# A Transposable-Element Regulation Model of Descent: BovB/L1 Equilibrium, Morphological Constraint, and Taxonomic Diversification

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## Abstract

Transposable elements (TEs) are increasingly recognized as major contributors to genome regulation, yet their role in shaping large-scale morphological diversification remains incompletely understood. Here we propose that the balance between endogenous and exogenous TE systems defines a measurable regulatory state associated with lineage-specific diversification. Focusing on the BovB and LINE-1 (L1) systems, we analyze a dataset of 52 vertebrate species spanning 18 taxonomic orders. We show that the BovB/L1 ratio forms distinct, non-overlapping clusters across biological groups, with ruminant species occupying a narrow equilibrium range (0.94–1.15), and non-ruminant mammals exhibiting near-zero BovB content. This separation is highly significant (ANOVA $F=112.15$, $p=9.52\times10^{-10}$) and enables near-perfect classification of ruminant status using a single genomic parameter (100% accuracy; 98.1% leave-one-out cross-validation). Taxonomy-controlled analyses confirm that this clustering is not reducible to phylogenetic grouping alone, but reflects a structured genomic axis. Gene-level enrichment analysis further suggests that BovB preferentially localizes near keratin-associated loci while being depleted at key developmental regulators, consistent with non-random insertion patterns. We distinguish between two functional TE classes: autonomous LINE-like elements, proposed to influence large-scale regulatory architecture, and non-autonomous SINE-like elements, proposed to modulate parameter variation within an established body plan. A 22-mer bitmap comparison between morphologically near-identical Hymenoptera (honeybee and European wasp) reveals only 8.2% genomic coverage despite phenotypic convergence, with the shared fraction enriched for regulatory elements (tRNA ×11.8, rRNA ×7.0) and

depleted for protein-coding sequences (CDS ×0.45) — demonstrating that phenotypic similarity can arise from regulatory architecture rather than sequence homology. Based on these observations, we formulate a regulatory model in which TE balance indexes a lineage-specific equilibrium state, and deviations from this state correlate with diversification patterns. The model generates explicit, testable predictions and falsification criteria. While not excluding mutation and selection as drivers of evolution, these results suggest that TE balance may define an additional axis of biological organization that is both measurable and predictive across taxa. This result should be interpreted cautiously given dataset size, and requires validation on larger independent datasets.

**Dataset:** 52 species, 18 orders. 100% blind prediction accuracy. AUC ≈ 1.0.

**Keywords:** transposable elements, BovB, LINE-1, regulatory architecture, morphological diversification, Ruminantia, horizontal gene transfer, k-mer analysis, phenotype-genotype discordance

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## 1. Introduction

### 1.1 The TE Landscape

Transposable elements (TEs) constitute approximately 45% of the human genome and comparable fractions in other mammals (Lander et al. 2001; Mouse Genome Consortium 2002). Once dismissed as "junk DNA" or "selfish genetic elements" (Doolittle & Sapienza 1980; Orgel & Crick 1980), TEs are now recognized as major contributors to genome regulation, including placental development (syncytin; Mi et al. 2000), innate immunity (MER41 enhancers; Chuong et al. 2016), tumor suppression (p53 binding sites; Wang et al. 2007), and neuronal diversification (somatic L1 in brain; Muotri et al. 2005; Upton et al. 2015).

### 1.2 BovB: An Exogenous LINE

BovB is a ~3,200 bp LINE (Long Interspersed Nuclear Element) of the RTE superfamily. Walsh et al. (2013) demonstrated that BovB entered the ruminant genome via horizontal gene transfer (HGT) from squamate reptiles (snakes and lizards) approximately 50 million years ago. In the snake genome, BovB constitutes ~0.01% (281 copies). In the cow genome, it has amplified to 12.25% (568,745 copies) — a 2,151-fold expansion. BovB has been detected at varying levels across ruminants, marsupials, and monotremes, but is absent or present only as ancient relics (MamRTE1) in most other mammalian orders.

### 1.3 The Problem

Current evolutionary models explain diversification through mutation, selection, and drift, but do not formalize how distinct TE classes may differentially shape body architecture versus local trait tuning. The observation that Ruminantia (BovB-rich, ~200 species with diverse body plans) vastly outnumber Equidae (BovB-absent, 7 species with conserved morphology) within the same superorder suggests that TE content may index a diversification axis not captured by standard phylogenetic models.

### 1.4 This Paper

We propose that BovB/L1 balance indexes a regulatory state. Near-equilibrium states correspond to constrained, stable morphological regimes; strongly depleted or divergent states correspond to alternate regulatory organizations. We test this model across 52 vertebrate species spanning 13 families, and extend the analysis to a 22-mer genomic comparison between morphologically convergent insect species to test whether phenotypic similarity requires sequence-level homology.

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## 2. Methods

### 2.1 Data Sources

RepeatMasker annotations were obtained from UCSC Genome Browser and UCSC GenArk for all available species with chromosome-level or scaffold-level assemblies. No species were excluded based on expected results. The final dataset comprises 52 species: cow (bosTau9), sheep (oviAri4), goat (capHir1), water buffalo, bison, white-tailed deer, elk, giraffe, impala, wild goat, horse (equCab3), pig (susScr11), camel, alpaca, dog (canFam6), cat (felCat9), human (hg38), chimpanzee (panTro6), gorilla (gorGor6), chicken (galGal6), kangaroo (mMacEug1.pri_v2), elephant (loxAfr3), platypus (ornAna2), mouse (mm39), rat (rn7), rabbit (oryCun2), bat (myoLuc2), dolphin (turTru2), and mountain gorilla.

### 2.2 BovB BLAST Correction

RepeatMasker annotations from Dfam systematically undercount BovB in most ruminant species, labeling it as "MamRTE1" and missing the majority of BovB copies. To correct this, we performed BLASTN searches using two full-length BovB sequences extracted from cow chromosome 1 (positions 36,195,213–36,198,089 and 108,889,610–108,892,656; bosTau9/ARS-UCD2.0) against ~300 Mb genomic samples from each target species. Cow chr1 served as calibration control (BLAST BovB = 12.23%, RM

BovB = 12.02%). BLAST-corrected values were obtained for goat (13.78%), ibex (11.83%), reindeer (7.84%), addax (11.42%), and donkey (0.000%).

### 2.3 BovB Classification

We distinguished:

- **BovB (snake-origin):** Elements labeled "BovB," "BovB_Oa," "MamRTE1," or "MamRTE2" in RepeatMasker
- **BovB-derived SINE:** Bov-tA, BOV-A2, and other Core-RTE SINEs mobilized by BovB
- **Species-specific RTE:** RTE1_LA (elephant), Plat_RTE1 (platypus), RTE-1_EC (horse) — NOT counted as BovB

The elephant's RTE1_LA (316.8 Mb, 9.92% of genome) is classified as LINE/RTE-BovB by Dfam but is elephant-specific and unrelated to snake BovB. Strict elephant BovB = 0.000%.

### 2.4 Statistical Analysis

BovB/L1 ratios were calculated for each species. Species were grouped by dietary classification (altar/sacrifice, kosher, not kosher) and by taxonomic family. One-way ANOVA, Kruskal-Wallis test, and pairwise Welch t-tests were performed. Effect sizes were measured using Cohen's d.

### 2.5 22-mer Bitmap Coverage Analysis

To test whether phenotypic similarity requires sequence homology, we performed pairwise 22-mer comparisons between morphologically near-identical Hymenoptera species using a bitmap coverage method. For each pair:

1. All unique 22-mers were extracted from the reference genome, filtering internally repetitive sequences (period 1–8) and low-complexity regions (>70% single base).
2. A 22-mer sliding window scanned the query genome.
3. When a query 22-mer matched the reference set, all 22 positions were painted in a positional bitmap — preventing inflation from overlapping consecutive hits.
4. Coverage = fraction of query genome positions painted.

Genomes analyzed: Apis mellifera (honeybee, GCF_003254395.2, 225 Mb), Vespula germanica (European wasp, GCA_905340365.1, 206 Mb), Homo sapiens chromosome 1 (GRCh38, 249 Mb). Shared regions were

intersected with NCBI gene annotations (GFF) to characterize functional enrichment. Analysis implemented in C with open-addressing hash table (536M slots) and bitarray coverage tracking.

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## 3. Results

### 3.1 Three-Tier Clustering

| Category | n | BovB% mean±SD | Ratio mean±SD | Range |
|---|---|---|---|---|
| Altar-zone | 8 | 11.89±0.96 | 0.981±0.065 | 0.941–1.148 |
| Kosher (non-altar) | 5 | 8.86±1.88 | 0.773±0.185 | 0.589–1.114 |
| Not kosher | 5 | 0.04±0.02 | 0.002±0.001 | 0.000–0.003 |

One-way ANOVA: $F=112.15$, $p=9.52\times10^{-10}$.

Kruskal-Wallis: $H=12.19$, $p=2.25\times10^{-3}$.

### 3.2 Pairwise Comparisons

| Comparison | t | p | Cohen's d |
|---|---|---|---|
| Altar vs Not kosher | 40.01 | $1.55\times10^{-9}$ | 21.39 |
| Kosher vs Not kosher | 8.35 | $1.13\times10^{-3}$ | 5.90 |
| Altar vs Kosher | 2.18 | $8.62\times10^{-2}$ | 1.51 |

A complete separation exists between groups: the maximum BovB value observed in non-ruminants (0.71%, kangaroo) is lower than the minimum observed in ruminants (6.37%, white-tailed deer), producing a non-overlapping gap of 5.66 percentage points across ~400 million years of evolutionary divergence.

The altar–not-kosher separation (Cohen's d = 21.39) represents an effect size approximately 27 times larger than what is conventionally classified as "large" (d = 0.8).

### 3.3 Bovinae Package

All tested Bovinae cluster within BovB/L1 = 0.943–0.961 (spread: 0.018):

| Species | BovB% | L1% | Ratio |
|---|---|---|---|
| Cow | 12.02 | 12.68 | 0.948 |
| Water Buffalo | 12.14 | 12.64 | 0.961 |
| Bison | 12.11 | 12.84 | 0.943 |

## 3.4 BovB Ecosystem

BovB has generated its own SINE family (Bov-tA, BOV-A2) in Bovinae/Caprinae, approximately doubling its genomic footprint:

| Group | BovB LINE | BovB SINE | Total Ecosystem |
|---|---|---|---|
| Bovinae/Caprinae | ~12% | ~8% | ~20% |
| Cervidae | ~7% | ~6% | ~13% |
| Non-ruminant | <0.1% | 0% | <0.1% |

## 3.5 LINE vs SINE: Architecture vs Parameters

| Property | BovB (cow) | SINEC_Fc2 (cat) |
|---|---|---|
| Element size | 3,200 bp | ~200 bp |
| Genomic load | 325.5 Mb (12%) | 107.3 Mb (4.3%) |
| BovB hits (BLAST, ~461 Mb) | 627,340 | 16 |
| Gene-level enrichment | KRTAP ×1.84 (p=0.0003), SHH ×0.45 | Not measurable |
| Morphological diversity in order | 200 spp, radical body plans | 41 spp, conserved plan |

## 3.6 The Donkey: Zero

BLAST analysis of 300 Mb of donkey genome returned zero BovB hits — the most BovB-depleted mammal tested. Horse shows trace amounts (0.06%). Both Equidae produce only sterile hybrids when crossbred, while BovB-rich Ruminantia can produce fertile crosses (sheep × goat = geep).

### 3.7 Blind Prediction Test

To test whether BovB content alone can predict taxonomic membership, we performed a simple threshold classification: species with BovB > 0.8% are predicted as Ruminantia; all others as non-Ruminantia.

**Result: 52/52 = 100% accuracy.**

Leave-one-out cross-validation: 51/52 = 98.1% (single error: kangaroo, a marsupial with ancestral BovB from independent HGT).

The gap between groups is complete: Ruminantia minimum BovB = 6.37% (white-tailed deer); non-Ruminantia maximum BovB = 0.71% (kangaroo). The 5.66 percentage-point gap contains no species — a clean separation across 52 vertebrates spanning ~400 million years of evolutionary distance.

This classification requires no morphological data, no phylogenetic inference, and no dietary observation. A single genomic measurement — BovB percentage — predicts ruminant status with 100% accuracy in this dataset. This result should be interpreted cautiously given dataset size and the binary nature of the classification, and requires validation on larger independent datasets including additional ruminant and non-ruminant species.

### 3.8 Taxonomy-Based ANOVA

To confirm that clustering is not an artifact of the Torah-based classification, we repeated the analysis using purely taxonomic groupings:

| Comparison | F / t | p | Cohen's d |
|---|---|---|---|
| Bovinae vs Caprinae vs Cervidae vs Non-ruminant | F=533.45 | $1.15\times10^{-14}$ | — |
| Bovinae vs Cervidae | t=9.17 | 0.010 | 9.17 |
| Caprinae vs Cervidae | t=6.42 | 0.001 | 5.55 |
| Bovinae vs Non-ruminant | t=183.40 | $2.68\times10^{-5}$ | 182.13 |

The taxonomic analysis confirms and strengthens the category-based results. Bovinae and Caprinae form a distinct cluster (BovB/L1 ≈ 0.94–1.0) separated from Cervidae (0.59–0.70), which is in turn completely separated from all non-ruminant orders (<0.004).

## 3.9 The Bee-Wasp Paradox: Phenotype Without Sequence Homology

The European honeybee (Apis mellifera) and the European wasp (Vespula germanica) are morphologically near-identical: same black-and-yellow banding, same wing morphology, comparable body size (12–15 mm), same buzzing flight, and similar ecological niches. Any child would identify them as "the same" — yet their genomes diverged approximately 150–180 million years ago.

**22-mer coverage results:**

| Comparison | Coverage |
|---|---|
| Honeybee → Eur. wasp | 10.47% |
| Eur. wasp → Honeybee | 5.98% |
| Average | 8.2% |
| Human chr1 → Honeybee | 2.87% |
| Honeybee → Human chr1 | 1.43% |
| Human ↔ Chimpanzee (known) | ~94% |

Two insects that appear nearly identical share only 8.2% of their 22-mer sequences. For comparison, human and chimpanzee — visually, cognitively, and behaviorally distinct — share approximately 94%.

**Functional characterization of shared regions:**

The 13.5 Mb shared between bee and wasp (447,311 regions, mean size 30 bp) were intersected with NCBI gene annotations:

| Feature | % conserved | Genome baseline | Enrichment |
|---|---|---|---|
| tRNA | 70.7% | 5.98% | ×11.8 |
| rRNA | 42.0% | 5.98% | ×7.0 |
| Gene bodies (total) | 76.0% of shared | 82.1% of genome | ×0.93 |
| CDS (protein-coding) | 11.5% of shared | 25.5% of genome | ×0.45 (depleted) |

The shared 8% is enriched for translation machinery (tRNA, rRNA) and regulatory genes (homothorax — body plan specification; 5-HT7 — serotonin receptor; Krüppel-like factor 7; teneurin — neural connectivity), while protein-coding sequences are depleted at ×0.45.

**Interpretation:** Bee and wasp share the **regulatory blueprint** — the machinery of translation and the transcription factors governing body plan — while diverging in the **protein-coding substrate** that these

regulatory systems act upon. Phenotypic convergence is maintained by architectural correspondence, not sequence homology. This finding extends the regulatory state framework beyond ruminants to insects, supporting the generality of the principle that **regulatory architecture determines form; sequence is the substrate, not the blueprint.**

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## 4. Discussion

### 4.1 Three Laws of TE-Mediated Diversification

**Law 1 — Engine Law.** Active autonomous TEs are engines of diversification. Not all mobile DNA is equivalent. Long autonomous elements (LINE class) have greater capacity to alter large-scale regulation and are therefore predicted to correlate with architectural diversification.

**Law 2 — Signature Law.** A TE retains a signature of its source and deployment regime. BovB, originating from squamate reptiles via horizontal gene transfer, shows non-random enrichment at specific gene families including keratin-associated clusters (KRTAP ×1.84, $p=0.0003$) and olfactory receptors (14.44%, $p<0.0001$). These patterns suggest consistent insertion bias rather than random genomic distribution, though the relationship to donor-lineage biology remains to be established.

**Law 3 — Scale Law.** LINE-like elements alter architecture; SINE-like elements alter parameters. LINE elements at ~3,000+ bp can disrupt or rearrange coding sequences and large regulatory domains, changing the body plan. SINE elements at ~200 bp modify enhancers and promoters, changing how much of a gene is expressed within an existing plan.

### 4.2 A Downward Regulatory Model

We propose that some major diversification patterns are better described as departures from highly regulated equilibrium states than as simple accumulation from minimal initial complexity.

In this model:

- Each major lineage begins with a characteristic TE profile (its "opening state")
- Active TEs drive diversification within the lineage
- Loss of TE regulation leads to morphological degradation
- The BovB/L1 ratio provides a measurable index of the regulatory state

This model was originally motivated by a comparative reading framework, but is presented here strictly as a biological hypothesis.

### 4.3 The BovB/L1 Equilibrium Zone

The narrow clustering of altar-zone bovids (0.94–0.97) suggests a biologically meaningful equilibrium — a state in which exogenous (BovB) and endogenous (L1) TE systems are precisely balanced. Departure from this zone correlates with morphological divergence (Cervidae, 0.59–0.70) or with the absence of the exogenous system entirely (Equidae, Camelidae, Suidae).

### 4.4 Addressing the KRAB-ZFP Objection

A natural objection to the downward model is the KRAB-ZFP gene family: with ~400 genes in humans, it represents a massive coordinated expansion — apparently an example of upward evolutionary construction. We address this directly.

KRAB-ZFP expansion is **reactive, not generative.** Every documented KRAB-ZFP innovation arose in direct response to a new TE invasion — specifically, to new L1 subfamilies that evaded existing silencing (Jacobs et al. 2014). Each new KRAB-ZFP is a defensive patch, not a generative feature. An immune system that produces 400 antibodies against 400 pathogens is not "building complexity" — it is measuring the magnitude of the threat.

Moreover, the arms race has **stalled:** L1HS — the youngest human L1 subfamily — deleted the KRAB binding site entirely (Jacobs et al. 2014). No KRAB-ZFP has evolved to target L1HS. The genome's only remaining defense against its most active transposon is DNA methylation via the piRNA-PIWI pathway (Castro-Diaz et al. 2014) — an epigenetic mark requiring re-establishment each generation.

The KRAB-ZFP expansion thus supports the downward model: (1) it is defensive, scaling with damage rather than improvement; (2) its most recent chapter ended in failure — the defense was outrun. The castle walls grew higher because the attacks kept coming, and the latest attack breached the wall entirely.

### 4.5 Phenotype-Genotype Discordance

The bee-wasp comparison (Section 3.9) reveals a fundamental challenge to models in which phenotype derives incrementally from genotype: two organisms with 92% different 22-mer sequences produce nearly identical phenotypes, while two organisms with only 6% different sequences (human and chimpanzee) produce radically different phenotypes. This observation is consistent with the regulatory state

framework: phenotypic form is determined by regulatory architecture (transcription factors, translation machinery, signaling networks), not by the protein-coding substrate those systems act upon.

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## 5. Predictions and Falsification

### 5.1 Predictions

1. **BovB/L1 equilibrium** should remain within 0.93–1.00 across all Bovidae tested (currently 8/8 confirmed)
2. **Species diversity** within an order should correlate positively with active TE burden
3. **Kangaroo BovB** should show enrichment near hindlimb-patterning loci (TBX4, PITX1) relative to forelimb loci
4. **Human somatic L1** activity should exceed that of chimpanzee > gorilla > orangutan in controlled rank order
5. **22-mer shared fraction** between morphologically similar but phylogenetically distant species should consistently show regulatory enrichment and CDS depletion

### 5.2 Falsification Criteria

The model is falsified if:

- Any Bovidae species shows BovB/L1 outside the range 0.85–1.10
- SINE-rich clades show greater architectural diversification than LINE-rich clades of comparable age
- No statistically significant BovB enrichment is found near developmental loci in ruminants
- No L1HS somatic activity gradient exists across primate species
- Morphologically convergent species pairs consistently show high sequence-level homology rather than regulatory-level conservation

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## 6. Conclusion

The model does not claim that transposable elements explain all descent. It claims that TE balance may define an overlooked regulatory axis of diversification — one that is measurable, taxonomically structured, and experimentally testable.

The data presented here — 52 species (18 orders), three-tier clustering at $p < 10^{-9}$, 100% blind prediction accuracy, gene-level enrichment analysis, LINE/SINE functional distinction, 22-mer phenotype-genotype discordance analysis, the KRAB-ZFP rebuttal, and five falsifiable predictions — constitute the empirical foundation for this claim. Whether the model survives further testing will determine its value. That is what science does.

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