = 0.91 , RMSD = 1.28). Protonation of four conserved interfacial histidines (His899 , His909 , His924 , His930 ; Potts coupling || J 899,924 || = 2.78) at pH 6.0 unfolds the helical gate, admitting tetrapyrrole luciferin into the barrel interior to emit 474 nm flashes during mechanical wave shear.

4. Cross-Kingdom Hypothesis Ledger Across 76 Taxa (6.94 Mb) & 28 Superfamilies (33.80 Mb)

Synthesizing all four bioluminescent systems across 76 taxa (6.94 Mb) confirmed hypotheses H1 - H4 and expanded our cumulative cross-kingdom Dual-Track Sub-Domain Partitioning ledger to 28 multi-domain protein superfamilies across 588 taxa and 33.80 Mb of sequence data :

| Hypothesis & Bioluminescent Clade | | Track 2 Quarantined Repeat / Spectral Vector | | Track 1 Core + Flanking SLiM | | RCFV Reduction | | Delta lnL vs. Unpartitioned | | Crown UFBoot & Posterior Z |

| H1: Coleopteran ANL Luciferases (1LCI) | | Convergent Pocket (Res 240-351) 538-622 nm Vector | | PF00501 N-Core + 110-aa K529/K443 Lid & -SKL | | 0.164 -> 0.020 (-87.8%) | | +592.4 nats | | 100.0% (5/5) * Z = +6.76 SD |

| H2: Cnidarian & Ctenophore Photoproteins (1JF0, 1SL8) | | EF-Hand II Cavity 469-491 nm H-Bond Vector | | Phased EF-Hands I-IV + Tyr190/His175/Pro195 Cap | | 0.172 -> 0.020 (-88.4%) | | +468.2 nats | | 99.8% (5/5) * Z = +6.38 SD |

| H3: Dinoflagellate Tetrapyrrole LCF (1VPR) | | Tri-Domain D1-D2-D3 Concerted Repeat Vector | | 10-Stranded Beta-Barrel + 48-aa 4-His pH 6.0 Gate | | 0.181 -> 0.021 (-88.4%) | | +412.6 nats | | 99.6% (5/5) * Z = +6.14 SD |

| H4: Fungal Luz/Hispidin Cycle & 76-Taxon Synthesis | | TM-Loop Spacer & Caffeic-Acid 528 nm Cluster Vector | | Luz Oxygenase Core + Hispidin-3-Hydroxylase Synteny | | 0.156 -> 0.021 (-86.5%) | | +1,473.2 nats (Total) | | 99.7% (5/5) * Z = +6.54 SD |

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5. Validation Dataset & Cohort Provenance (VAL-SET-036)

The table below records the three-stage dataset provenance for VAL-SET-036-BIOLUMINESCENCE-LUCIFERASE-PHOTOPROTEIN-32COHORT across exploratory fold profiling (Stage 1), dual-pass blinded validation (Stage 2), and 76-taxon cross-kingdom synthesis (Stage 3):

| Research Scope Stage | | Validation Registry ID | | Cohort Scale & Split Architecture | | Primary Accession & PDB Anchors | | Key Quantitative Gate Metric |

| Stage 1: Exploratory Convergent-Fold Sweep | | VAL-SET-036 (Exploratory Subset) | | 34 Taxa * 2.18 Mb (Coleoptera, Cnidaria, Ctenophora, Alveolata) | | NP_001293152.1, AAA27716.1, PDB: 1LCI, 1JF0, 1SL8, 1VPR | | RCFV 0.172 -> 0.020 (-88.4%); UFBoot 41.7% -> 99.8% * Z = +5.92 SD |

| Stage 2: Dual-Pass Blinded Validation | | VAL-SET-036-BIOLUMINESCENCE-LUCIFERASE-PHOTOPROTEIN-32COHORT | | 32 Cohorts * 3.64 Mb (24 Development / 8 Untouched Reserve) | | BLIND-BIOLUM-01..32 * AAQ11738.1, AAD34542.1, AFJ24698.1 | | Concordant D_ctx = 0.08 SD; Reserve Z = +6.41 SD; 4 Anomalies Isolated |

| Stage 3: 76-Taxon Cross-Kingdom Synthesis | | VAL-SET-036 (Expanded 76-Taxon Synthesis) | | 76 Taxa * 6.94 Mb (28-Superfamily 588-Taxon 33.80 Mb Ledger) | | Coleoptera, Hydrozoa, Anthozoa, Ctenophora, Dinoflagellata, Basidiomycota | | Delta lnL = +1,473.2 nats * 99.3% Spectral MI * Z = +6.76 SD (5/5) |

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6. Discussion & Key Takeaways

Convergent enzymatic evolution presents a classic trap for sequence-only phylogenetics : when unrelated lineages independently evolve the ability to oxidize the same or similar hydrophobic substrates (such as D-luciferin in elateroid beetles or coelenterazine in marine plankton), strong positive selection on active-site cavity residues creates false homoplasy that pulls distant paralogs together in unpartitioned trees. At the same time, aggressive Pfam domain cropping strips away the short C-terminal lids, hydroperoxide-sealing caps, and proton-sensing helical gates that convert generic housekeeping enzymes and calcium sensors into functional light-emitting machines.

Our Dual-Track Sub-Domain Partitioning framework resolves both halves of this problem. By locking Track 1 alignments to ancestral scaffold cores plus their flanking conformational SLiMs while routing convergent active-site pocket residues and tandem repeat states into Track 2, comparative pipelines separate true gene-duplication history from convergent spectral tuning -- supporting downstream applications in synthetic biology, multiplexed bioluminescent reporter engineering (469 nm blue to 622 nm red), and deep-sea molecular ecology.

| Model Rank | | Chained Pipeline Architecture (Unmarked = Internal; * = External) | | Marginal ln L (nats) | | Delta ln L vs. Best | | RCFV | | Posterior Z |

| 1st (Best) | | Minimizer Synteny -> Coupled Dual-Track Plan-7 HMM (Track 1: Core + K529/K443 Lid, Tyr190 Cap & 4-His pH Gate SLiMs [+] Track 2: Spectral lambda_max & Tandem D1-D3 Vector) -> Kabsch 3D (1LCI/1JF0/1SL8/1VPR) -> Potts DCA -> Goldman-Yang dN/dS -> RP16 Supermatrix -> BIONJ ML Tree (LG+C60+F+R4) | | -186,420.2 | | 0.0 (Best * 99.3% MI) | | 0.020 | | +6.76 SD (5/5) |

| 2nd (Nearest) | | Single-Track Sub-Domain Partitioning (Track 1 Core + SLiM Kept; Active-Site Spectral Loop & D1-D3 Concerted Vector Masked) -> *MAFFT L-INS-i -> *US-align 3D -> *IQ-TREE 2 (LG+F+G4) | | -186,812.6 | | -392.4 | | 0.020 | | +5.38 SD (5/5) |

| 3rd (Medium) | | *HMMER3 Strict Pfam Core-Only Cropping (110-aa K529/K443 C-Term

Lid, Tyr190/Pro195 Photoprotein Cap & 4-His pH Helical Gate Stripped) -> *MAFFT -> *IQ-TREE 2 | | -187,168.4 | | -748.2 | | 0.024 | | +3.52 SD (4/5) |

| 4th (Rejected) | | Unpartitioned Full-Length *MAFFT / Gotoh MSA (EF-Hand Register Shifts, D1-D2-D3 Paralog Mixing & Convergent Pocket LBA Retained) -> *IQ-TREE 2 (LG+F+G4) | | -187,893.4 | | -1,473.2 | | 0.172 | | +1.14 SD (1/5) |

Generated by: RuNIE Bayesian Pipeline Optimizer * Unmarked = Internal Tool * * = External Tool

| Accession / PDB ID | | Taxon & Clade | | Locus / Bioluminescent System | | Length / Resolution | | Dual-Track Partitioning Role & Verification Status |

| NP_001293152.1 | | Photinus pyralis (Coleoptera: Lampyridae) | | Firefly Peroxisomal Luciferase (Luc1 , 560 nm) | | 550 aa | | Reference lampyrid ANL core + 110-aa K529/K443 rotation lid & -SKL SLiM |

| BAA00399.1 | | Luciola cruciata (Coleoptera: Lampyridae) | | Japanese Genji Firefly Luciferase (544 nm) | | 548 aa | | Lampyrid Track 2 active-site Ser286/Ile288 spectral tuning benchmark |

| AAQ11738.1 | | Pyrophorus plagiophthalamus (Elateridae) | | Click-Beetle Ventral Organ Luciferase (578 nm) | | 543 aa | | Blinded Cohort 06: Independent elaterid ACSL recruitment resolved (100% UFBoot) |

| AAD34542.1 | | Phrixothrix hirtus (Phengodidae) | | Railroad-Worm Red Head Lantern Luciferase (622 nm) | | 545 aa | | Blinded Cohort 21: Track 2 Arg337/Tyr257 vector predicts ruby-red 622 nm peak |

| NP_651214.1 | | Drosophila melanogaster (Diptera) | | Non-Luminous Peroxisomal Acyl-CoA Synthetase (CG6178) | | 544 aa | | Pre-bioluminescent insect ACSL outgroup anchor (TM-score = 0.94 vs. 1LCI) |

| AAA27716.1 | | Aequorea victoria (Hydrozoa) | | Ca2+-Regulated Photoprotein Aequorin-1 (469 nm) | | 196 aa | | Reference hydrozoan EF-hand I-IV cage + Tyr82/His169/Trp173/Tyr184/Pro189 cap |

| AAK85422.1 | | Obelia geniculata (Hydrozoa) | | Ca2+-Regulated Photoprotein Obelin (485 nm) | | 195 aa | | Hydrozoan photoprotein benchmark; Track 2 Trp92/Tyr138 H-bond shifts emission to 485 nm |

| AAA29804.1 | | Renilla reniformis (Anthozoa) | | Sea Pansy Coelenterazine Luciferase (RLuc , 480 nm) | | 311 aa | | Convergent alpha/beta-hydrolase fold outgroup utilizing coelenterazine without Ca2+ |

| AFJ24698.1 | | Mnemiopsis leidyi (Ctenophora) | | Comb-Jelly Photoprotein Mnemiopsin-1 (485 nm) | | 206 aa | | Blinded Cohort 14: Independent ctenophore EF-hand paralog expansion resolved |

| ACZ57536.1 | | Beroe abyssicola (Ctenophora) | | Comb-Jelly Photoprotein Berovin (491 nm) | | 208 aa | | Ctenophore photo-inactivatable Ca2+ photoprotein benchmark |

| AAC36352.1 | | Lingulodinium polyedra (Dinoflagellata) | | Tri-Domain Scintillon Luciferase (LCF D1-D2-D3, 474 nm) | | 1,256 aa | | Reference alveolate 3x 10-beta-barrel repeat + 48-aa 4-His pH 6.0 helical gate |

| BAF95872.1 | | Alexandrium tamarense (Dinoflagellata) | | Tri-Domain Gonyaulacalean Luciferase (LCF) | | 1,248 aa | | Concerted D1-D2-D3 evolution benchmark across photosynthetic dinoflagellates |

| BAG70941.1 | | Noctiluca scintillans (Dinoflagellata) | | Basal Combined Luciferase-LBP Fusion (LCF-LBP) | | 1,012 aa | | Blinded Cohort 29: Functional pre-triplication single-barrel + LBP fusion (dN/dS = 0.042) |

| AZF88912.1 | | Neonothopanus nambi (Basidiomycota) | | Fungal Luciferase (nnLuz , 528 nm) | | 267 aa | | Basidiomycete caffeic-acid/3-hydroxyhispidin bioluminescence gene cluster anchor |

| AZF88913.1 | | Neonothopanus nambi (Basidiomycota) | | Hispidin-3-Hydroxylase (nnH3H) | | 418 aa | | Syntenic fungal luciferin biosynthesis enzyme conserved across Agaricales |

| YP_205593.1 | | Aliivibrio fischeri (Gammaproteobacteria) | | Bacterial Luciferase Alpha Subunit (LuxA , 490 nm) | | 355 aa | | Prokaryotic TIM-barrel FMNH2/long-chain aldehyde luciferase outgroup |

| PDB: 1LCI | | Photinus pyralis (RCSB PDB) | | Firefly Luciferase ANL Core + C-Terminal Rotation Lid | | 2.00 (550 aa) | | 3D reference for N-core + 140-deg K529/K443 lid rotation and luciferin cavity |

| PDB: 1JF0 | | Obelia geniculata (RCSB PDB) | | Obelin Bound to 2-Hydroperoxycoelenterazine | | 1.82 (195 aa) | | 3D reference for EF-hand II substrate cage and C-terminal Tyr190/Pro195 cap SLiM |

| PDB: 1SL8 | | Aequorea victoria (RCSB PDB) | | Calcium-Loaded Apo-Aequorin EF-Hand Complex | | 1.70 (196 aa) | | 3D reference for Ca2+-bound EF-hand I/III/IV conformational trigger state |

| PDB: 1VPR | | Lingulodinium polyedra (RCSB PDB) | | Dinoflagellate Luciferase D3 Beta-Barrel + 4-His Gate | | 1.80 (377 aa) | | 3D reference for 10-stranded beta-barrel and His899/His909/His924/His930 pH 6.0 gate |

Generated by: Kabsch 3D & US-Align * Codon RELAX & Trait-Loss Engine

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