Decoding Silkworm Host Plant Interactions: A Comprehensive Review of Chemosensory and Genetic Mechanisms in *Bombyx mori* and *Antheraea assamensis*

Indrani Nath [a*], Pankaj Lushan Dutta [a] and Manasee Hazarika Ahmed [b]

[a] *Department of Sericulture, Forest College and Research Institute, Mettupalayam, Tamil Nadu Agricultural University, Tamil Nadu-641301, India.*
[b] *Department of Sericulture, College of Sericulture, Assam Agricultural University, Jorhat-785013, Assam, India.*

Authors' contributions

This work was carried out in collaboration among all authors. The author IN conceptualised the review, conducted the primary literature search and wrote the initial draft of the manuscript. Author PLD assisted in literature search and data analysis, contributed to the writing and revision of the manuscript and provided critical feedback on the draft. Author MHA provided expertise on specific topics covered in the review, reviewed and edited the manuscript for important intellectual content and approved the final version for submission. All authors read and approved the final manuscript.

Review Article

_____

*Corresponding author: Email: nathindrani8@gmail.com;

ABSTRACT

Understanding the intricacies of silkworm–host plant interactions is pivotal for advancing sustainable sericulture and improving silk productivity. This review comprehensively examines the behavioral, chemical, and molecular mechanisms governing host plant recognition and feeding in *Bombyx mori* (monophagous) and *Antheraea assamensis* (polyphagous). We detail how silkworm larvae rely on a sophisticated two-step chemosensory process involving maxillary palp and galea, with specialized gustatory receptors responding to stimulants such as chlorogenic acid, β-sitosterol, and sucrose. In *B. mori*, feeding is highly selective, driven by gustatory and olfactory receptor genes like *Gr66*, *Gr6*, and *Gr9*, which enforce mulberry specificity. Gene-editing studies reveal that these receptors act as molecular gatekeepers of host fidelity. Conversely, *A. assamensis* exhibits broader chemosensory plasticity, accepting a range of Lauraceae species due to a more diverse receptor repertoire and less stringent phytochemical thresholds. We also explore the role of phytochemicals in muga host plants such as *Persea bombycina*, and highlight the need for functional genomics studies to decode the sensory basis of polyphagy in non-mulberry silkworms. Insights from this review offer new avenues for artificial diet development, genetic improvement of silkworm strains, and sericultural resource optimization. Furthermore, comparative findings between monophagy and polyphagy contribute to our broader understanding of insect–plant co-evolution and sensory ecology.

1. INTRODUCTION

Sericulture is a traditional agro-based industry that integrates the cultivation of host plants, rearing of silkworms, and the processing of cocoons through reeling and spinning to produce high-quality silk yarn. It is widely recognized for its sustainability, labor-intensive nature, and socio-economic importance, particularly in developing nations such as India and China. With its potential to generate quick financial returns within a short span, sericulture has become an increasingly vital source of income for rural and semi-urban populations. The industry is broadly classified into two main sectors based on the feeding behavior and host plant specificity of silkworms: mulberry and non-mulberry sericulture (Padaki et al., 2014; Das et al., 2020). The mulberry sector primarily involves the rearing of the domesticated silkworm *Bombyx mori* L. for producing fine, commercial-grade silk. In contrast, the non-mulberry sector includes the rearing of wild silkworms, or "vanya" silks, such as muga (*Antheraea assamensis*), eri (*Samiaricini*), tropical tasar (*Antheraea mylitta*), and temperate tasar (*Antheraea proylei*) (Saikia & Saikia, 2022).

The diversity of sericulture systems is closely tied to the feeding behavior of silkworms, which, in turn, reflects a broader pattern observed across insect taxa. Insects constitute the most diverse and numerous animal groups on Earth, representing nearly 50–70% of all described species (Caers et al., 2012; Bellés, 2010). This biodiversity is largely shaped by their wide-ranging feeding ecologies and adaptive strategies across habitats (Song et al., 2021). Insects can be broadly grouped based on dietary habits into phytophagous (plant-feeding), carnivorous, and omnivorous types (Regier et al., 2015). Within phytophagous insects, feeding specialization varies from strict monophagy, where insects feed on a single plant species to oligophagy and euryphagy, where insects consume a limited or wide range of plant taxa, respectively (Morris, 2007).

This variation in host plant use has profound implications for sericulture. The host plant not only serves as the primary food source but also directly influences silkworm physiology, growth, cocoon formation, and silk quality (Saranya et al., 2019). *Bombyx mori*, being monophagous, feeds exclusively on mulberry (*Morus* spp.) leaves, which are nutritionally rich and capable of meeting the complete dietary needs of the silkworm (Fraenkel, 1959; Nagaraju, 2002; Fambayun et al., 2022). The quality and availability of these leaves are therefore pivotal to successful silkworm rearing. Factors such as plant cultivar, leaf maturity, environmental conditions, and the concentration of secondary metabolites collectively determine the nutritional profile of the foliage. These variables significantly influence key biological traits in

silkworms including larval survival, growth rate, cocoon yield, and filament quality (Samami et al., 2019).

Silkworms, like other phytophagous insects, employ complex chemosensory systems to recognize, assess, and accept suitable host plants. The feeding process is initiated and regulated by a combination of physical characteristics (such as texture, shape, and color) and chemical cues, particularly plant volatiles and surface compounds (Miller &Strickler, 1984; Rausher, 1978; Renwick, 1990; Carter & Feeny, 1999). Host plant location is typically guided by olfactory and visual cues at long range, whereas tactile and gustatory perception becomes dominant at close range (Bernays & Chapman, 1994). Once the silkworm larva comes into contact with a leaf surface, its gustatory receptor neurons are activated to evaluate the presence of stimulatory or inhibitory compounds, thereby influencing feeding decisions (Watanabe, 1958; Thorsteinson, 1960; Ishikawa et al, 1969).

A substantial body of research has demonstrated the importance of secondary plant metabolites in mediating host plant selection and feeding behavior in lepidopteran larvae (Haynes et al., 1991; Lopez et al., 2000; Legay, 1958). Compounds such as phenolics, flavonoids, sterols, and terpenoids act either as phagostimulants, encouraging feeding, or as deterrents, depending on their concentration and the insect's gustatory receptor response. In *B. mori*, specific chemicals like chlorogenic acid, isoquercetin, and β-sitosterol have been shown to elicit strong feeding responses and promote larval development (Ito & Tanaka, 1959; Nayar & Fraenkel, 1962; Neog et al., 2011), highlighting the critical role of host plant chemistry in silkworm biology.

Further complicating this interaction is the role of adult female behavior in oviposition site selection. In insects with limited larval mobility, such as silkworms, the choice of oviposition site by the female strongly determines larval success. Females rely on a suite of environmental and chemical cues to locate optimal host plants that ensure suitable larval habitats and food resources (Gotthard et al., 2005; Bossart & Scriber, 1999). Therefore, the relative acceptability of a host plant is governed by a dynamic interplay of intrinsic factors such as genetic and neurophysiological makeup and extrinsic factors, including surface chemistry and plant volatiles (Sokame et al., 2020; Scheirs et al., 2000).

Among the diverse types of silk produced worldwide, mulberry and muga silk stand out due to their exceptional quality, fine texture, natural sheen, and high market value. These qualities have led to their widespread popularity in the textile industry and cultural heritage sectors. Given their superior attributes and commercial importance, the present review focuses primarily on these two silkworm species—*Bombyx mori* and *Antheraea assamensis* with the objective of unraveling the chemical and molecular mechanisms that underlie their feeding behavior and host plant interactions.

Although advances have been made in understanding the ecological and physiological aspects of silkworm–host plant relationships, the deeper molecular mechanisms, especially those linked to chemoreception, receptor gene expression, and downstream signaling remain incompletely understood. This review seeks to bridge this knowledge gap by compiling and analyzing current findings on the chemical ecology and molecular biology of silkworm feeding, with special emphasis on gustatory receptor functions, secondary plant metabolites, and genetic determinants that shape host specificity and adaptability in *B. mori* and *A. assamensis*.

2. HOST PLANTS OF MULBERRY SILKWORM

The domesticated silkworm, *Bombyx mori* L., is a phytophagous insect of significant economic importance, primarily reared for silk production. Although it is traditionally viewed as a monophagous species due to its strong preference for mulberry (*Morus* spp.) leaves, which provide a complete nutritional profile essential for its growth, development, and cocoon formation (Fraenkel, 1959), its feeding behavior is more accurately described as oligophagous. In addition to mulberry, *B. mori* has been experimentally observed to accept leaves from other plant families, including Ulmaceae (e.g., wild elm), Compositae (e.g., lettuce and dandelion), and Urticaceae (Fraenkel, 1959; Ishikawa et al., 1969). However, these alternative host plants are markedly inferior in nutritional quality compared to mulberry, often resulting in poor larval development, reduced silk production, or even mortality due to phytochemical incompatibility or toxicity

(Fraenkel et al., 1959). Historical and comparative analyses (Zhang et al., 2013; Legay, 1958; Fraenkel, 1959; Jacobson, 2019) also support the classification of *B. mori* as an oligophagous insect, with restricted but observable feeding flexibility beyond the Moraceae family. Nonetheless, under practical rearing conditions, mulberry remains the only viable and nutritionally optimal host plant for sustainable and profitable silkworm cultivation.

3. CHEMOSENSORY MECHANISMS IN SILKWORM FEEDING BEHAVIOR

Silkworm feeding behavior is orchestrated by a complex interplay of behavioral, physiological, and molecular mechanisms involving specialized chemosensory organs. Both *Bombyx mori* (the monophagous mulberry silkworm) and *Antheraea assamensis* (the polyphagous muga silkworm) rely on finely tuned sensory systems to recognize and discriminate among host plants, though their degree of selectivity and sensory adaptations differ considerably. Understanding these mechanisms is critical not only for elucidating silkworm–plant interactions but also for advancing sericultural practices, artificial diet development, and host plant improvement.

3.1 Behavioral and Electrophysiological Basis of Host Recognition

Initial host plant recognition in silkworms begins with long-range olfactory cues detected by chemoreceptors located on the antennae and maxillary palps (Sato & Touhara, 2008; Hansson, 1995; Johnson et al., 2011; Nissan et al., 2009).

These cues, often in the form of plant-emitted volatile organic compounds, guide larvae to potential food sources (Ishikawa et al., 1969). Upon contact, tactile and gustatory cues dominate, with test biting behavior serving as a crucial evaluative step (Van & Carlson, 2006). This is mediated by gustatory receptors located on the maxillary galea and labrum, which sense surface phytochemicals and exuded sap from host leaves (Bernays & Chapman, 1994, 2001; Watanabe, 1958; Watanabe et al., 2011; Miles et al., 2005; Van & Schoonhoven, 1999) (Fig. 1).

Electrophysiological studies in *B. mori* have demonstrated that the larvae respond selectively to specific host-derived compounds, such as chlorogenic acid, β-sitosterol, and flavonoids like isoquercetin, found in *Morus* spp. leaves (Ito & Tanaka, 1959; Nayar & Fraenkel, 1962). Activation of sensory neurons upon detection of these compounds initiates feeding. Similar behavior has been observed in *A. assamensis*, though the range of acceptable host plants is broader, and the spectrum of responsive compounds is more diverse due to its polyphagous nature (Mech & Vijay, 2022; Haloi et al., 2023).

3.2 Two-Factor Host Acceptance Model in *Bombyx mori*

Recent advances have clarified the two-step chemosensory mechanism in *B. mori*, as proposed by Tsuneto et al. (2020) (Fig. 2). In this model, host acceptance involves sequential input from two key maxillary structures:
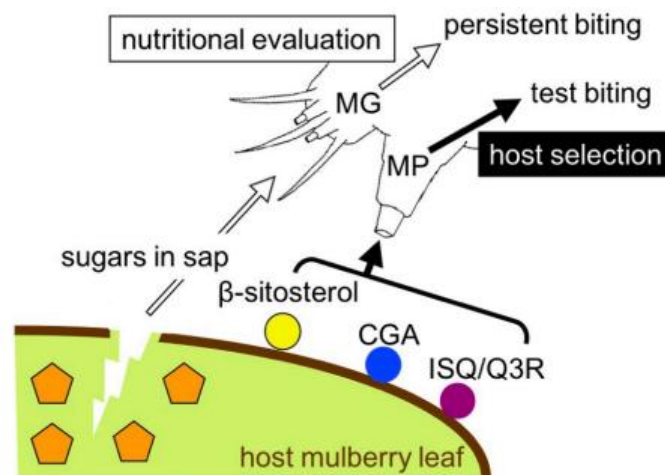
Fig. 1. Host recognition and acceptance by *B. mori*
(Tsuneto et al., 2020)

- The maxillary palp (MP) plays a critical role in the initial recognition phase. It houses ultra-sensitive gustatory neurons capable of detecting host-specific phytochemicals, including chlorogenic acid, β-sitosterol, and isoquercetin, at extremely low concentrations (attomolar to femtomolar levels). These compounds are found on the leaf surface waxes of mulberry and serve as reliable chemical signatures for *B. mori*. Activation of MP receptors by these molecules triggers the larva to engage in test biting behavior.

- Following this, the maxillary galea (MG) becomes active during the test bite stage, where it evaluates compounds released from the leaf sap. Sugars like sucrose and myo-inositol, which leak from the damaged plant tissues, act as feeding stimulants when detected by MG receptors (Ishikawa et al., 1969; Wanner & Robertson, 2009). The detection of these compounds confirms the palatability and nutritional suitability of the plant, prompting the larva to initiate persistent feeding.
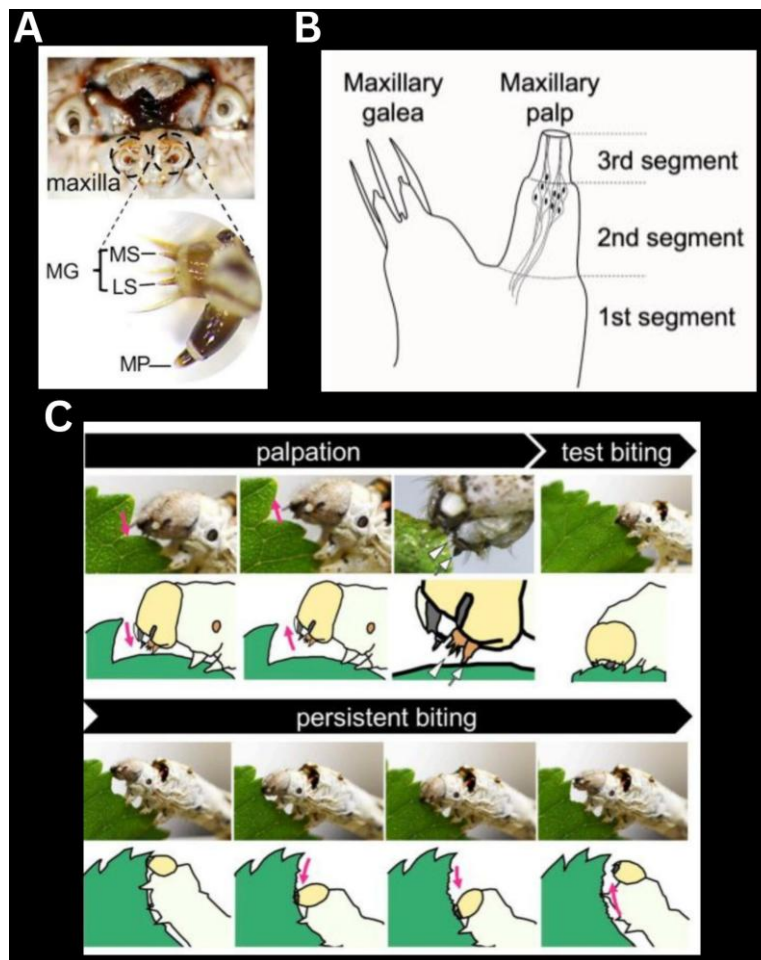
Fig. 2. Sequential Feeding Behavior in *Bombyx mori* Larvae Mediated by Maxillary palp (MP) and Maxillary galea (MG). (A) Mouthparts of a silkworm larva. The maxilla consists of the MG and MP. The MG has 2 gustatory sensilla, the lateral styloconicsensillum (LS) and median styloconicsensillum (MS). (B) Schematic diagram of the maxilla of a silkworm larva. (C) Feeding on mulberry leaves by silkworm larvae. (1) Palpation: a silkworm larva first palpates the leaf surface with its maxilla (MP and MG) for 5–30 seconds. The white arrow and arrowhead indicate MP and MG. (2) Test biting: the larva bites the leaf edge several times intermittently during palpation. (3) Persistent biting: the larva nibbles the leaf edge repeatedly (2–3 times per second) with its head moving in the dorsoventral direction along the leaf edge. Magenta arrows indicate the direction of head movement
(Tsuneto et al., 2020; Endo et al., 2024)

4. KEY PHYTOCHEMICALS INFLUEN-CING SILKWORM FEEDING

The feeding behavior of silkworms, particularly *Bombyx mori* and *Antheraea assamensis*, is primarily governed by a complex interaction between phytochemicals present on the leaf surface and within the sap. These compounds function either as stimulants or deterrents, modulating silkworm host plant selection, feeding initiation, and continuation. The maxillary palp (MP) and maxillary galea (MG) of silkworm house specialized gustatory receptors that detect these compounds and trigger appropriate behavioral responses (Ishikawa et al*.,* 1969; Endo et al*.,* 2024).

4.1 Feeding Stimulants

4.1.1 Chlorogenic acid

Chlorogenic acid has been consistently identified as one of the most effective feeding stimulants in *B. mori*. It acts during the palpation and test biting phase and is detected by sensory neurons in the MP. Endo et al*.* (2024) demonstrated that chlorogenic acid, when applied at attomolar concentrations, is sufficient to elicit test biting. Earlier work by Ito & Tanaka (1959) confirmed its bioactivity even in isolation from the leaf matrix and also reported strong feeding stimulation in response to chlorogenic acid extracted from mulberry leaves, linking its presence to increased larval acceptability.

4.1.2 β-Sitosterol and quercetin glycosides

These phytochemicals also play a critical role in feeding initiation. β-Sitosterol and quercetin glycosides, often co-occurring with chlorogenic acid, significantly increase test biting frequency (Endo et al*.,* 2024; Tsuneto et al*.,*2020; Chun, 1972; Devitt & Smith, 1985). According to behavioral assays, their combined presence triggers a greater than 50% acceptance rate in larvae during initial inspection (Endo et al*.,* 2024). These compounds may also act as leaf surface recognition cues, mimicking essential sterols and flavonoids needed for larval development.

4.1.3 Sucrose and myo-inositol

Post-test biting, silkworm larvae evaluate internal sap for sugars that signal nutritional adequacy. Two specific gustatory receptors in the MG, BmGr6, which responds to sucrose, and BmGr9, which responds to myo-inositol, mediate this response (Endo et al*.,* 2024; Morinaga et al*.,* 2022). This receptor activation leads to persistent biting, a hallmark of host acceptance (Chun, 1972; Devitt & Smith, 1985). Nayar & Fraenkel (1962) similarly observed that sucrose solutions directly applied to leaf tissue increased biting frequency and reduced hesitation time. In *A. assamensis*, although receptor-specific data are limited, similar sugars and polyols in som (*Persea bombycina*) and soalu (*Litsea monopetala*) sap are believed to contribute to host plant recognition (Haloi et al*.,* 2023).

4.2 Feeding Deterrents

4.2.1 Antagonistic compounds in non-host plants

Compounds found in non-host plants such as *Artemisia vulgaris* have been shown to interfere with gustatory signaling. Ethanol extracts of *A. vulgaris* suppressed sucrose-induced activation in MG neurons, reducing the likelihood of persistent biting (Endo et al*.,* 2024). This is consistent with findings by Xu et al*.* (2024), who demonstrated that sesquiterpene lactones and alkaloids in bitter plants could block sugar receptor pathways.

4.2.2 Absence of key stimulants

Another form of deterrence is passive rejection, when test biting fails to yield sufficient levels of phagostimulants like chlorogenic acid, β-sitosterol, or sugars. Endo et al*.* (2024) noted that leaves lacking these three signature compounds triggered minimal feeding behavior. This explains why *B. mori*, though oligophagous, exhibits near-monophagous behavior under natural conditions.

5. MOLECULAR GENETICS OF HOST PREFERENCE

The host preference of the domesticated silkworm, *Bombyx mori*, presents a compelling model to explore the molecular genetic mechanisms underlying insect-plant interactions. As an oligophagous insect, *B. mori* feeds almost exclusively on mulberry (*Morus spp.*) leaves, despite having the capacity to accept a limited range of alternative host plants under artificial conditions. This narrow dietary preference is regulated not only by behavioral and physiological traits but also, and more importantly, by an intricate genetic network

involving chemosensory receptors, particularly those governing gustatory and olfactory perception. With the advent of high-throughput molecular tools, including whole-genome sequencing, transcriptomic profiling, and gene-editing technologies, significant advances have been made in identifying key genes and pathways that shape the feeding specificity of *B. mori*.

5.1 Gustatory System and Host Discrimination

The gustatory system plays a foundational role in host plant discrimination by enabling the silkworm to detect non-volatile compounds through specialized gustatory receptor neurons (GRNs) located on its maxillary galea. Electrophysiological investigations of the styloconicsensilla (SS-I and SS-II) revealed that these structures respond robustly to certain phagostimulants, especially vitamin C, sucrose, and inositol, which are abundant in mulberry leaves (Cui et al., 2001) (Table 1). Interestingly, these compounds can also exhibit mutual inhibitory effects on sensory neurons; for instance, vitamin C suppresses the response of SS-I to sucrose and inositol and vice versa, indicating a complex regulatory crosstalk between stimulatory and inhibitory signals at the peripheral sensory level.

At the molecular level, gustatory receptors (Grs), which belong to a distinct family of seven-transmembrane domain proteins, are central to decoding the chemical profile of potential food sources. Genome-wide annotations have identified up to 76 Gr genes in *B. mori*, several of which are expressed in chemosensory tissues such as the maxillae, antennae, and even in the central nervous system (Guo et al., 2017). Among them, BmGr6, BmGr8, and BmGr4–10 function as sugar receptors, recognizing compounds like inositol and epi-inositol, which further reinforce mulberry specificity (Zhang et al., 2011; Mang et al., 2016). Notably, the maxillary galea, a critical gustatory organ—plays a fundamental role in assessing the nutritional quality of a leaf following test biting, the initial stage of feeding. Within this structure, BmGr6 and BmGr9 serve as molecular sensors for sugars present in leaf sap, and their activation determines whether the larva proceeds to sustained feeding (Endo et al., 2024). In contrast, BmGr53, BmGr16, BmGr18, and BmGr66 are categorized as bitter receptors, responding to deterrent compounds such as

coumarin, caffeine, and pilocarpine (Kasubuchi et al., 2018). These bitter Grs are critical for rejecting unsuitable or toxic plant material, adding another layer of selectivity to the silkworm's feeding behavior.

Genetic studies have provided compelling evidence linking specific Gr genes to host preference. Using the CRISPR/Cas9 system, Baci et al. (2021) demonstrated that targeted disruption of the hestia gene converted *B. mori* from an oligophagous insect to one capable of consuming alternative foods such as apple and corn. Similarly, Zhang et al. (2019) reported that knockout of the bitter receptor gene Gr66 resulted in silkworm larvae that readily accepted atypical food sources, losing their inherent selectivity for mulberry. These findings underscore the genetic control of feeding preference and suggest that specific Grs function as molecular gatekeepers in host recognition.

5.2 Olfactory Contributions to Feeding Behavior

In parallel with gustation, the olfactory system plays a critical role in long-range host detection. Located on the antennae, the olfactory apparatus includes odorant receptors (Ors), odorant-binding proteins (OBPs), and odorant-degrading enzymes (ODEs). These components work in concert to detect, transduce, and terminate responses to volatile semiochemicals released by host plants.

Odorant-binding proteins serve as the first interface between environmental volatiles and neuronal receptors. Gong et al. (2009) demonstrated that proteins such as GOBP, ABP, and PBPs (PBP1–3) are differentially expressed in the olfactory tissues of *B. mori* and are involved in transporting volatile molecules through the sensillar lymph to their corresponding Ors. Among these, PBP1 binds sex pheromones like bombykol and bombykal and transfers them to BmOr1 and BmOr3, respectively, facilitating not only mating behavior but also feeding-related responses.

Olfactory receptors themselves play a direct role in modulating feeding. For instance, BmOr56 has been shown to exhibit high sensitivity to cis-jasmone, a potent attractant in mulberry leaves, and mediates behavioral attraction in larvae (Tanaka et al., 2009). Xin & Zhang (2020) further demonstrated that BmOr54 and BmOr56 exert opposing effects on feeding, Or56 promotes

feeding while Or54 suppresses it. Simultaneous disruption of both genes using CRISPR/Cas9 significantly altered larval feeding patterns, establishing these genes as key regulators of olfactory-driven host selection.

The co-receptor Orco, essential for functional olfactory signaling complexes, is also implicated in feeding regulation. Sun et al. (2022) observed that Orco expression correlates with feeding intensity and is downregulated under starvation, suggesting that it contributes to olfactory sensitivity and, by extension, feeding behavior. Supporting this, odorant-degrading enzymes such as BmGSTD1 (a glutathione-S-transferase) and CYP6AE21 (a cytochrome P450) act to rapidly degrade odorant molecules after signal transduction, maintaining olfactory acuity and preventing sensory desensitization (Liu et al., 2024; Wang et al., 2011).

5.3 Evolutionary Implications and Genomic Architecture

Comparative genomic analyses reveal that the chemosensory genes involved in host preference have undergone significant duplication and divergence. Zhang et al. (2011) noted that many Gr and Or genes are arranged in tandem on the same chromosomes, particularly chromosomes 7 and 17, implying evolutionary expansion through gene duplication events. These genes are believed to have originated from common ancestral loci and diversified to enable species-specific adaptation. Notably, Gr66 and its homologs appear to play pivotal roles in maintaining mulberry specificity, whereas mutations in these genes result in expanded dietary flexibility, suggesting a strong link between genotype and host preference phenotype.

6. INSIGHTS FROM MUGA SILKWORM (*Antheraea assamensis*)

6.1 Feeding Preferences and Host Plants

The golden-hued muga silk is produced by the semi-domesticated silkworm *Antheraea assamensis* Helfer, a polyphagous lepidopteran species known for its ability to utilize a diverse array of host plants. The natural distribution of its food plants spans extensively across the northeastern region of India, particularly in states such as Assam, Meghalaya, Manipur, Mizoram, Nagaland, Tripura, and Sikkim. Additionally, several northern and eastern states, including Himachal Pradesh, Uttarakhand, Uttar Pradesh, Gujarat, West Bengal, and the Union Territory of Puducherry, also support the growth of these host plants. In Arunachal Pradesh, their occurrence is more sporadic (Mech & Vijay, 2022; Haloi et al., 2023).

Among the various host species, *Persea bombycina* (locally known as som) and *Litsea monopetala* (soalu) are regarded as the primary food plants, providing optimal nutrition and supporting healthy larval growth. Secondary host plants include *Litsea salicifolia* (dighloti) and *Litsea citrata* (mejankori), which are also commonly used but are considered slightly inferior in nutritional quality. Beyond these, several additional species serve as minor or tertiary hosts, including *Cinnamomum glaucescens*, *Actinodaphne obovata*, *Michelia champaca*, *Zizyphus jujuba*, *Zanthoxylum rhetsa*, and *Celastrus monosperma* (Neog et al., 2005). These alternative hosts, although not commonly used in commercial rearing, can support larval development under specific ecological or seasonal constraints. A comprehensive list of host plants for *A. assamensis* is detailed in Table 2, highlighting the species' broad polyphagous feeding nature and adaptability to varied ecological conditions.

The muga silkworm, *Antheraea assamensis*, is a polyphagous insect that exhibits strong feeding preferences for members of the Lauraceae family, primarily *Persea bombycina*, *Litsea polyantha*, and *Litsea citrata*. Among these, the tender leaves of *Litsea polyantha* showed the highest concentration of soluble protein (17.17 mg/g), whereas the tender leaves of *Persea bombycina* recorded the highest total phenol content (119.79 mg/100 g) (Table 3). In contrast, the mature and medium leaves of *Litsea citrata* exhibited the lowest levels of soluble protein (8.86 mg/g) and total phenols (15.50 mg/100g), which contribute to both nutritional quality and chemical signaling essential for larval development (Haloi et al., 2023; Neog et al., 2005).

6.2 Role of Chemical Stimulants

Feeding stimulation in *A. assamensis* is driven by an array of phytochemicals. Flavonoids such as myricetin and 7,2',4'-trimethoxy-dihydroxy flavone, along with β-sitosterol (0.69–1.06 %), are crucial in eliciting biting and acceptance behaviors. Additionally, volatile terpenoids like caryophyllene and linalyl acetate, detected via

Table 1. Factors influencing feeding behavior in *B. mori*

Classification	Silkworm-related and general functions	Factors	Function	Reference
Gustatory	Styloconicsensilla on the maxillary galea (SSI and SSII)	Vitamin C, sucrose and inositol	SSI and SSII are the primary sensory sites initiating feeding. Vitamin C suppress their response of SSI to sucrose and inositol. Conversely, sucrose and inositol can inhibit the response of SS-I and SS-II to vitamin C.	Cui & Xu, 2001
	Gustatory receptors (Grs)- involved in food preference and selection	BmGr9, BmGr8, BmGr4-10,	Function as Sugar receptor	Mang et al., 2016; Zhang et al., 2011
		BmGr53, BmGr16, BmGr18, BmGr66	Function as Bitter receptor	Zhang et al., 2011; Kasubuchiet al., 2018; Zhang et al., 2019
Olfactory	Odorant binding proteins (OBPs)- facilitate transport of odor molecules to sensory neurons, triggering signal transmission	GOBP	Capable of binding a range of odor molecules from food and the environment	Zhang, 2009
	Olfactory receptors (Ors)- convert odorant chemical signals into electrical responses via ion channel changes	BmOr56	Highly responsive to cis-jasmone, a strong attractant from mulberry leaves; mediates behavioral attraction.	Tanaka et al., 2009
		BmOr54 and BmOr56	Or56 stimulates feeding, whereas Or54 suppresses it. These two receptors work antagonistically to regulate larval feeding	Liu, 2017
Mulberry leaf	Attracting factors	α, β-hexenal, β, γ-hexenol, citral, linalyl acetate and linalol	Elicit feeding behavior in larvae	Watanabe et al., 1958; Hamamura & Naito, 1961
	Biting factors	β-sitosterol	Induces biting activity	Takeda & Ueda, 1984; Nagata et al.,2011
	Swallowing factors	Cellulose, phosphate and silica, Sucrose, inositol, high levels of casein	Enhance feeding and swallowing responses	Nagata et al.,2011; Song et al., 2022; Naito et al.,

Classification	Silkworm-related and general functions	Factors	Function	Reference
		and ascorbic acid isoquercetin, morin, quercetin, chlorogenic acid, vanillin, polyphenolic acid, choline, certain vegetable oils and fatty acids		1965; Kato and Yamada, 1966; Hamamura et al., 1966; Hayashiya, 1965
	Inhibitory factors	Tartaric acid, malic acid, sorbic acid, acetic acid and phosphoric acid	Suppress the growth and feeding of silkworms.	Tsai et al., 1978; Cui et al., 1998
	Avoidance factor	Artemisinin	Suppresses feeding behavior in larvae	Zhang, 2012

(Song et al., 2021)

Table 2. Host plants of muga silkworm

Status of Food Plant	Host Plants	Family
Primary	*Persea bombycina*	Lauraceae
	Litsea monopetala	Lauraceae
Secondary	*Cinnamomum camphora*	Lauraceae
	Cinnamomum tamala	Lauraceae
	Litsea citrata	Lauraceae
	Litsea salicifolia	Lauraceae
	Actinodaphne augustifolia	Lauraceae
	Actinodaphne obovata	Lauraceae
	Celastrus monosperma	Celastraceae
Tertiary	*Cinnamomum cecidodaphne*	Lauraceae
	Cinnamomum glanduliferum	Lauraceae
	Cinnamomum obtusifolium	Lauraceae
	Gmelina arborea	Verbenaceae
	Litsea nitida	Lauraceae
	Machilus odoratissima	Lauraceae
	Magnolia pterocarpa	Magnoliaceae
	Michelia champaca	Magnoliaceae
	Michelia oblonga	Magnoliaceae
	Symplocos grandiflora	Symplocaceae
	Symplocos paniculata	Symplocaceae
	Symplocos ramosissima	Symplocaceae

(Tikader et al., 2013; Das et al., 2020)

Table 3. Comparative analysis of protein, phenolic content, and PAL activity in leaves of host plants at different maturity stages

Host Plant	Maturity Level	Protein Content (mg/g)	Total Phenol Content (mg/100 g)	PAL Activity (nmole/mg/min)
Persea bombycina	Tender	16.23	119.79	3.48
	Medium	11.61	47.26	4.14
	Mature	9.98	53.12	2.06
Litsea polyantha	Tender	17.17	40.41	3.03
	Medium	13.67	101.39	3.22
	Mature	11.19	34.30	1.44
Litsea salicifolia	Tender	14.23	31.10	2.54
	Medium	13.03	47.51	2.42
	Mature	9.44	101.97	1.19
Litsea citrata	Tender	12.13	34.51	2.52
	Medium	9.93	15.50	1.81
	Mature	8.86	28.43	0.96

(Neog et al., 2011 b)

olfactory pathways act as attractants that guide larvae toward suitable foliage. These chemicals, often concentrated in younger leaves, serve as both feeding cues and developmental enhancers (Mech & Vijay, 2022; Tikaderet al*.,* 2013).

6.3 Secondary Metabolite Analysis

High-performance liquid chromatography (HPLC) profiling of *P. bombycina* leaves has revealed high concentrations of chlorogenic acid (1.45–2.06%) and β-sitosterol in tender and semi-mature stages, which contribute to palatability and possess antioxidant and antimicrobial properties. Such compounds play a significant role not only in stimulating larval feeding but also in enhancing cocoon quality and larval immunity (Das et al*.,* 2020; Tikader et al*.,* 2013) (Table 4).

6.4 Chemosensory Flexibility in *Antheraea assamensis*

In contrast to the strict selectivity of *B. mori*, *A. assamensis* displays remarkable chemosensory plasticity, which supports its polyphagous lifestyle. The larvae accept a broad spectrum of host plants, primarily from the Lauraceae family (*Persea bombycina*, *Litsea monopetala*), but also including secondary and tertiary hosts like *Michelia champaca* and *Cinnamomum glaucescens* (Tikader et al*.,* 2013; Das et al*.,* 2020) (Table 5). Although fewer

Table 4. Quantitative profiling of secondary metabolites and phenolic compounds in *Persea bombycina* leaves at different maturity stages

Sl. No.	Secondary Metabolites	Tender	Medium	Mature
1	β-sitosterol (%)	1.06	0.82	0.69
2	Chlorogenic acid (%)	1.81	2.06	1.45
3	Phytic acid (mg/100g)	83.33	1642.20	2310.05
4	Total phenol (%)	1.946	1.182	0.712
5	Acid detergent fibre (%)	16.90	23.35	26.50
6	Acid detergent lignin (%)	8.02	13.52	15.83
7	Tannin (%)	6.71	2.05	3.00
Sl. No.	**Phenolic Compound**	**Tender (g/100 g)**	**Medium (g/100 g)**	**Mature (g/100 g)**
1	Quercetin	0.008	0.015	0.025
2	3', 4' Dimethyl Quercetin	0.026	0.035	0.042
3	Morin	0.028	0.035	0.045
4	Myrecetin	0.040	0.025	0.018
5	7, 2', 4' Trimethoxy dihydroxy flavone	0.038	0.030	0.015
6	2', 4' Dimethyl Morin	0.012	0.025	0.033

(Neog et al., 2011a, b)

Table 5. Behavioral response of Muga silkworm larvae to various chemical stimuli

Sl. No.	Name of the Chemical	Attraction	Biting
1	Myrcetin	No action	+ve
2	Morin	No action	No action
3	Quercetin	No action	No action
4	7, 2′, 4′ Trimethoxy dihydroxy flavone	No action	+ve
5	3′, 4′ Dimethyl Quercetin	No action	No action
6	2′, 4′ Dimethyl Morin	No action	No action
7	Beta sitosterol	No action	+ve
8	Myrcetin+ Beta sitosterol	Highly +ve	Highly +ve
9	7, 2′, 4′ Trimethoxy dihydroxy flavone +Beta sitosterol	Highly +ve	Highly +ve
10	Citral	+ve	-ve
11	Linalool	+ve	-ve
12	Linalyl Acetate	Highly +ve	-ve
13	Myrcetin+7, 2′, 4′ Trimethoxy dihydroxy flavone +Beta sitosterol	+ve	-ve
14	Geraniol	No action	No action
15	Hexanol	No action	No action
16	Caryophyllene	+ve	+ve
17	Decyl aldehyde	+ve	+ve
18	Dodecyl aldehyde	+ve	+ve
19	Geraniol+ Hexanol+ Caryophyllene	Highly +ve	Highly +ve
20	Gallic acid	-ve	+ve
21	Azainidole	-ve	Highly -ve
22	Control (water)	No action	No action

(Neog et al., 2011 b)

electrophysiological studies have been conducted on *A. assamensis*, analogous research on *Antheraea pernyi and Antheraea yamamai* suggests the presence of a well-developed array of gustatory and olfactory receptor genes expressed in the maxillary organs, antennae, and palps (Jiang et al*., 2023; Li et al., 2020).

Behaviorally, muga larvae also exhibit test biting followed by committed feeding, implying that a similar two-step chemosensory process may operate. However, the thresholds for stimulant detection are likely broader, and receptor tuning less specific, allowing the species to adapt to varying host chemical profiles. This sensory generalism is advantageous for survival in fluctuating environments where host plant availability changes seasonally.

Adult oviposition behavior in both species is chemically mediated. Females detect surface volatiles and cuticular compounds of leaves via chemoreceptors on the tarsi and ovipositor, ensuring eggs are laid on suitable host plants (Gothard et al*., 2005; Bossart & Scriber, 1999). In *A. assamensis*, the wider oviposition range corresponds with larval polyphagy, whereas in *B. mori*, oviposition is limited due to domestication and dependence on cultivated mulberry.

7. COMPARATIVE CHEMOSENSORY MECHANISMS UNDERLYING MONOPHAGY AND POLYPHAGY IN SILKWORMS

The divergence in feeding strategies between *Bombyx mori* and *Antheraea assamensis* reflects their distinct evolutionary histories and varying degrees of domestication. *B. mori*, a fully domesticated lepidopteran, exhibits strict monophagy, feeding exclusively on mulberry (*Morus* spp.). This limited host range is driven by a highly specialized and genetically constrained chemosensory system. Gustatory receptors (Grs), particularly Gr66, play a critical role in selective host plant recognition, ensuring high host fidelity and restricting dietary flexibility (Zhang et al*., 2019).

In contrast, *A. assamensis*, the muga silkworm, exhibits polyphagous behavior, feeding on a variety of host plants within the Lauraceae family, including *Persea bombycina*, *Litsea polyantha*, and *L. citrata*. This broader host acceptance is facilitated by a more diverse and adaptable set of gustatory and olfactory receptors, allowing larvae to respond to a wide array of phytochemical cues. The species' semi-domesticated status and its ecological association with diverse forest environments likely contribute to the
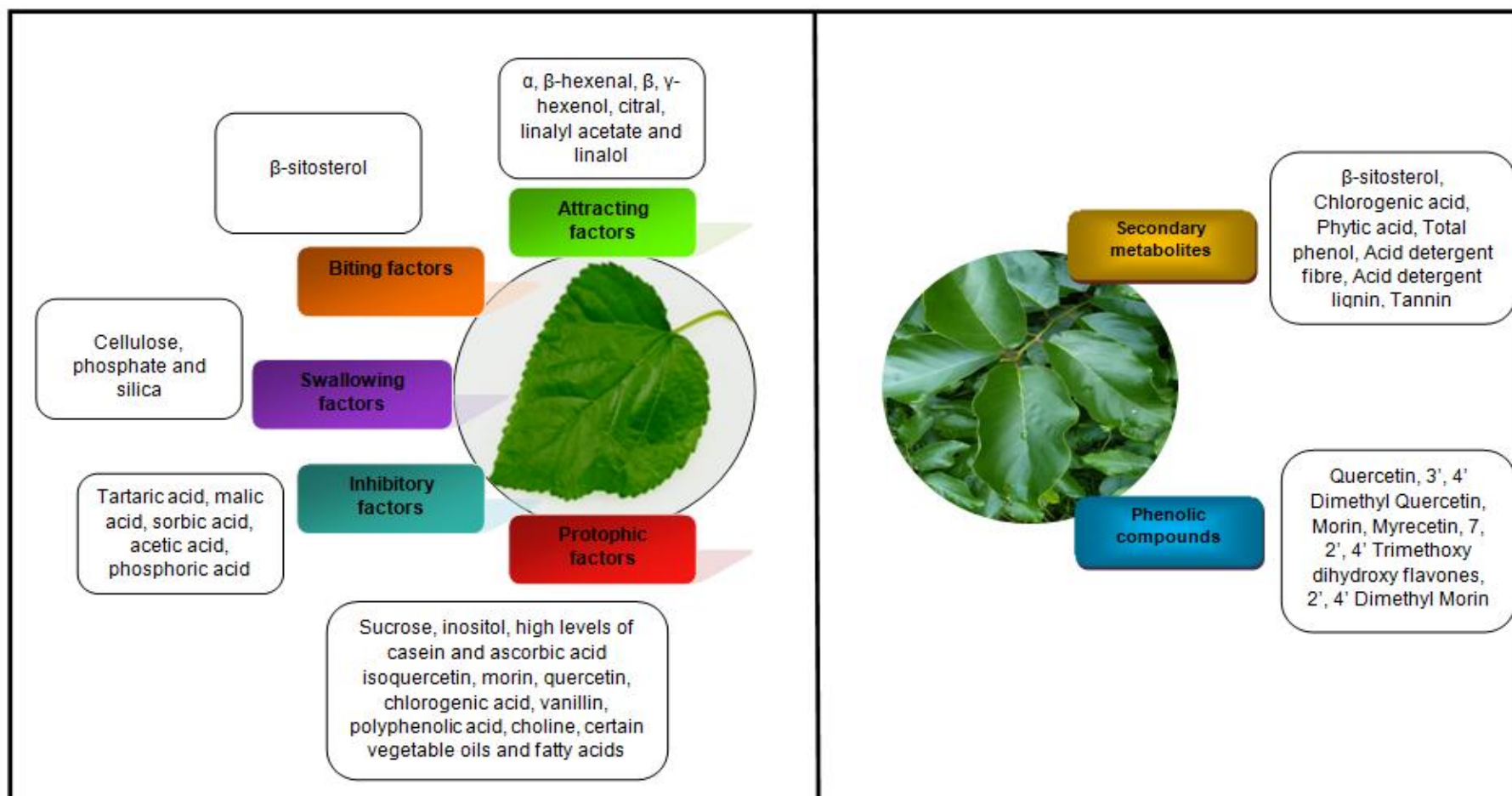
Fig. 3. Comparative analysis of phytochemical feeding cues in mulberry (*Morus* spp.) and Som (*Persea bombycina*) leaves influencing silkworm behavior

maintenance of this chemosensory plasticity. While extensive research has elucidated the molecular mechanisms governing host recognition and feeding behavior in *B. mori*, such as the role of specific feeding stimulants like β-sitosterol, sucrose, chlorogenic acid, and volatile organic compounds, the corresponding mechanisms in *A. assamensis* remain poorly understood. The phytochemical composition of its primary host, *Persea bombycina* (Som), and its influence on larval feeding behavior has not been comprehensively investigated.

To bridge this knowledge gap, further studies are required to identify and functionally characterize the gustatory receptor (Gr) genes in *A. assamensis*. Comparative transcriptomic analyses, receptor-ligand interaction assays, and behavioral studies are essential to uncover the molecular and neuroethological basis of polyphagy in this species. Such research will not only advance fundamental understanding of host plant adaptation but also support practical applications in muga silkworm breeding, host plant selection, and artificial diet formulation. Overall, comparative insights into the chemosensory systems of monophagous and polyphagous silkworms can significantly inform strategies for sustainable sericulture, species conservation, and the management of host plant resources.

8. APPLICATIONS AND FUTURE DIRECTIONS

8.1 Artificial Diet Formulation

The elucidation of key phytochemical stimulants, such as chlorogenic acid, β-sitosterol, quercetin glycosides, and sugars like sucrose, paves the way for designing nutritionally and behaviorally effective artificial diets. By incorporating these compounds into synthetic feed matrices, researchers can significantly improve the palatability and acceptability of artificial diets, especially for *B. mori*, which traditionally exhibits reluctance toward non-mulberry feeds.

8.2 Silkworm Breeding and Genetic Engineering

Advancements in molecular biology and genome editing techniques (e.g., CRISPR-Cas9) provide new opportunities to manipulate gustatory receptor genes like Gr66, Gr6, and Gr9. Modifying these receptors could yield silkworm strains capable of feeding on alternative or less resource-intensive host plants, enhancing sustainability and adaptability under changing agro-ecological conditions.

8.3 Pest Management Strategies

The knowledge derived from silkworm host plant interactions can be extended to agricultural pest species. Understanding chemosensory mechanisms can help develop targeted pest deterrents or resistant crop varieties by manipulating surface chemistry or metabolic pathways involved in host recognition.

8.4 Future Research Directions

While considerable research has elucidated the molecular and chemical basis of feeding in *Bombyx mori*, there remains a substantial gap in our understanding of the equivalent mechanisms in *Antheraea assamensis*. Future research should prioritize the identification and functional characterization of gustatory and olfactory receptor genes in *A. assamensis*, as well as the downstream neural circuits involved in host plant selection. Comparative transcriptomic analyses between larval stages fed on different host plants could reveal regulatory networks that govern polyphagy.

Furthermore, behavioral assays combined with metabolomic profiling of host plants can help delineate the precise chemical cues guiding muga silkworm feeding behavior. Integration of these approaches with genome editing tools will be instrumental in developing improved silkworm strains and refining sericultural practices tailored to the unique biology of muga silkworms. These insights hold promise not only for sericulture improvement but also for broader applications in insect ecology, evolutionary biology, and integrated pest management.

9. CONCLUSION

Silkworm feeding behavior is driven by a complex integration of plant-derived phytochemicals, chemosensory detection, and genetic regulation. In *Bombyx mori*, feeding is highly specific to mulberry due to the action of gustatory receptors such as Gr66, Gr6, and Gr9. These receptors recognize stimulants like chlorogenic acid, β-sitosterol, and sugars, triggering a precise sequence of feeding behaviors. Gene editing studies have confirmed that these receptors are key determinants of host fidelity. In contrast, the polyphagous muga

silkworm, *Antheraea assamensis*, responds to a broader array of phytochemicals including flavonoids and terpenoids from multiple Lauraceae host plants. While its feeding ecology is well-documented, the molecular basis of its host selection remains underexplored, highlighting a critical area for future investigation.

These insights not only illuminate evolutionary differences in host adaptation but also offer practical applications. Artificial diets incorporating identified stimulants can improve feed acceptance, while receptor-targeted genetic modifications may broaden host range. Additionally, this knowledge has implications for pest management and crop protection. Future research should focus on expanding molecular and functional studies in non-mulberry silkworms like *A. assamensis*, including receptor profiling and behavioral assays. Such efforts will support sustainable sericulture and advance our broader understanding of insect-plant interactions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

ACKNOWLEDGEMENTS

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

Baci, G. M., Cucu, A. A., Giurgiu, A. I., Muscă, A. S., Bagameri, L., Moise, A. R., et al. (2021). Advances in editing silkworms (*Bombyx mori*) genome by using the CRISPR-Cas system. *Insects, 13*(1), 28. https://doi.org/10.3390/insects13010028

Bellés, X. (2010). Beyond *Drosophila*: RNAi in vivo and functional genomics in insects. *Annual Review of Entomology, 55*(1), 111–128. https://doi.org/10.1146/annurev-ento-112408-085301

Bernays, E. A., & Chapman, R. F. (1994). Behavior: The process of host-plant selection. In *Host-plant selection by phytophagous insects* (Contemporary Topics in Entomology, Vol. 2, pp. 61–94). Chapman and Hall. https://doi.org/10.1007/978-0-585-30455-7_5

Bernays, E. A., & Chapman, R. F. (2001). Taste cell responses in the polyphagous arctiid, *Grammia geneura*: Towards a general pattern for caterpillars. *Journal of Insect Physiology, 47*(9), 1029–1043. https://doi.org/10.1016/S0022-1910(01)00079-8

Bossart, J. L., & Scriber, J. M. (1999). Preference variation in the polyphagous tiger swallowtail butterfly (Lepidoptera: Papilionidae). *Environmental Entomology, 28*(4), 628–637. https://doi.org/10.1093/ee/28.4.628

Caers, J., Verlinden, H., Zels, S., Vandersmissen, H. P., Vuerinckx, K., & Schoofs, L. (2012). More than two decades of research on insect neuropeptide GPCRs: An overview. *Frontiers in Endocrinology, 3*, 151. https://doi.org/10.3389/fendo.2012.00151

Carter, M., & Feeny, P. (1999). Host-plant chemistry influences oviposition choice of the spicebush swallowtail butterfly. *Journal of Chemical Ecology, 25*(9), 1999–2009. https://doi.org/10.1023/A:1021076404423

Chun, M. W. (1972). *Dynamics of feeding responses in Pieris brassicae Linn. as a function of chemosensory input: A behavioural, ultrastructural and electrophysiological study* (Doctoral dissertation, Wageningen University and Research). *ProQuest Dissertations & Theses Global*, 72, 1–162.

Cui WeiZheng, C. W., Wang YanWen, W. Y., Mu ZhiMei, M. Z., Hu ZengJuan, H. Z., & Xu JunLiang, X. J. (2001). Gustation electrophysiological response to vitamin C of silkworm (*Bombyx mori*). *Acta Sericologica Sinica, 27*(9), 92–95.

Das, S. K., Sahu, B. K., & Singh, D. (2020). Host plant diversity of non-mulberry silkworms: A review. *Journal of Pharmacognosy and Phytochemistry, 9*(3), 109–113.

Devitt, B. D., & Smith, J. J. B. (1985). Action of mouthparts during feeding in the dark-

sided cutworm, *Euxoa messoria* (Lepidoptera: Noctuidae). *The Canadian Entomologist, 117*(3), 343–349. https://doi.org/10.4039/Ent117343-3

Endo, H., Tsuneto, K., Mang, D., Zhang, W., Yamagishi, T., Ito, K., et al. (2024). Molecular basis of host plant recognition by silkworm larvae. *Journal of Insect Physiology, 154*, 104628. https://doi.org/10.1016/j.jinsphys.2024.104 628

Fambayun, R. A., Agustarini, R., & Andadari, L. (2022). Cultivation and breeding techniques for increase silk productivity in Indonesia. In *IOP Conference Series: Earth and Environmental Science, 995*(1), 012055. IOP Publishing. http://dx.doi.org/10.1088/1755-1315/995/1/012055

Fraenkel, G. S. (1959). The raison d'être of secondary plant substances: These odd chemicals arose as a means of protecting plants from insects and now guide insects to food. *Science, 129*(3361), 1466–1470. https://doi.org/10.1126/science.129.3361.1 466

Gong, D. P., Zhang, H. J., Zhao, P., Xia, Q. Y., & Xiang, Z. H. (2009). The odorant binding protein gene family from the genome of silkworm, *Bombyx mori*. *BMC Genomics, 10*(1), 332. https://doi.org/10.1186/1471-2164-10-332

Gotthard, K., Margraf, N., Rasmann, S., & Rahier, M. (2005). The evolution of larval foraging behaviour in response to host plant variation in a leaf beetle. *Oikos, 109*(3), 503–512. https://doi.org/10.1111/j.0030-1299.2005.14074.x

Guo, H., Cheng, T., Chen, Z., Jiang, L., Guo, Y., Liu, J., et al. (2017). Expression map of a complete set of gustatory receptor genes in chemosensory organs of *Bombyx mori*. *Insect Biochemistry and Molecular Biology, 82*, 74–82. https://doi.org/10.1016/j.ibmb.2017.02.001

Haloi, K., Kalita, M. K., & Devi, D. (2023). Regulation and characterization of amylase enzyme secretion in the digestive tract of *Antheraea assamensis* Helfer. *Indian Journal of Entomology, 85*(3), 556–562. http://dx.doi.org/10.55446/IJE.2023.962

Hamamura, Y., & Naito, K. (1961). Food selection by silkworm larvae, *Bombyx mori*. Citral, linalyl acetate, linalol, and terpinyl acetate as attractants of larvae. *Nature, 190*, 879–880. https://doi.org/10.1038/190880a0

Hamamura, Y., Kuwata, K., & Masuda, H. (1966). Effect of gallic acid on the growth of the silkworm larvae *Bombyx mori* L. *Nature, 212*(5068), 1386–1387. https://doi.org/10.1038/2121386a0

Hansson, B. S. (1995). Olfaction in Lepidoptera. *Experientia, 51*(11), 1003–1027. https://doi.org/10.1007/BF01946910

Hayashiya, K., Kato, M., & Hamamura, Y. (1965). Acetylcholine as a growth factor in early larval development of the silkworm. *Nature, 205*(4971), 620–621. https://doi.org/10.1038/205620a0

Haynes, K. F., Zhao, J. Z., & Latif, A. (1991). Identification of floral compounds from *Abelia grandiflora* that stimulate upwind flight in cabbage looper moths. *Journal of Chemical Ecology, 17*(3), 637–646. https://doi.org/10.1007/BF00982132

Ishikawa, S., Hirao, T., & Arai, N. (1969). Chemosensory basis of hostplant selection in the silkworm. *Entomologia Experimentalis et Applicata, 12*(5), 544–554. https://doi.org/10.1111/j.1570-7458.1969.tb02552.x

Ito, T., & Tanaka, M. (1959). Per os administration of the nutrients to the silkworm larvae, I. Effect of the administration of glucose solution. *Sanshi Shikenjo Hokoku, 15*, 353–364.

Jacobson, M. (2019). *Glossary of plant derived insect deterrents* (1st ed., ebook). CRC Press. https://doi.org/10.1201/9781351072274

Jiang, T., Li, X. Y., Chen, M. M., Liu, S. T., Li, Y. P., Xia, R. X., et al. (2023). Genome-wide identification and transcriptome-based expression pattern of chemosensory genes in two wild silkmoths, *Antheraea pernyi* and *Antheraea yamamai*. *Journal of Insects as Food and Feed, 9*(6), 823–840. http://dx.doi.org/10.3920/JIFF2022.0160

Johnson, B. R., van Wilgenburg, E., & Tsutsui, N. D. (2011). Nestmate recognition in social insects: Overcoming physiological constraints with collective decision making. *Behavioral Ecology and Sociobiology, 65*(5), 935–944. https://doi.org/10.1007/s00265-010-1094-x

Kasubuchi, M., Shii, F., Tsuneto, K., Yamagishi, T., Adegawa, S., Endo, H., & Sato, R. (2018). Insect taste receptors relevant to

host identification by recognition of secondary metabolite patterns of non-host plants. *Biochemical and Biophysical Research Communications, 499*(4), 901–906. https://doi.org/10.1016/j.bbrc.2018.04.014

Kato, M., & Yamada, H. (1966). Chlorogenic acid promotes the utilization of oil in the growth of silkworm. *Proceedings of the Japan Academy, 42*(10), 1185–1188. https://doi.org/10.2183/pjab1945.42.1185

Legay, J. M. (1958). Recent advances in silkworm nutrition. *Annual Review of Entomology, 3*, 75–86. https://doi.org/10.1146/annurev.en.03.0101 58.000451

Li, J., Wang, X., & Zhang, L. (2020). Sex pheromones and olfactory proteins in *Antheraea* moths: *A. pernyi* and *A. polyphemus* (Lepidoptera: Saturniidae). *Archives of Insect Biochemistry and Physiology, 105*(2), e21729. https://doi.org/10.1002/arch.21729

Liu, Y., Tian, X., Gui, L., Wang, F., & Zhang, G. (2024). Molecular and functional characterization of an antenna-enriched glutathione S-transferase *BminGSTd3* involved in undecanol degradation in the citrus fruit fly, *Bactrocera minax* (Enderlein) (Diptera: Tephritidae). *International Journal of Biological Macromolecules, 256*, 128514. https://doi.org/10.1016/j.ijbiomac.2023.128 514

Lopez Jr, J. D., Shaver, T. N., Beerwinkle, K. R., & Lingren, P. D. (2000). *U.S. Patent No. 6,074,634.* U.S. Patent and Trademark Office.

Mang, D., Shu, M., Endo, H., Yoshizawa, Y., Nagata, S., Kikuta, S., & Sato, R. (2016). Expression of a sugar clade gustatory receptor, *BmGr6*, in the oral sensory organs, midgut, and central nervous system of larvae of the silkworm *Bombyx mori. Insect Biochemistry and Molecular Biology, 70*, 85–98. https://doi.org/10.1016/j.ibmb.2015.12.008

Mech, D., & Vijay, N. (2022). Indigenous technical knowledge for higher fecundity of Muga silkworm seeds. *Plant Archives, 22*(Special Issue VSOG), 88–91. https://doi.org/10.51470/PLANTARCHIVES .2022.v22.splecialissue.018

Miles, C. I., Campo, M. L. D., & Renwick, J. A. A. (2005). Behavioral and chemosensory responses to a host recognition cue by larvae of *Pieris rapae. Journal of Comparative Physiology A, 191*(2), 147–155. https://doi.org/10.1007/s00359-004-0580-x

Miller, J. R., & Strickler, K. L. (1984). Finding and accepting host plants. In W. J. Bell & R. T. Cardé (Eds.), *Chemical ecology of insects* (pp. 127–157). Springer. https://doi.org/10.1007/978-1-4899-3368-3_6

Morinaga, S., Nagata, K., Ihara, S., Yumita, T., Niimura, Y., Sato, K., & Touhara, K. (2022). Structural model for ligand binding and channel opening of an insect gustatory receptor. *Journal of Biological Chemistry, 298*(11), 102573. http://dx.doi.org/10.1016/j.jbc.2022.102573

Morris, S. C. (2007). Review of the book *Evolution of the insects*, by D. Grimaldi & M. S. Engel. *Geological Magazine, 144*(6), 1035–1036. https://doi.org/10.1017/S00167568070037 2X

Nagaraju, J. (2002). Application of genetic principles for improving silk production. *Current Science, 83*(4), 409–414.

Nagata, S., Morooka, N., Matsumoto, S., Kawai, T., & Nagasawa, H. (2011). Effects of neuropeptides on feeding initiation in larvae of the silkworm, *Bombyx mori. General and Comparative Endocrinology, 172*(1), 90–95. https://doi.org/10.1016/j.ygcen.2011.03.00 4

Naito, K. (1965). Studies on the micro constituent in mulberry leaves. Part VI. Isolation of chlorogenic acid. *Journal of Agricultural and Biological Chemistry, 39*, 237.

Nayar, J. K., & Fraenkel, G. (1962). The chemical basis of hostplant selection in the silkworm, *Bombyx mori* (L.). *Journal of Insect Physiology, 8*(5), 505–525. https://doi.org/10.1016/0022-1910(62)90062-8

Neog, K., Das, A., Unni, B. G., Ahmed, G. U., & Rajan, R. K. (2011a). Studies on secondary metabolites of Som (*Persea bombycina* Kost), a primary host plant of Muga silkworm (*Antheraea assamensis* Helfer). *International Journal of Pharmaceutical Science and Research, 3*(3), 1441–1447.

Neog, K., Gogoi, S. N., & Chakravorty, R. (2005). Present status and constraints of Muga silkworm host plant germplasm conservation. In *Proceedings of the Workshop on Strategies for Maintenance*

of Non-Mulberry Silkworm and Host Plant Germplasm, Central Muga Eri Research & Training Institute, Lahdoigarh, Jorhat, Assam, India, March 10 (Vol. 11, pp. 1–10).

Neog, K., Unni, B., & Ahmed, G. (2011a). Studies on the influence of host plants and effect of chemical stimulants on the feeding behavior in the muga silkworm, *Antheraea assamensis. Journal of Insect Science, 11*(1), 133. https://doi.org/10.1673/031.011.13301

Nissan, E. (2009). Peter McGregor (ed.), *Animal Communication*. Tristram D. Wyatt, *Pheromones and Animal Behaviour: Communication by Smell and Taste. Pragmatics & Cognition, 17*(2), 482–490.
    https://doi.org/10.1075/pc.17.2.16nis

Padaki, N. V., Bhattacharya, A., Das, B., Choudhury, B., Mishra, S. N., & Singh, B. K. (2014). Studies on the influence of seasonal and regional aspects on the quality of muga silk. *Research Journal of Textile and Apparel, 18*(1), 25–30. https://doi.org/10.1108/RJTA-18-01-2014-B004

Rausher, M. D. (1978). Search image for leaf shape in a butterfly. *Science, 200*(4345), 1071–1073.
    https://doi.org/10.1126/science.200.4345.1071

Regier, J. C., Mitter, C., Davis, D. R., Harrison, T. L., Sohn, J. C., Cummings, M. P., et al. (2015). A molecular phylogeny and revised classification for the oldest ditrysian moth lineages (*Lepidoptera: Tineoidea*), with implications for ancestral feeding habits of the mega-diverse Ditrysia. *Systematic Entomology, 40*(2), 409–432. https://doi.org/10.1111/syen.12110

Renwick, J. A. A. (2018). Oviposition stimulants and deterrents. In *Handbook of natural pesticides* (pp. 151–160). CRC Press.

Saikia, S., & Saikia, M. (2022). Physical and chemical properties of Indian silk fibres. *The Pharma Innovation Journal, 11*, 732–738.

Samami, R., Seidavi, A., Eila, N., Moarefi, M., Ziaja, D. J., Lis, J. A., et al. (2019). Production performance and economic traits of silkworms (*Bombyx mori* L., 1758) fed with mulberry tree leaves (*Morus alba*, var. Ichinose) significantly differ according to hybrid lines. *Livestock Science, 226*, 133–137.
    https://doi.org/10.1016/j.livsci.2019.06.015

Saranya, M., Krishnamoorthy, S., & Murugesh, K. (2019). Fortification of mulberry leaves with indigenous probiotic bacteria on larval growth and economic traits of silkworm (*Bombyx mori* L.). *Journal of Entomology and Zoology Studies, 7*(4), 780–784.

Sato, K., & Touhara, K. (2008). Insect olfaction: Receptors, signal transduction, and behavior. In S. Korsching & W. Meyerhof (Eds.), *Chemosensory systems in mammals, fishes, and insects* (Results and Problems in Cell Differentiation, Vol. 47, pp. 203–220). Springer. https://doi.org/10.1007/400_2008_10

Scheirs, J., Bruyn, L. D., & Verhagen, R. (2000). Optimization of adult performance determines host choice in a grass miner. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 267*(1457), 2065–2069.
    https://doi.org/10.1098/rspb.2000.1250

Sokame, B. M., Subramanian, S., Kilalo, D. C., Juma, G., & Calatayud, P. A. (2020). Larval dispersal of the invasive fall armyworm, *Spodoptera frugiperda*, the exotic stemborer *Chilo partellus*, and indigenous maize stemborers in Africa. *Entomologia Experimentalis et Applicata, 168*(4), 322–331.
    https://doi.org/10.1111/eea.12899

Song, W. T., Zhu, F. F., & Chen, K. P. (2021). The molecular mechanisms and factors affecting the feeding habits of silkworm (*Lepidoptera: Bombyxidae*). *Journal of Asia-Pacific Entomology, 24*(4), 955–962.
    https://doi.org/10.1016/j.aspen.2021.08.010

Song, W., Zhu, F., Andoh, V., & Chen, K. (2022). Analysis of genes influencing the feeding of *Bombyx mori* by genome resequencing. *Invertebrate Survival Journal*, 136–168. https://doi.org/10.25431/1824-307X/isj.v19i1.136%20-%20168

Sun, Y., Tao, S., Zhang, W., Jiang, B., Dai, H. Y., Liu, B. S., et al. (2022). Transcriptome profile analysis reveals the emamectin benzoate-induced genes associated with olfaction and metabolic detoxification in *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae). *All Life, 15*(1), 340–357.
    https://doi.org/10.1080/26895293.2022.2052190

Takeda, S., & Ueda, S. (1984). Effect of the interaction among n-hexacosanol, morin

and β-sitosterol on the larval feeding activity of silkworm, *Bombyx mori*, reared on an artificial diet without mulberry leaves. *The Journal of Sericultural Science of Japan, 53*(5), 373–379. https://doi.org/10.11416/kontyushigen1930.53.373

Tanaka, K., Uda, Y., Ono, Y., Nakagawa, T., Suwa, M., Yamaoka, R., & Touhara, K. (2009). Highly selective tuning of a silkworm olfactory receptor to a key mulberry leaf volatile. *Current Biology, 19*(11), 881–890.

Thorsteinson, A. J. (1960). Host selection in phytophagous insects. *Annual Review of Entomology, 5*(1), 193–218. https://doi.org/10.1146/annurev.en.05.010160.001205

Tikader, A., Vijayan, K., & Saratchandra, B. (2013). Improvement of host plants of Muga silkworm (*Antheraea assamensis*) for higher productivity and better adaptation – A review. *Plant Knowledge Journal, 2*(2), 83–88.

Tsai, Y. M., Wang, H. L., Ho, C. L., & Li, S. C. (1978). Studies on the artificial diet of silkworm *Bombyx mori* L.: The effects of dietary physico-chemical factors on the feeding and growth of the silkworm. *Acta Entomologica Sinica, 21*(4), 369–384.

Tsuneto, K., Endo, H., Shii, F., Sasaki, K., Nagata, S., & Sato, R. (2020). Diet choice: The two-factor host acceptance system of silkworm larvae. *PLOS Biology, 18*(9), e3000828. https://doi.org/10.1371/journal.pbio.3000828

Van Der Goes Van Naters, W., & Carlson, J. R. (2006). Insects as chemosensors of humans and crops. *Nature, 444*(7117), 302–307. https://doi.org/10.1038/nature05403

van Loon, J. J., & Schoonhoven, L. M. (1999). Specialist deterrent chemoreceptors enable *Pieris* caterpillars to discriminate between chemically different deterrents. *Entomologia Experimentalis et Applicata, 91*(1), 29–35. https://doi.org/10.1046/j.1570-7458.1999.00463.x

Wang, D., Li, B., Lin, C., Chen, Y., Xu, Y., & Shen, W. (2011). Cloning, expression analysis and subcellular localization of P450 gene *CYP6AE21* from *Bombyx mori. Acta Sericologica Sinica, 54*(1), 1–8.

Wanner, K. W., & Robertson, H. M. (2008). The gustatory receptor family in the silkworm moth *Bombyx mori* is characterized by a large expansion of a single lineage of putative bitter receptors. *Insect Molecular Biology, 17*(6), 621–629. https://doi.org/10.1111/j.1365-2583.2008.00836.x

Watanabe, K., Toba, G., Koganezawa, M., & Yamamoto, D. (2011). Gr39a, a highly diversified gustatory receptor in *Drosophila*, has a role in sexual behavior. *Behavior Genetics, 41*(5), 746–753. https://doi.org/10.1007/s10519-011-9461-6

Watanabe, T. (1958). Substances in mulberry leaves which attract silkworm larvae (*Bombyx mori*). *Nature, 182*(4631), 325–326. https://doi.org/10.1038/182325a0

Xin, S., & Zhang, W. (2020). Construction and analysis of the protein–protein interaction network for the olfactory system of the silkworm *Bombyx mori. Archives of Insect Biochemistry and Physiology, 105*(3), e21737. https://doi.org/10.1002/arch.21737

Xu, Y., Wang, Y., Li, L., Lu, N., Zhu, Y., Huang, Z., & McLoughlin, S. (2024). Plant–insect interactions across the Triassic–Jurassic boundary in the Sichuan Basin, South China. *Frontiers in Ecology and Evolution, 11*, 1338865. http://dx.doi.org/10.3389/fevo.2023.1338865

Zhang, H. J. (2012). An observation on food selection behavior of silkworm larvae to non-Moraceae plants with four-arm olfactometer. *Scientific Sericulture, 38*, 74–81.

Zhang, H. J., Anderson, A. R., Trowell, S. C., Luo, A. R., Xiang, Z. H., & Xia, Q. Y. (2011). Topological and functional characterization of an insect gustatory receptor. *PLOS ONE, 6*(8), e24111. https://doi.org/10.1371/journal.pone.0024111

Zhang, H. J., Faucher, C. P., Anderson, A., Berna, A. Z., Trowell, S., Chen, Q. M., et al. (2013). Comparisons of contact chemoreception and food acceptance by larvae of polyphagous *Helicoverpa armigera* and oligophagous *Bombyx mori. Journal of Chemical Ecology, 39*(8), 1070–1080.

Zhang, Z. J., Zhang, S. S., Niu, B. L., Ji, D. F., Liu, X. J., Li, M. W., et al. (2019). A determining factor for insect feeding

preference in the silkworm, *Bombyx mori. PLOS Biology, 17*(2), e3000162.

https://doi.org/10.1371/journal.pbio.3000162

Peer-review history:
The peer review history for this paper can be accessed here:
https://pr.sdiarticle5.com/review-history/141705