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Research Paper

Animal milk oligosaccharides: structural diversity, biological functions, and health relevance

Apurwa Singh[1], Parinita Tripathy[2*]
[1,2*]Department of Science (Chemistry), Kalinga University, Raipur, Chhattisgarh, 492101, India.

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ABSTRACT

Plant-derived Milk oligosaccharides (MOs) are mammalian milk glycans with varied structure and high biological activity. Human milk oligosaccharides (HMOs) are well known for their prebiotic, antimicrobial, and immunomodulatory functions, whereas animal milk oligosaccharides cow, goat, sheep, and buffalo are increasingly recognized for their health-promoting potential. This review summarizes and critically evaluates the existing scientific literature on animal-derived MOs' structure, biosynthesis, and healthy functions in animals, highlighting their similarities and differences with HMOs. With high-quality research paper sources, we discuss how bovine and caprine milk oligosaccharides contribute to a healthy gut, regulate immunity, and support its development. Comparative tabulation and visual inspection highlight the structural diversity and biological significance of animal-derived milk oligosaccharides for functional food and infant formula applications.

Corresponding Author:
Parinita Tripathy
Department of Science (Chemistry), Kalinga University, Raipur, Chhattisgarh, 492101, India.
Email: tripathy.parinita2002@gmail.com

1. INTRODUCTION

Milk being the major nutritional source in mammalian neonates, is not only a food source but also a bioactive fluid. Milk contains many compounds with a role in early development, immune system formation, and microbial implantation in the infant gut [1]. Among these components, milk

oligosaccharides (MOs) have received growing interest from scientists because of their multidirectional biological activities. These glycan's, made up of a number of units of different monosaccharides such as glucose, galactose, N-acetyl glucosamine, fucose, and sialic acid [2], are not digestible by the host but are selectively consumed by gut commensal bacteria, making them effective prebiotic compounds [3]. For human milk oligosaccharides (HMOs), in-depth research has shed light on their critical functions in infant health, such as gut microbiota modulation, defense against pathogens, promotion of brain development, and immune response enhancement [4], [5]. HMOs are the third most concentrated solid constituent of human milk, following lactose and lipids, with more than 200 structurally unique forms characterized to date. This structural heterogeneity is due to differences in glycosidic linkages [6], polymerization levels, and terminal modifications like fucosylation and sialylation, which make them heterogeneously functional. Previously, animal milk oligosaccharides, like those of bovine, caprine, ovine, and buffalo milk, were nutritionally less important as they were found in lesser quantities and with more basic structures when compared to HMOs. Nonetheless, recent advancements in mass spectrometry and liquid chromatography analysis have shown that animal milks too have a range of MOs, structurally or functionally similar to some extent to HMOs [7], [8] For example, many sialylated and neutral core structures in goat and cow milk have similarities to those in human milk, opening possibilities for their use as infant formula supplement and functional food ingredients [9].

a. Evolutionary Perspective and Comparative Glycomics

The evolutionary history of milk oligosaccharides points towards their phylogenetically conserved function in mammalian biology. Although it is humans who have evolved to make a highly diversified and rich set of oligosaccharides in milk, possibly as an adaptation to extended infant dependency and susceptibility to microbes, other animals like bovines and caprines have adopted more reduced milk oligosaccharide profiles adequate for their shorter neonatal development windows. Comparative glycomic analysis indicates that although human milk has 50–80% fucosylated oligosaccharides, bovine milk yields trace of fucosylated species [9]. Goat milk, however, has a greater proportion of sialylated oligosaccharides compared to cow milk and therefore comes across as the nearest substitute to HMOs in functional glycan content [6].

b. Compositional Profiles Across Animal Species

The concentration and composition of milk oligosaccharides vary widely among species. Human milk contains between 5–15 g/L of oligosaccharides, depending on factors such as genetics (secretor vs. non-secretor status), lactation stage, and maternal nutrition. In contrast, bovine milk contains only 0.05–0.3 g/L of milk oligosaccharides, though it is available in large volumes, making it an attractive raw material for industrial-scale oligosaccharide extraction [6]. Goat and sheep milk have comparatively greater concentrations (0.25–0.6 g/L), and their oligosaccharide compositions are more abundant in sialylated and neutral non-fucosylated structures, some of which have mimicked functionality of important HMOs such as 3′-sialyllactose and 6′-sialyllactose. The goat milk has more than 30 different oligosaccharide structures, some of which were considered unique to human milk [10], [11]. Buffalo milk, while less extensively studied, has been found to harbour complex sialylated oligosaccharides with suspected neurodevelopmental and anti-inflammatory activity.

c. Biosynthesis and Structural Diversity

Milk Milk oligosaccharides are biosynthesized in mammary epithelial cell Golgi apparatus by the concerted activity of glycosyltransferases that append monosaccharides in defined linkages to lactose (the central disaccharide) [6], [12]. The structural pattern of species-specific MOs is governed by the relative abundance of such enzymes as fucosyltransferases (FUT2, FUT3), sialyltransferases (ST3GAL, ST6GAL), and N-acetylglucosaminyltransferases [13]. In humans, the polymorphism of genes such as FUT2 and FUT3 leads to varying HMO phenotypes, which affect infant disease susceptibility and colonization patterns in the gut [14]. In animal milk, the restricted occurrence of fucosyltransferases is paralleled by the low concentration of fucosylated MOs, although certain unusual structures such as lacto-N-fucopentaose

(LNFP) have been found in minute quantities in cow milk [14], [15]. However, sialyltransferases are exceptionally active in ruminant animals and are thus responsible for the relative prevalence of sialylated oligosaccharides such as 3′-sialyllactose (3′-SL) and 6′-sialyllactose (6′-SL) the former of which is also under research for its cognitive and anti-infective properties [16].

d. Functional Implications and Health Relevance

In addition to their nutritional innocuity, animal-derived milk oligosaccharides have exhibited prebiotic, antimicrobial, anti-inflammatory, and cognition-enhancing activities in vitro and in vivo [13], [15]. For instance, it has been demonstrated that bovine-derived 3′-SL and 6′-SL inhibit the adhesion of pathogenic bacteria like Escherichia coli and Campylobacter jejuni to intestinal epithelial cells [17]. These oligosaccharides have also been found to stimulate the growth of probiotic bacteria like Bifidobacterium longum subsp. infantis, albeit less selectively and strongly than HMOs. Caprine milk oligosaccharides, particularly sialylated structure-rich ones, have been associated with increased brain development and immune modulation in neonatal animal models [18], [19]. The presence in animal milk oligosaccharides of N-glycolylneuraminic acid (Neu5Gc), not found in human milk, has questioned their long-term immunogenicity in humans. Yet, enzymatic and microbiome modifications during processing may soften these fears [19].

e. Application in Infant Nutrition and Functional Foods

With an increasing demand for HMO analogues, especially for non-breastfed infants, dairy companies are using more capital to extract, purify, and enzymatically produce animal-sourced milk oligosaccharides. Most infant formulas on the market today contain galacto-oligosaccharides (GOS) and fructo-oligosaccharides (FOS), which do not possess the structural sophistication and biological activity of HMOs [20]. Adding oligosaccharides of animal origin, particularly bovine and caprine sialyllactoses, provides a viable pathway to bridge the gap between formula and mother's milk. Emerging breakthroughs in membrane filtration, enzymatic glycoengineering, and microbial biosynthesis are opening doors towards scalable manufacture of structurally defined animal milk oligosaccharides [20]. The European Food Safety Authority (EFSA) and U.S. FDA have already approved the utilization of certain milk oligosaccharides, such as 2′-fucosyllactose and lacto-N-neotetraose, for formula uses, which further pushed the research on their animal counterparts.

2. RELATED WORK

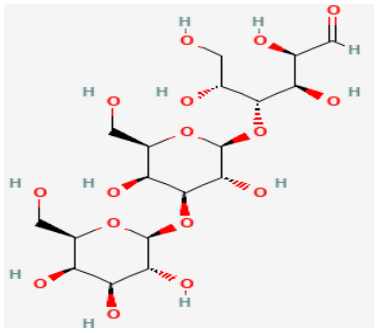
a. Structural Diversity of Animal Milk Oligosaccharides

Animal-derived milk oligosaccharides differ in monosaccharide composition, glycosidic linkage, degree of fucosylation, and sialylation as shown in Table 1 and Figure 1.

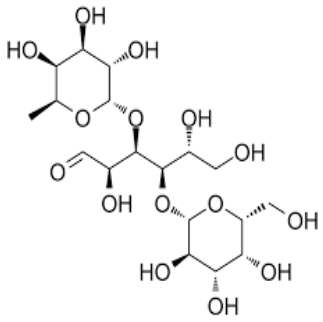
Table 1. Composition of Milk Oligosaccharides in Different Species

Milk Source	Estimated Oligosaccharide Count	Major Monosaccharides	Fucosylation	Sialylation	Reference
Human	~160+	Glc, Gal, GlcNAc, Fuc, Neu5Ac	High (50–80%)	Moderate	[17], [5]
Cow	~40	Glc, Gal, GlcNAc, Neu5Ac	Low (<10%)	High	[8]
Goat	~55	Similar to cow	Moderate	High	[7]
Sheep	~35	Similar to cow/goat	Low	High	[9], [27], [28], [12], [25], [26], [11], [13], [15], [14]
Buffalo	~30	Similar	Very Low	High	[41]

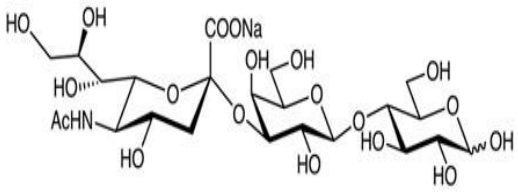
2.1. Key Structural Classes



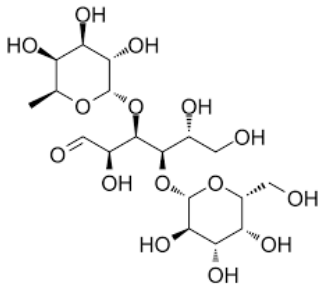
Neutral OS (e.g., 3'-Galactosyllactose)



Fucosylated OS (Common in HMOs but Rare in Bovine MOs)



Sialylated OS (e.g., 3′-Sialyllactose, 6′-Sialyllactose 3′-Sialyllactose



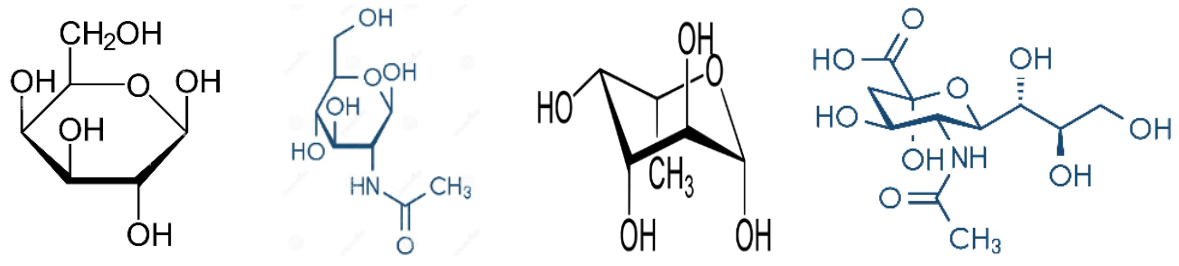
Sialylated OS (e.g., 3′-Sialyllactose, 6′-Sialyllactose 6′-Sialyllactose

Figure 1. Structural Diversity of Monosaccharides

Studies using HPLC-MS and NMR have identified over 50 oligosaccharide structures in goat milk and a more limited set in bovine milk [20], [21].

b. Biosynthesis and Analytical Advances

Animals trigger biosynthesis of milk oligosaccharides (MOs) within the mammary gland, where a cascade of glycosyltransferase-catalyzed enzymatic reactions begins from a lactose core [22]. Enzyme after enzyme adds monosaccharide units of galactose, N-acetylglucosamine, fucose, and sialic acid, as shown in Figure 2, to it to construct branched and linear oligosaccharide structures. Whereas the core biosynthetic pathway is evolutionarily conserved, interspecies variability in glycosyltransferase activity and expression results in milk structural variability from animal to animal [22], [23], [24].



Galactose N-Acetylglucosamine Fucose Sialic acid

Figure 2. Enzyme after Enzyme Adds Monosaccharide Units

Advances in the past few years in analytical technology have dramatically advanced the knowledge of milk oligosaccharides of animals. Glycomics in combination with proteomics and metabolomics has enabled high-resolution structural analysis of oligosaccharides such as linkages, anomeric configuration, and terminal modification. Techniques such as liquid chromatography–mass spectrometry (LC-MS), matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF), and nuclear magnetic resonance

(NMR) spectroscopy have become an integral component of milk oligosaccharide profiling and quantitation [23], [24], [25], [26], [27], [28]. They are aided by computational and bioinformatics tools, such as MilkOligoDB, that classify and compare MO profiles across species, revealing conserved glycan motifs and enhancing structural annotation [29].

Furthermore, computational simulation and machine learning bear the possibility of developing predictive models on computational ways of analyzing oligosaccharide biosynthesis pathways. Through them, one can simulate enzymatic specificity, predict structural isomers, and deduce biosynthetic constraints and thus gain more insight into interspecies diversity and synthetic mimicry opportunities [30]. These collaborative analytical breakthroughs have furthered not just the understanding of naturally occurring milk oligosaccharide biosynthesis, but also the effort at bioengineering useful milk oligosaccharides for nutritional and therapeutic applications [1], [2], [6].

c. Biologic Functions and Health Implications

Animal-derived milk oligosaccharides, although more structurally homogeneous than HMOs, have been finding a wide range of biological activities with crosstalk bearing important implications on the health and well-being of animals and human beings. Just by virtue of their very structural resemblance to HMOs with a more or less particular emphasis being given to prebiotic regulation, antimicrobial defense, and immunomodulation oligosaccharides have created a big market for themselves in infant nutrition, functional foods, and therapeutics [1], [2], [6].

Prebiotic Activity

This is probably the best-known activity of animal milk oligosaccharides [1], [2]. Bovine milk oligosaccharides and goat milk were found to selectively stimulate gut commensal microbiota, especially the families of Bifidobacterium and Lactobacillus [8], [31]. These microorganisms actually ensure intestinal homeostasis, enhance gut barrier function, and shield against the colonization of pathogens. Comparative research has indicated that some bovine milk oligosaccharides have a similar structure to the HMO structures and can thus mimic the same bifidogenic effects when added to infant formula.

Pathogen Inhibition

Milk oligosaccharides from animal origin also function as decoy receptors by mimicking the epithelial cell surface glycans naturally targeted by pathogens for adhesion. This antiadhesive nature makes milk oligosaccharides competitive in inhibiting microbial attachment and hence avoiding the risk of infection. Interestingly, certain bovine and porcine milk oligosaccharides were reported to inhibit adhesion and colonization by Escherichia coli, Campylobacter jejuni, Salmonella enterica, and Helicobacter pylori gastrointestinal pathogens of worldwide prevalence [32], [33]. Such activities have promise for use in milk oligosaccharide-based anti-infective therapeutic and prophylactic development not dependent on antibiotics [34].

Immunomodulation

Aside from their antimicrobial and prebiotic action, animal milk oligosaccharides also display immunomodulatory action that modulates systemic and mucosal immunity. Various studies have established their capacity to modulate patterns of cytokine secretion, boost regulatory T cell (Treg) activity, and induce anti-inflammatory responses [34], [35]. All these roles result in a lower frequency of immune-mediated illnesses like allergies when given early in life. Milk oligosaccharides can have the potential to aid in neonatal immune system development and may have clinical nutrition and immune therapeutic uses [20].

3. METHODOLOGY

This review paper accounts for a detailed summary and critical evaluation of some of the current literature concerning animal-derived milk oligosaccharides (MOs). The method was to collate information

from well-reputed earlier research papers to discuss and analyze the structure, biosynthesis, and biological functionalities of milk oligosaccharides [36], [37]. In the most general terms, animal milk oligosaccharides (MOs) are glucomannans that are found in the milk of mammalian animals such as cows, goats, sheep, and buffaloes [38], [39]. They are less abundant and less diverse than human milk oligosaccharides but have been recently recognized for possessing some health benefits, such as being prebiotic, antimicrobial, and immunomodulatory [40]. This would make them quite attractive for their application in infant formulas and functional foods.

a. Methodology for Studying Animal Milk Oligosaccharides

Animal milk oligosaccharides are scrutinized and analyzed using a combination of some of the most advanced analytical methodologies, combined with computational tools and techniques in modern science. Such identification and quantitation remain unimaginable without these techniques, along with the deeper understanding of MO structures and their biological functions.

Sample Preparation

The process begins with the extraction of oligosaccharides from raw milk. The procedure usually encompasses a few steps:

- Removal of Caseins and Fats: Removal of fats and proteins is performed as a preliminary stage. The fats may be removed by centrifugation, and the proteinaceous components, mainly casein, can be precipitated by means of acid treatment [7], [8], [9], [10], [11].
- Whey Separation: The flyweight occurring liquid in the lake of solids is termed whey. It contains the oligosaccharides along with lactose and some other incomplete proteins [7], [8], [9], [10], [11].
- Purification: The oligosaccharides are then purified from the whey. The plants are usually chromatography-based, like size-exclusion chromatography or solid-phase extraction, to remove minute splits like lactose and salts [7], [8], [9], [10], [11].

b. Analytical Techniques

Advanced analytical methods are crucial for deciphering the structural diversity of MOs.

- Liquid Chromatography-Mass Spectrometry (LC-MS): LC-MS is the primary technique used for separating and identifying MOs. Liquid Chromatography-Mass Spectrometry (LC-MS): LC-MS is the primary technique used for separating and identifying MOs. LC separates individual oligosaccharides based on their physicochemical characteristics, while MS provides accurate mass measurements to identify and characterize the monosaccharide units (e.g., glucose, galactose, N-acetylglucosamine, fucose, and sialic acid) and composition of each oligosaccharide. LC-MS is also applied to quantify MOs [32], [33], [34], [35].
- NMR Spectroscopy: Provides detailed information on structure, such as specific glycosidic linkages (including 3' or 6' linkages) and anomeric configurations of sugar moieties. It is crucial for establishing the detailed structure of a novel oligosaccharide [32], [33], [34], [35].
- Mass Spectrometry with Matrix-Assisted Laser Desorption/Ionization Time-of-Flight (MALDI-TOF): This technique is employed for rapid high-throughput profiling of oligosaccharide mixtures. It yields a quick "fingerprint" of various MOs in a sample based on their mass-to-charge ratio. This is especially advantageous for comparative analysis between various animal species [32], [33], [34], [35].

c. Bioinformatics and Computational Analyses

Any large dataset that these analytical methods might generate requires interpretation on sophisticated computational tools.

- **Bioinformatics Tools:** Bioinformatics tools such as Databases are employed to compare the structure of the given MOs with a database of previously recognized oligosaccharides in mammalian organisms. This helps in revealing conserved motifs of structure and determination of the evolutionary relationship of MOs [10]

- **Computational Simulations:** Machine learning and molecular modeling are used to simulate the biosynthetic pathways of MOs. The models can reproduce enzymatic specificity and predict the hypothetical isomers of an oligosaccharide and why various animals have different MO profiles. The models also allow for the prediction of hypothetical biological activities of novel MO structures that have been isolated [10].

4. RESULTS AND DISCUSSION

a. Comparative Analysis of Milk Oligosaccharides

Comparative evaluation of the oligosaccharide content of different types of milk, including human, cow, and goat milk. Figure 2 highlights considerable disparity in both quantity and structural complexity of oligosaccharides among species.

- **Human Milk (HMOs):** Human milk is found to have the highest oligosaccharide count, with over 160 different structures identified. It also has high fucosylation, with 50-80% of its oligosaccharides containing fucose units. This structural diversity and volume directly relate to the sheer biological benefits of HMOs, such as their intense prebiotic and anti-pathogen activity [23], [32], [33].
- **Cow Milk (BMOs):** In contrast, the graph indicates that bovine milk (cow's milk) has a much lower level of oligosaccharides (around 40 structures) and minimal fucosylation, with less than 10% of its oligosaccharides containing fucose. Less diversified as they may be, such oligosaccharides, particularly sialylated structures like 3'- and 6'-sialyllactose, are still of value to human health and are currently studied as functional food components [23], [41].
- **Goat Milk (GMOs):** Goat milk falls intermediate between cow and human milk in terms of number of oligosaccharides and fucosylation. The Figure 3 shows that it is more heterogeneous (with approximately 55 structures) and moderately fucosylated compared to cow milk. Goat milk thus emerges as a nearer functionally equivalent alternative to human milk, especially with the abundance of sialylated oligosaccharides which have been shown to induce gut health and immunity [7], [23].

The comparison, as indicated in Figure 3, highlights the distinct evolutionary history of every mammalian species, with humans creating a very intricate set of oligosaccharides to sustain the long-term growth of their young. Although less intricate than that of humans, the individual oligosaccharide profiles of animal milks present specific advantages for application in infant formula and other functional foods. The following is a visual contrast of oligosaccharide numbers and fucosylation among major types of milk Figure 3.

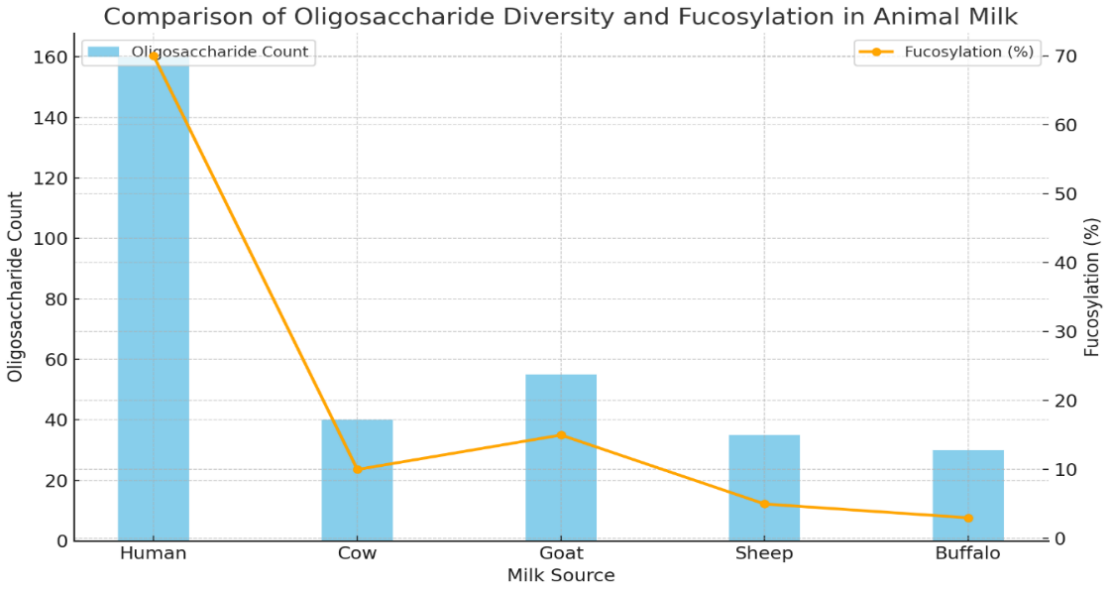


Figure 3. Oligosaccharide Count vs. Fucosylation

- Human milk exhibits the highest oligosaccharide count and fucosylation.
- Goat milk surpasses cow milk in diversity and functional similarity to HMOs.

b. Applications

Animal-derived milk oligosaccharides (MOs) are increasingly attracting attention with their promise of translational utility in nutrition, medicine, and biotechnology. Among the most significant areas of application is the fortification of infant formula. Goat and bovine milk oligosaccharides, based on their partial structural similarity to human milk oligosaccharides (HMOs), are being extensively investigated as effective HMO analogues to be used in infant nutrition products [36], [37]. Such analogues could mitigate the differences between breastfed and formula-fed infants in terms of immune development and composition of gut microbiota [38]. Other than infant nutrition, animal MOs could be applied therapeutically. Their anti-inflammatory, immunomodulatory, and anti-adhesive properties render them suitable for the treatment of gut and respiratory infections [39], [40]. For instance, oligosaccharides mimicking host cell surface glycans may act as decoys to block pathogen adhesion and thereby reduce infection outcome or infection severity by E. coli, Campylobacter, and Helicobacter pylori [41], [42].

Synergistically, advances in biotechnology are facilitating scalable production of structurally intricate milk oligosaccharides, including fucosylated milk oligosaccharides—characteristics generally more common in HMOs. Microbial fermentation and enzymatic production with directed glycosyltransferases have both been successful in producing customized oligosaccharides with specific functional properties [43], [44]. These technologies improve not only availability but also facilitate tailoring oligosaccharide compositions for specific health effects [44], [45].

5. CONCLUSION

Animal milk oligosaccharides, i.e., from bovine and caprine sources, represent a sector with high promise for biomedical and nutritional innovation. Irrespective of less structural diversity than HMOs, their bioactivity and accessibility make them plausible for functional food formulations and infant diet. Future investigation into glycosylation pathways, as well as microbial synthesis has the potential to curtail the difference between animal and human milk oligosaccharides in future applications.

Growing interest in oligosaccharides from animal milk (milk oligosaccharides) underscores the need for coordinated, interdisciplinary strategies to unlock their full biological and therapeutic potential. The future should involve thorough glycomic analysis of more domesticated and wild mammalian species. This will uncover new oligosaccharide structures and interspecies variations that can possess special biological properties. One such pathway concerns synthetic biology and bioengineering approaches toward the scaling-up of production of rare and complex milk oligosaccharides, especially fucosylated and sialylated types, short in supply in non-human milk. The organisms can be genetically manipulated (e.g., Lactococcus lactis, Escherichia coli, Saccharomyces cerevisiae) along with the in vitro enzyme systems to produce MOs with maximum precision and yield. Such technologies may enable the development of cost-effective manufacturing streams, adaptable for pharmaceutical, nutraceutical, and infant formula industries. Clinical testing in human and animal models must further be undertaken to identify animal milk oligosaccharide efficacy, safety, and effective dose ranges. Gut health, immunomodulation, neurodevelopment, and metabolic impacts should be investigated as a function of age and state of health. Whereas merging AI-guided molecular modeling and systems biology platforms will be capable of further accelerating functional predictions, structure–activity relationships, and host–microbe interaction mapping, regulatory policies must also evolve in order to facilitate commercialization of animal-derived milk oligosaccharides, balancing safety standards and stimulating innovation.

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Author Contributions Statement

Name of Author	C	M	So	Va	Fo	I	R	D	O	E	Vi	Su	P	Fu
Apurwa Singh	✓				✓	✓		✓	✓				✓	
Parinita Tripathy	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		

C : **C**onceptualization
M : **M**ethodology
So : **So**ftware
Va : **Va**lidation
Fo : **Fo**rmal analysis
I : **I**nvestigation
R : **R**esources
D : **D**ata Curation
O : Writing - **O**riginal Draft
E : Writing - Review & **E**diting
Vi : **Vi**sualization
Su : **Su**pervision
P : **P**roject administration
Fu : **Fu**nding acquisition

Conflict of Interest Statement

No conflict of interest.

Informed Consent

We have obtained informed consent from all individuals included in this study.

Ethical Approval

Not applicable.

Data Availability

Data availability does not apply to this paper as no new data were created or analyzed in this study.

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BIOGRAPHIE OF AUTHORS

Apurwa Singh, received the M.Sc. degree from Bilaspur University, Bilaspur, Chhattisgarh, India, and is presently pursuing a Ph.D. from Kalinga University, Raipur, Chhattisgarh, India. She has published more than 5 papers on the isolation, extraction, and bioactivity of medicinal plants with one national design patent. Her research interests are in organic chemistry, natural products, medicinal chemistry, green chemistry, carbohydrate chemistry, as well as their spectral analysis. Email: singhapurwa73@gmail.com

Parinita Tripathy, received the M.Sc. degree in chemistry from Kalinga University, Raipur, Chhattisgarh, India, with the Dissertation "Synthesis of Fibres from Urginea indica Kunth". She is a Research Scholar in Kalinga University, Raipur, Chhattisgarh, India. She has published more than 20 papers on the isolation, extraction, and bioactivity of medicinal plants, as well as computational chemistry and nanomedicine, with one book and an international patent. Her research interests are in organic chemistry, natural products, medicinal chemistry, green chemistry, carbohydrate chemistry, as well as their spectral analysis. She gets the 20th Chhattisgarh Congress Young Scientist Award 2025, in the field of chemical science, by the Chhattisgarh Council of Science and Technology. She is currently working as a research assistant in the Department of Chemistry, Kalinga University, Raipur, Chhattisgarh, India. Email: parinitatripathy2023@gmail.com