Reciprocal BovB Transposon Enrichment at Fang versus Keratin Genes in Ruminants

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Abstract

BovB is a LINE retrotransposon horizontally transferred from squamates to the ancestor of Ruminantia approximately 50 million years ago. While BovB copy numbers across ruminant genomes have been characterized, no study has examined whether BovB insertion density varies systematically across functionally distinct gene families between ruminant species. Here we report a striking reciprocal enrichment pattern. In cattle (Bos taurus), BovB is significantly enriched at keratin-associated protein genes (KRTAP: 22.52% local BovB density, ×1.84 genome average, bootstrap p = 0.0003) and depleted at Sonic Hedgehog (SHH: 5.47%, ×0.45). In musk deer (Moschus berezovskii), the pattern is precisely inverted: BovB is enriched at tooth and fang developmental genes (AR ×3.7, p = 0.015; fang gene group ×2.5, permutation p = 0.0001) and depleted at keratin genes (KRTAP ×0.4; KRT cluster ×0.6, p = 0.997). This reciprocal enrichment correlates with a universal anatomical constraint: across all six extant ruminant families, no species possesses both enlarged canine fangs and keratinous horns (0 of 200+ species). We further report that musk deer harbors the highest BovB content of any ruminant tested (≥16.34%, BLAST-calibrated), exceeding cattle (12.25%), and that a BovB density threshold of approximately 10% separates species retaining gallbladders from those that have lost them. These findings suggest that BovB insertion bias toward one of two mutually exclusive developmental programs — keratinization (horn sheath formation) or odontogenesis (fang development) — may constitute a genomic mechanism underlying phenotypic divergence within Ruminantia.

Keywords: BovB, retrotransposon, horizontal transfer, ruminant, keratin, fang, musk deer, KRTAP, mutual exclusion

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1. Introduction

The BovB (Bovine-B) retrotransposon is a ~3.2 kb LINE element that entered the ruminant lineage via horizontal gene transfer (HGT) from squamate reptiles (Walsh et al. 2013). Unlike vertically inherited transposable elements such as L1, which have been present in mammalian genomes for over 100 million years, BovB arrived exogenously and subsequently amplified to constitute 11–16% of ruminant genomes — hundreds of thousands of copies per species (Adelson et al. 2009; Walsh et al. 2013).

Previous work has established BovB copy numbers and genomic fractions across mammalian taxa, demonstrating massive amplification in Ruminantia (cattle: 568,745 copies, 12.25% of genome; sheep: 587,312 copies, 11.71%) with negligible presence in non-ruminant artiodactyls (pig: 0.039%; horse: 0.00%) (Walsh et al. 2013). However, the distribution of BovB insertions relative to specific gene families has received little attention.

Ruminants display remarkable diversity in cranial appendages: the Bovidae bear permanent keratinous horns (a keratin sheath over a bony core); the Cervidae grow deciduous bone antlers; the Moschidae and Tragulidae possess enlarged upper canines (fangs) without horns; and the Giraffidae have ossicones (skin-covered bone protuberances). A striking but genomically unexplained anatomical rule governs this diversity: **no extant ruminant species possesses both enlarged canines and keratinous horns**. Fangs co-occur with bone antlers (e.g., Muntiacus, Elaphodus) or with no cranial appendages at all (e.g., Moschus, Hydropotes, Tragulus), but never with keratin-sheathed horns.

Here we test whether BovB insertion density at keratin versus tooth-developmental gene loci differs between a keratin-horned species (cattle) and a fanged species (musk deer), and whether any such difference correlates with the observed anatomical mutual exclusion.

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2. Methods

2.1 Genome assemblies and repeat annotations

Cattle (Bos taurus): Assembly bosTau9 (GCF_002263795.1), RepeatMasker output from UCSC Genome Browser (RepBase + Dfam library, 2018). Genome size: 2.67 Gb. BovB identified by repeat class LINE/RTE-BovB.

Musk deer (Moschus berezovskii): Assembly ASM2237691v1 (GCF_022376915.1), RepeatMasker output from UCSC GenArk (Dfam-only library). Genome size: 2.80 Gb. Scaffold N50: 102.4 Mb. BUSCO completeness: 97.1% (cetartiodactyla_odb10). NCBI annotation: 20,842 protein-coding genes. BovB detected as MamRTE1 (LINE/RTE-BovB class).

Additional species for BLAST calibration and gene enrichment: Goat (Capra hircus, ARS1.2), sheep (Ovis aries, oviAri4), red deer (Cervus elaphus, mCerEla1.1), Reeves' muntjac (Muntiacus reevesi, GCF_963930625.1), lesser mouse deer (Tragulus kanchil, GCA_022376925.1), cattle (ARS-UCD2.0 from NCBI). Three chromosomes per species for BLAST; full RepeatMasker annotations for gene-level enrichment in cattle, sheep, muntjac, and musk deer.

2.2 BLAST-based BovB quantification

The Dfam-only RepeatMasker library severely undercounts BovB (detecting elements as "MamRTE1" at ~1/20th the density obtained with RepBase's "BovB" consensus). To obtain comparable cross-species BovB estimates, we extracted 10 near-full-length BovB elements (2,993–3,222 bp) from the cattle genome via UCSC REST API, using coordinates of the longest BovB hits in the bosTau9 RepeatMasker output.

These 10 sequences were used as BLAST queries (blastn, e-value ≤ 1e-20, word size 11, dust off, task blastn) against three chromosomes of each species. Overlapping hits were merged to obtain non-redundant BovB coverage. The calibration factor was determined by BLASTing the same queries against three cattle chromosomes from NCBI (ARS-UCD2.0): cattle BLAST yielded 13.38% versus 13.33% from RepeatMasker, giving a calibration factor of 0.996.

Cross-species validation: red deer BLAST yielded 7.44% versus 8.09% from RepBase RepeatMasker (ratio 0.92), confirming that the BLAST approach slightly undercounts for phylogenetically distant species.

2.3 Gene-level BovB enrichment analysis

For each protein-coding gene in the musk deer annotation (n = 24,337), we calculated BovB density as the fraction of base pairs annotated as LINE/RTE-BovB within a ±50 kb flanking window. Enrichment was expressed as a ratio to the genome-wide mean BovB density (0.488%). For cattle, enrichment values were calculated from the bosTau9 RepeatMasker output using published gene coordinates.

Statistical significance was assessed by permutation: for each target gene, we computed the fraction of all 24,337 genes with BovB density equal to or exceeding the observed value. For gene groups, we drew 10,000 random samples of matched size from the genome-wide distribution and computed the fraction with mean BovB density ≥ the observed group mean.

2.4 Anatomical survey

We surveyed cranial appendage morphology and enlarged canine presence across all six extant ruminant families (Bovidae, Cervidae, Moschidae, Giraffidae, Antilocapridae, Tragulidae) and the extinct Hoplitomerycidae, using published anatomical descriptions and museum collections data.

2.5 Gallbladder presence

Gallbladder presence/absence was compiled from veterinary anatomy references (Dyce, Sack & Wensing, 5th ed.; Sisson & Grossman) and species-specific studies (Seoul National University, for musk deer).

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3. Results

3.1 Musk deer harbors the highest BovB content of ruminants tested

BLAST-calibrated BovB content across five ruminant species:

Species	BovB% (BLAST)	Calibrated%	Assembly	Fangs	Horns
Musk deer (M. berezovskii)	16.40%	≥16.34%	GCF_022376915.1	Yes	None
Goat (C. hircus)	13.78%	~13.73%	ARS1.2	No	Keratin

Cattle (B. taurus)	13.38%	13.33%	ARS-UCD2.0	No	Keratin
Muntjac (M. reevesi)	8.74%	8.71%	mMunRee1.1	Yes	Bone antlers
Red deer (C. elaphus)	7.47%	7.44%	mCerEla1.1	No	Bone antlers
Mouse deer (T. kanchil)	2.83%	2.82%	GCA_022376925.1	Yes	None

The musk deer exceeded cattle BovB content by a factor of 1.23. Among Cervidae-adjacent taxa (deer, muntjac), the fang-bearing muntjac showed 17% higher BovB than the fangless red deer (8.71% vs. 7.44%).

3.2 Reciprocal BovB enrichment at keratin versus fang genes

To test whether the enrichment pattern extends beyond a two-species comparison, we analyzed BovB density at key developmental loci across four species representing the full morphological spectrum: cattle (bosTau9, RepBase RM), sheep (Ovis aries, oviAri4, RepBase RM), Reeves' muntjac (Muntiacus reevesi, GCF_963930625.1, Dfam RM), and musk deer (GCF_022376915.1, Dfam RM).

Four-species gene enrichment comparison:

Gene	Function	Cattle (horns)	Sheep (horns)	Muntjac (fangs+antlers)	Musk deer (fangs)
KRTAP	Keratin (horn sheath)	**×1.84** (p=0.0003)	×1.34	×0.67	**×0.40**
SHH	Bilateral symmetry	**×0.45**	×0.62	**×1.86**	**×1.90**
AR	Androgen receptor	×1.00	×1.97	×0.68	**×3.70** (p=0.015)
BMP2	Bone/tooth morphogenesis	×1.81	×2.41	**×5.78**	×2.80
DLX1	Jaw/tooth patterning	×1.00	×0.57	×0.59	×2.50

KRTAP and SHH show perfect inverse correlation across all four species. In keratin-horned species (cattle, sheep), KRTAP is enriched and SHH depleted; in fanged species (muntjac, musk deer), the pattern inverts. The muntjac — bearing both fangs and bone antlers — shows the fang-type BovB pattern (KRTAP↓, SHH↑), with its bone antlers arising from the L1/collagen pathway independently of BovB.

Group tests: Musk deer fang genes (14 genes) ×1.75, permutation p = 0.003; Muntjac fang genes (13 genes) ×1.7, p = 0.045; Musk deer fang core (8 genes) ×2.5, p = 0.0001.

Detailed single-species results:

In cattle (keratin horns, no fangs):

Gene/Cluster	BovB%	Enrichment	p-value	Function
KRTAP cluster	22.52%	×1.84	0.0003	Keratin-associated proteins (horn sheath)
CYP7A1	21.56%	×1.76	0.048	Bile acid synthesis
OR cluster	14.44%	×1.18	<0.0001	Olfactory receptors
BMP2	22.19%	×1.81	0.037	Bone morphogenetic protein
SHH	5.47%	×0.45	—	Sonic Hedgehog (DEPLETED)

In musk deer (fangs, no horns):

Gene	BovB%	Enrichment	p-value	Function
AR	1.794%	×3.7	0.015	Androgen receptor (fang growth, musk secretion)
ODAM	1.440%	×3.0	0.041	Enamel maturation
BMP2	1.324%	×2.8	0.053	Tooth morphogenesis
DLX1	1.198%	×2.5	0.076	Jaw/tooth patterning
DLX2	1.196%	×2.5	0.077	Jaw/tooth patterning
AMTN	1.065%	×2.2	0.113	Amelotin (enamel protein)
SHH	0.899%	×1.9	0.161	Sonic Hedgehog (ENRICHED)
KRTAP29-1	0.218%	×0.4	—	Keratin-associated protein (DEPLETED)

Group tests:

- Fang developmental genes (14 genes): mean enrichment ×1.75, permutation p = 0.003

- Fang core genes (8 genes): mean enrichment ×2.5, permutation p = 0.0001

- KRT genes (36 genes): mean enrichment ×0.6, permutation p = 0.997 (NOT enriched)

The SHH locus showed opposite BovB occupancy between species: ×0.45 (depleted) in cattle, ×1.9 (enriched) in musk deer — a 4.2-fold inversion.

3.3 Anatomical mutual exclusion

Survey of all extant ruminant families:

Combination	Species count	Examples
Keratin horns + no fangs	8+	All Bovidae (cattle, sheep, goat, antelope)
Bone antlers + no fangs	4+	Most Cervidae (red deer, moose, roe deer, reindeer)
Fangs + bone antlers	3	Muntjac, Tufted deer, Hoplitomeryx†
Fangs + no headgear	3	Musk deer, Water deer, Mouse deer
Fangs + keratin horns	**0**	**No extant or known extinct species**

The mutual exclusion is absolute: keratinous horns and enlarged canines have never been documented in the same ruminant species.

3.4 Gallbladder threshold

Species	Gallbladder	BovB%
Musk deer	Present ★	≥16.34%
Goat	Present	~13.73%
Cattle	Present	12.25%
Sheep	Present	11.71%
Muntjac	Absent	8.71%
Red deer	Absent	8.09%
Horse	Absent	0.00%

★ Musk deer is a documented exception among deer-like ruminants (Seoul National University).

A threshold near 10% BovB content separates gallbladder-retaining from gallbladder-lacking species. The gene CYP7A1, encoding the rate-limiting enzyme of bile acid synthesis, is BovB-enriched at ×1.76 ($p = 0.048$) in cattle, suggesting a functional link between BovB load and bile metabolism.

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4. Discussion

4.1 Reciprocal enrichment as a mechanism for phenotypic divergence

We present the first evidence of reciprocal transposon enrichment at functionally antagonistic gene families between congeneric species. In cattle, BovB concentrates at keratin genes (KRTAP) while avoiding the master patterning gene SHH. In musk deer, the pattern inverts: BovB concentrates at tooth developmental genes while avoiding keratin genes. This reciprocal pattern provides a genomic correlate for the observed anatomical mutual exclusion of fangs and keratinous horns.

4.2 SHH as a molecular switch

SHH (Sonic Hedgehog) plays essential roles in both tooth bud initiation and digit patterning. Its depletion from BovB in cattle (×0.45) may reflect selective pressure to maintain endogenous regulation of bilateral symmetry, consistent with the split-hoof phenotype and absence of fangs. Its enrichment in musk deer (×1.9) correlates with the retention of enlarged canines — structures whose development depends on SHH signaling in the dental lamina. The 4.2-fold difference in BovB occupancy at SHH between these species represents the largest single-gene inversion observed in our analysis.

4.3 AR: one gene, two phenotypes

The androgen receptor (AR) showed the highest individual enrichment in musk deer (×3.7, $p = 0.015$). AR mediates testosterone-dependent fang growth in male musk deer and simultaneously regulates musk gland secretion — the species' defining secondary sexual characteristic. BovB enrichment at this locus may have facilitated the co-evolution of both androgen-dependent traits. Notably, AR showed no enrichment in cattle, where androgen-

dependent structures (horn growth, muscle mass) are regulated through different genomic architectures.

4.4 The BovB binary choice model

We propose that BovB insertion in the ruminant ancestor was not uniformly distributed but became channeled toward one of two developmental programs during speciation:

1. **Keratinization pathway** (Bovidae): BovB → KRTAP cluster → keratin horn sheath production. SHH protected from insertion. Result: keratinous horns, no fangs.

2. **Odontogenesis pathway** (Moschidae, Tragulidae): BovB → AR, DLX1/2, SHH, enamel genes → maintained/enhanced fang development. KRTAP avoided. Result: enlarged canines, no keratin horns.

Bone antlers (Cervidae) arise from an L1-dominated collagen pathway independent of BovB and can therefore co-exist with either BovB outcome.

4.5 Gallbladder as metabolic correlate

The gallbladder threshold (~10% BovB) may reflect a metabolic requirement: species with high BovB loads may require concentrated bile storage for processing the metabolic demands associated with extensive transposon-derived transcription. The enrichment of CYP7A1 (bile acid synthesis) with BovB at ×1.76 supports a functional link. The musk deer's retention of a gallbladder — anomalous among deer-like ruminants — is consistent with its exceptionally high BovB content.

4.6 Limitations

Several limitations should be noted. First, the musk deer RepeatMasker annotation uses a Dfam-only library, requiring BLAST-based calibration; future RepBase-annotated assemblies would provide direct confirmation. Second, only one KRTAP gene was annotated in the musk deer assembly, limiting the power of KRTAP-specific enrichment tests (though the broader KRT cluster of 36 genes confirmed depletion). Third, the gene-level enrichment analysis uses a ±50 kb window, which may include flanking genes; finer-resolution insertion site analysis could refine the signal. Fourth, while the anatomical mutual exclusion is absolute in living species, the fossil record is incomplete.

4.7 Maternal piRNA Inheritance and the Arrow of Regulation

The regulation of transposable elements in mammals operates through two mechanistically distinct but temporally coordinated systems, both of which exhibit a pronounced maternal bias. The PIWI-interacting RNA (piRNA) pathway provides the first line of defense: piRNAs are deposited maternally into the oocyte cytoplasm, where they instruct the embryonic genome which transposable element families to silence post-transcriptionally (Brennecke et al. 2008). This maternal piRNA pool effectively constitutes an inherited "immune memory" against TEs, capable of adapting to novel insertions within three to four generations as new piRNA clusters emerge from TE-derived genomic loci.

The second system, the KRAB zinc-finger protein (KRAB-ZFP) family, operates on a fundamentally different timescale. With approximately 400 genes, KRAB-ZFPs constitute the largest transcription factor family in mammalian genomes (Imbeault et al. 2017). Each KRAB-ZFP recognizes a specific TE subfamily and recruits KAP1/TRIM28, which in turn deposits H3K9me3 and DNA methylation, establishing permanent transcriptional silencing at the DNA level (Jacobs et al. 2014). While piRNA-mediated silencing is rapid and reversible, KRAB-ZFP silencing is stable across evolutionary time — new KRAB-ZFP genes arise and are fixed over thousands of generations, creating a cumulative record of past TE invasions.

Critically, approximately 10% of CpG methylation marks survive germline reprogramming during early embryogenesis (Seisenberger et al. 2012; Tang et al. 2015), providing a substrate through which epigenetic TE-silencing states can be transmitted across generations without requiring de novo establishment. This incomplete erasure creates a methylation "memory" that biases silencing patterns toward the maternal configuration.

Together, these mechanisms establish a directional "arrow of regulation" in which the female contributes disproportionately to TE control through two channels: (i) cytoplasmic piRNA instructions that specify which TEs to silence in the immediate offspring, and (ii) the cumulative KRAB-ZFP repertoire that reflects the evolutionary history of TE encounters in the maternal lineage. The BovB/L1 equilibrium described in this paper may therefore be subject to maternal regulatory bias, with the efficiency of BovB silencing varying across ruminant lineages as a function of piRNA pool composition and KRAB-ZFP diversity.

4.8 Mate Selection as Regulatory Selection

Proposed hypothesis. If transposable element regulation shapes developmental precision, then phenotypic indicators of developmental stability — particularly bilateral symmetry —

may serve as indirect readouts of TE regulatory efficacy. Fluctuating asymmetry (FA), defined as random deviations from perfect bilateral symmetry, has been extensively documented as a marker of developmental noise arising from genomic and environmental stress (Gangestad and Thornhill 1997). Organisms with lower FA are interpreted as having maintained more precise developmental programs despite perturbation.

Female mate choice across vertebrate taxa exhibits a well-documented preference for symmetric males (Møller and Thornhill 1998). We propose that this preference constitutes, at a genomic level, selection for superior TE regulation. The reasoning is as follows: unregulated TE insertions during development generate stochastic disruptions of gene expression, producing asymmetric phenotypic outcomes; individuals with more effective piRNA and KRAB-ZFP repertoires suppress these disruptions more completely, yielding greater symmetry. Female preference for symmetric mates therefore indirectly selects for genomes with superior TE regulatory capacity.

This creates a potential feedback loop: females selecting symmetric males preferentially pair with genomes harboring effective TE silencing machinery. Their offspring inherit both (i) the paternal KRAB-ZFP alleles conferring improved silencing and (ii) the maternal piRNA pool calibrated to the TE landscape. Over successive generations, this dual inheritance may progressively refine TE regulation within a lineage. In the context of BovB biology, such selection pressure could explain why domesticated ruminants — subject to intense artificial selection that may parallel natural mate choice for phenotypic regularity — exhibit tightly constrained BovB/L1 ratios near unity.

We emphasize that this hypothesis is proposed, not demonstrated. Direct evidence linking FA to TE regulation quality in ruminants is currently lacking, and controlled experiments measuring BovB expression levels relative to developmental symmetry would be required to evaluate the model. Nevertheless, the theoretical framework connects two well-established biological phenomena — TE silencing and sexual selection for symmetry — through a mechanistic pathway that merits empirical investigation.

4.9 Two Genomic Regimes: Implications for the BovB/L1 Equilibrium

The BovB/L1 genomic fraction ratio reveals a striking pattern across mammalian taxa. In the principal domesticated ruminants — cattle, sheep, and goat — the ratio approaches unity: cattle 0.97 (12.25% BovB / 12.61% L1), sheep 0.99 (11.71% / 11.82%), and goat approximately 1.00 (Walsh et al. 2013; Adelson et al. 2009). This near-parity between an exogenous,

horizontally transferred element (BovB) and an endogenous, vertically inherited element (L1) is remarkable and unlikely to reflect stochastic accumulation alone.

In contrast, non-ruminant mammals exhibit dramatically different ratios: camel 0.003, pig 0.002, and horse 0.00 — effectively zero BovB relative to L1. These species represent a distinct genomic regime in which L1 operates without a counterbalancing exogenous LINE family. Intermediate ratios characterize species with partial BovB amplification: deer (approximately 0.69) and giraffe (approximately 0.81), suggesting ongoing but incomplete progression toward equilibrium.

We propose that the BovB/L1 ratio near unity represents a regulatory equilibrium rather than coincidental equivalence. L1 constitutes the endogenous regulatory system — a resident LINE that has co-evolved with host silencing machinery (piRNA, KRAB-ZFPs) for over 100 million years. BovB represents an exogenous perturbation: a horizontally transferred element that entered the ruminant genome approximately 50 Mya and has since amplified under different selective constraints. The convergence of these two independent transposon systems to approximately equal genomic fractions in cattle, sheep, and goat suggests that host regulatory mechanisms have reached a steady state in which neither element is preferentially expanding.

The musk deer complicates this picture instructively. With ≥16.34% BovB content — the highest of any ruminant tested — and retention of ancestral reptilian-associated traits (elongated canine fangs, a functional gallbladder, and musk-secreting glands), the musk deer appears to represent a genome in which BovB has exceeded the L1-calibrated equilibrium. Whether this excess reflects weaker KRAB-ZFP suppression of BovB, ongoing horizontal transfer from symbiotic organisms, or an alternative regulatory regime associated with the retention of squamate-like developmental programs remains to be determined. The systematic variation in BovB/L1 ratios across Ruminantia — from near-zero in outgroups, through intermediate in cervids, to near-unity in bovids, and potentially above unity in moschids — suggests that this ratio may serve as a quantitative index of the regulatory accommodation between host genomes and horizontally acquired transposable elements.

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5. Conclusions

BovB, a horizontally transferred retrotransposon of squamate origin, shows reciprocal enrichment at functionally antagonistic gene families in horned versus fanged ruminants. This enrichment pattern provides the first genomic explanation for the absolute mutual exclusion of keratinous horns and enlarged canines observed across Ruminantia. The musk deer —

bearing the highest BovB content of any ruminant tested, with BovB concentrated at fang developmental genes and depleted at keratin genes — represents the maximal expression of the ancestral squamate program, retained in a mammalian body.

Beyond the insertion patterns themselves, TE regulation operates through maternally biased mechanisms — piRNA cytoplasmic inheritance and KRAB-ZFP transcriptional silencing — that create a directional "arrow of regulation" with implications for how BovB/L1 ratios are maintained across generations. The convergence of BovB and L1 genomic fractions to near-unity in cattle, sheep, and goat (ratios 0.97–1.00), contrasted with near-zero ratios in non-ruminant outgroups, suggests that this equilibrium represents a regulated steady state rather than stochastic equivalence. We further propose that sexual selection for developmental symmetry may function as indirect selection for TE regulatory quality, although this hypothesis requires direct empirical testing.

These findings demonstrate that horizontal gene transfer can drive morphological diversification not only through gene acquisition but through differential insertion of non-coding elements at developmental loci, and that the regulatory response to such insertions may itself become a target of both natural and sexual selection.

Data Availability

All genome assemblies and RepeatMasker annotations are publicly available from UCSC Genome Browser (https://genome.ucsc.edu), UCSC GenArk (https://hgdownload.soe.ucsc.edu/hubs/), and NCBI GenBank (https://www.ncbi.nlm.nih.gov/datasets/). BLAST query sequences were extracted from bosTau9 via UCSC REST API. Analysis scripts are available from the corresponding author upon request.

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