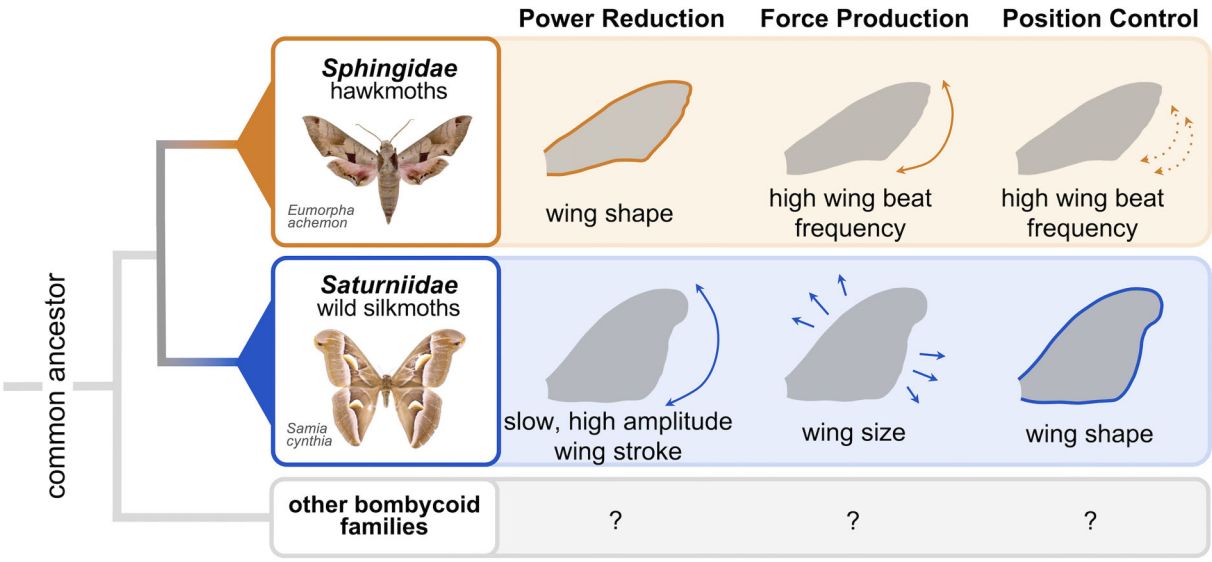

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SYMPOSIUM ARTICLE

Bombycoid Moths: An Emerging Model Clade for Studying Insect Flight

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Synopsis Flying insects achieve extraordinary locomotor performance through diverse combinations of physiological, morphological, and mechanical traits, exemplifying the many-to-one mapping between biological components and emergent flight behavior. Here, we argue that the moth superfamily Bombycoidea is a tractable and compelling emerging model clade that facilitates integration between controlled experimentation and phylogenetically informed comparative analyses, complementing single-species studies to understand the evolution of insect flight. Bombycoidea is a monophyletic group with a well-resolved phylogeny that includes approximately 6000 described species in 10 families distributed globally. Bombycoidea includes the hawkmoths (Sphingidae) and wild silkmoths (Saturniidae), which are known for their contrasting life history and flight behavioral strategies. Most hawkmoths perform agile hover feeding behavior, while silkmoths display erratic flight behavior and do not feed as adults, limiting the silkmoth energy budget. Hawkmoths and silkmoths perform divergent flight behaviors using different combinations of wing shape, size, and kinematics. In addition to the stark divergence in flight behavior and related traits, hawkmoths and silkmoths have extensive interspecific variation, including multiple examples of convergent evolution in life history (e.g., loss of functional adult mouth parts), wing morphologies (e.g., hindwing tails), and wing patterning (e.g., hindwing spots) that occur both within and between these two families and across other bombycoid families. Hawkmoths also include the Tobacco hornworm (*Manduca sexta*), and extensive research on flight in this species provides a foundation needed for comparison across Bombycoidea. These features of Bombycoidea, in addition to the recent advancements in technology, enable a tractable avenue for large-scale comparative work at unprecedented scales and resolution. Finally, we highlight recent advances in insect flight research using bombycoid moths and outline how this clade can inform future studies aimed at uncovering general principles of insect flight, animal behavior, and locomotion.

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Introduction

Flying insects are capable of incredibly agile locomotor behaviors. Insects solve the problem of flapping flight with great diversity in neural control, muscle, exoskeleton, and wing properties (Dudley 2000). The many-to-one mapping of component-level variation to flight performance highlights the importance of neuromechanical integration: how physiological subsystems are composed to give rise to emergent animal movement (Wainwright et al. 2005; Padilla and Tsukimura 2014; Sponberg 2017). In insects, the neuromechanical processes working together to produce flight (Fig. 1) have been characterized in a few well-studied disparate species, like the fruit fly (*Drosophila melanogaster*), hawkmoth (*Manduca sexta*), and desert locust (*Schistocerca gregaria*) (e.g., Zarnack and Möhl 1977; Robertson and Pearson 1983, 1985; Ramirez and Pearson 1993; Sherman and Dickinson 2003; Taylor and Thomas 2003; Dickinson 2005; Sane et al. 2007; Hedrick et al. 2009; Ayali and Lange 2010; Hinterwirth and Daniel 2010; Dyhr et al. 2013; Dickerson et al. 2014). Studying model organisms in depth for behavior, neuromechanics, and physiology is partially enabled by the powerful system-specific tools (e.g., neurogenetic driver lines), the large communities of scientists aligning efforts, and the wealth of knowledge on which to build. However, model organisms typically represent $<$ 1% of a diverse clade, and therefore restrict our understanding to a few species and the behaviors they manifest (Beach 1950; Brenowitz and Zakon 2015; Katz 2019). One complementary approach to the study of disparate model species is to diversify the organisms studied (Brenowitz and Zakon 2015; Yartsev 2017), often invoking the Krogh principle: seeking specific organisms that demonstrate exceptional performance, great accessibility, or other suitable features for investigating a given question (Krogh 1929). Other approaches include the inverse Krogh principle: selecting a given organism (or other biological unit) first and using it to create a tractable research question (Clark et al. 2023). Comparative approaches leverage interspecific variation to uncover robust patterns of trait evolution, and here we argue that specific insect "model clades" (Jourjine and Hoekstra 2021; Mabry et al. 2024) can offer an alternative synergistic, systematic approach for the exploration of neuromechanical strategies of insect flight.

A model clade acts as a unit of study (as opposed to a single species, or even a comparison of disparate, unrelated species) enabling researchers to integrate controlled experiments with evolutionary comparisons across related species. Model clades present opportunities (often through the use of phylogenetic comparative methods, PCMs) to identify how and why traits evolve relative to each other, and how underlying traits work together to produce emergent behavior (Jourjine and Hoekstra 2021); the application of PCMs to a model clade could yield deeper insights into these questions in comparison to the application of PCMs applies to a more disparate set of taxa. A model clade could be formed from any group of closely related extant species that share a single common ancestor and demonstrate natural trait variation between the species. The variation in traits and behaviors across species can then be leveraged to better understand whether the combination of underlying components responsible for generating an emergent behavior are conserved, convergent, or a collection of different, independent solutions. Performance and function are often assessed at the level of whole organism features, but arise from the lability in underlying components (Fig. 1). So, a model clade can serve as an important evolutionary unit in which to explore what component traits (or trait combinations) are phenotypically plastic, evolutionary labile, or constrained in shaping emergent behavior and performance. While the formulation of a model clade is relatively new, the approach of utilizing clades with a well resolved phylogeny to investigate how different neuromechanical traits work together to give rise to emergent animal movement across species has been successful across various systems and behaviors (e.g., Westneat et al. 2005; Patek et al. 2013; Anderson and Patek 2015; Aiello et al. 2017; Corn et al. 2022).

A model clade exhibits several features that support the phylogenetically grounded investigation of how and why traits evolve across species. For a model clade to be a tractable research system it should be (1) comprehensively sampled and phylogenetically well-resolved with a single common ancestor (monophyletic), and (2) disparate, displaying systematic patterns of trait evolution (Jourjine and Hoekstra 2021; Mabry et al. 2024). A clade possessing these features provides the resolution for a more nuanced identification of relationships among traits across species and understanding of how specific traits have diversified across the clade. In other words, these features of a clade allow the application of PCMs and other comparative analyses to demonstrate how trait variation is distributed and evolves relative to related traits (Jourjine and Hoekstra 2021), revealing how the various underlying components the neuromechanical system can evolve relative to each other to produce flight. In addition, the species of the clade will ideally share the same basic body plan (e.g., general morphology and nervous system) that generates a given behavior. For example, comparisons between moth species are likely easier to interpret as compared to a juxtaposition between a moth and a fly, as the latter comparison differs in flight morphology (e.g., an overlapping forewing-hindwing pair in Lepidoptera vs. forewing driven flight

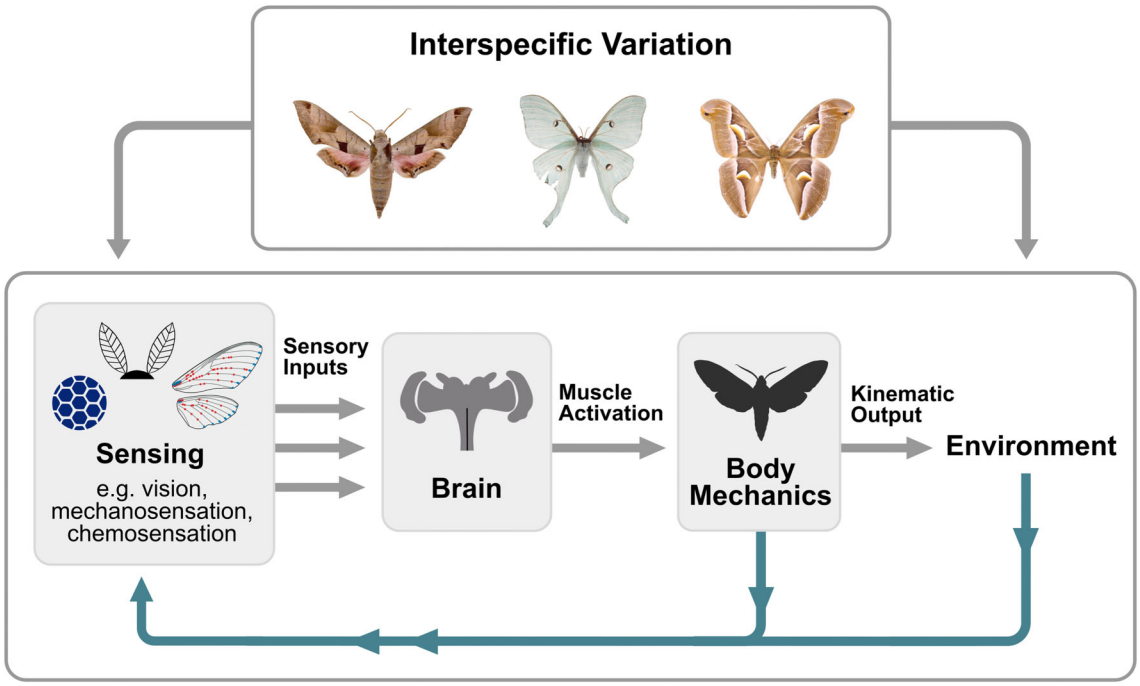

Fig. 1 Simplified control diagram demonstrating neuromechanical components that work to produce an emergent behavior. Within the block diagram, central arrows represent the interconnections between various components of a neuromechanical system and lower arrows represent the flow of sensory feedback from both the body and the environment back to the body. This sensory feedback can be processed by the central nervous system, used to modulate motor commands, which, in combination with the mechanics of the organism, will generate a behavioral output. Historically, the processes represented by each block have been studied in a few disparate species. A model clade that possesses interspecific variation in flight-related traits can be used to help reveal which components evolve in response to various selective pressures and ultimately help identify generalized principles of animal locomotion.

in Diptera) and neural control of flight muscles (synchronous vs. asynchronous) (Gau et al. 2023). While not essential, a model clade will be more powerful if it also (3) demonstrates patterns of convergence and (4) possesses one or more conventional model species (Jourjine and Hoekstra 2021; Mabry et al. 2024). Like for the Krogh principle applied to specific species, there is likely a clade that is particularly well suited to answer a given set of questions (Jourjine and Hoekstra 2021).

The model clade concept (and the fulfillment of the requirements needed to use them more regularly in comparative research) is emerging and being utilized in diverse branches of study to reveal how traits and behavior are related across a wide range of species (Jourjine and Hoekstra 2021; Jernigan et al. 2024; Mabry et al. 2024). In Jourjine and Hoekstra's (2021) seminal formulation of a model clade, additional consideration is presented on the trade offs when choosing the correct model clade, methodological limitations, and various open questions in evolutionary neuroscience that can benefit from the model clade approach. The historical use of the word model can range from its application to describe a traditional model organism (e.g., the mouse) versus a nontraditional model organism (e.g., a frog used to study jumping, which is sometimes referred to as a Krogh Model; see Clark et al. 2023). A model clade includes features of both uses of the word model. Like a Krogh (nontraditional) model organism, there will naturally be some clades that better fulfill the features of a model clade to make it more or less tractable for answering a given type of evolutionary question. For example, just as it would be difficult to study jumping in a turtle (Clark et al. 2023), it would be equally impractical to attempt to answer evolutionary questions on jumping using a clade of turtles. Under the more traditional use of model, insights from a model clade, like a model organism, can be leveraged to infer the functional consequences of flight-related traits in other, sometimes less accessible clades and even bioinspired robots. Thus, in the context of insect flight, the representational target of a model clade is to uncover generalized principles of insect flight, which generates a representational scope that, in some cases, could extend to aid in the understanding of other clades of flying insects.

The application of the model clade approach to insect flight will help provide a robust, mechanistic understanding of how different physiological and mechanical processes function together to produce flight behavior. While the classic Krogh approach generates insight from countless nontraditional model organisms (see

Green et al. 2018; Clark et al. 2023), even comparisons between these often disparate species do not address the question of generality on their own. The answer to some questions is not possible through comparisons of disparate, distantly related species and could benefit from utilizing a model clade. For example, the distribution of wing campaniform sensilla, mechanosensors providing critical feedback for flight performance, compared across a few disparate insect species revealed general trends in the placement of these sensors across the proximal wing (Aiello et al. 2021c). However, due to the relatively limited number of species, distant evolutionary relationships between species, and the inability to phylogenetically control for interspecific differences in flight behavior, wing size, wing shape, and wing movement, questions such as "how correlated is the evolution of wing size, shape, and sensor distribution?" and "what are the functional roles of sparsely distributed distal wing sensors?" remained unanswered and could directly benefit from the model clade approach.

Historically, the thorough study of many species across a model clade would be time and resource limited. Recent technological advances make detailed, multi-species research into insect flight both more tractable and efficient. High-throughput tools such as automated behavioral and kinematic analysis (e.g., DeepLabCut, YOLO) (Mathis et al. 2018; Chan et al. 2025), nondestructive imaging techniques like microCT and DiceCT (e.g., Gignac et al. 2016; Gignac and Kley 2018), gene sequencing, large-scale neural recordings using multielectrode arrays (e.g., Pachitariu et al. 2024; Ling et al. 2025), and semiautomated data analysis pipelines (e.g., Hedrick 2008; Brainerd et al. 2010), many of which are open source (e.g., Buccino et al. 2020), now allow researchers to more easily collect detailed anatomical, physiological, behavioral, genetic, and evolutionary data across many species. These tools, coupled with centralized databases (e.g., ZMA Portal), improved communication networks, and the development of robust phylogenies from large-scale genomic data, not only preserve the detailed collection of species-level data but also enable robust comparative analyses that reveal how and why traits evolve and work together across species.

Here, we identify a moth superfamily that meets the features of a model clade for the study of insect flight. Any group of insects possessing the features of a model clade likely resulted from uncoordinated efforts across historically siloed subfields (e.g., systematics, neuroscience, comparative biomechanics, etc); these uncoordinated efforts led to the production of a well-resolved phylogeny in a group that displays documented interspecific variation in traits of interest suitable for answering a given question and contains a traditional model species. Our primary goal is to demonstrate that the moth superfamily Bombycoidea, which includes the hawkmoths, wild silkmoths, and relatives, possesses all the features of a model clade. Next, we highlight recent uses of bombycoid moths to advance our understanding of insect flight, demonstrating its utility as an emerging model clade for studying insect flight. Finally, we provide other comparisons that can be made within the clade, and between this clade and others, to uncover generalized principles of insect flight.

Bombycoidea possesses the features of a model clade for studying insect flight

Here, we demonstrate that Bombycoidea possesses the four primary features of a model clade: (1) comprehensively sampled and phylogenetically well-resolved with a single common ancestor (monophyletic), and (2) disparate, displaying systematic patterns of trait evolution (3) demonstrates patterns of convergence and (4) possesses one or more conventional model species (Jourjine and Hoekstra 2021; Mabry et al. 2024). By the possession of these features demonstrated through decades of work, Bombycoidea is emerging as an ideal model clade to answer questions about the neuromechanics of insect flight.

Bombycoidea is a speciose, comprehensively sampled monophyletic clade with a well-resolved phylogeny

The superfamily Bombycoidea comprises a diverse, globally distributed radiation of more than 6000 moth species in 520 genera (Kitching et al. 2018). While no maximum number of species is required, a more speciose clade provides more data points and more statistical power when applying PCMs to infer evolutionary patterns of trait diversification, correlations between traits, or whether adaptive changes are independent of common ancestry (Jourjine and Hoekstra 2021). A particularly interesting feature of Bombycoidea is that hobbyists and community scientists across the globe have long been captivated by these diverse flyers, providing unprecedented help in the collection, access, and guides to rearing a large number of different species within the clade. Thus, when considering a trade-off of a model clade between the number of species in which one can obtain and feasibly study and the power needed to perform more robust phylogenetic analyses across more species (Jourjine and Hoekstra 2021), the advent of new technologies for data collection and analysis potentially enable comparative work to be comprehensively completed at the genus-level in this clade.

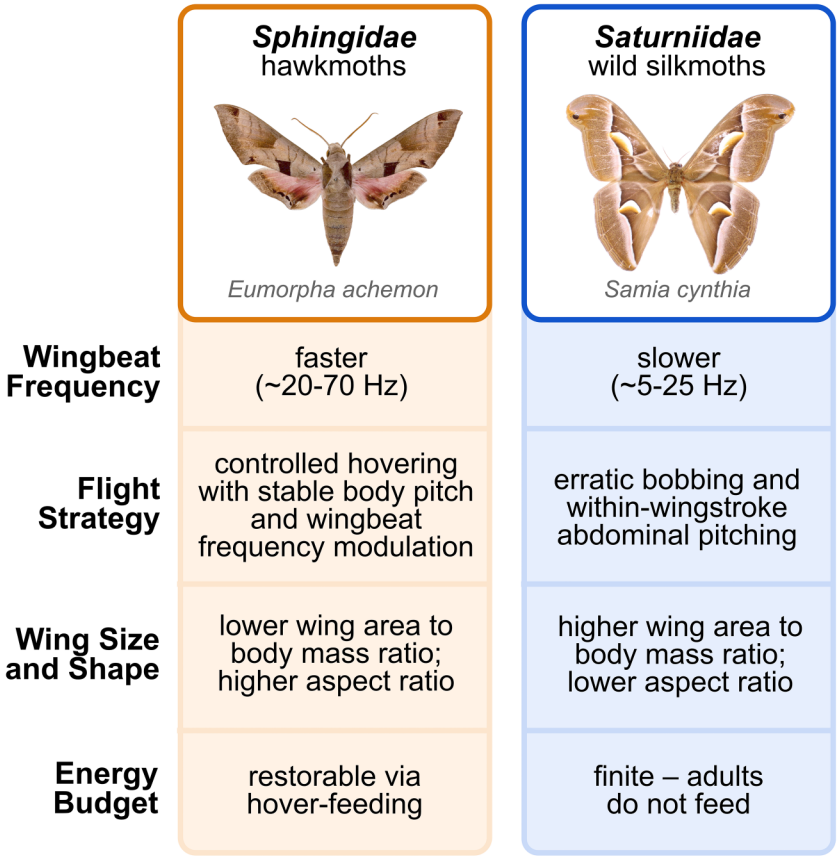

Fig. 2 Summary of the general, primary differences in flight strategy and life history between hawkmoths and wild silkmoths. It is important to note that exceptions to these family-specific generalizations have convergently evolved in a few cases in both families. For example, some hawkmoths have convergently lost the ability to feed in the adult stage. While these features of life history, flight behavior, and flight morphology have been closely examined in hawkmoths and wild silkmoths, the other, smaller, bombycoid moth families offer further opportunities to decipher the complex relationships between ecology, life history, and flight behavior.

A key strength of Bombycoidea as a model clade is the availability of a well-resolved, comprehensively sampled phylogeny. Phylogenomic work has produced evolutionary hypotheses for relationships across the superfamily, resolving deep, time-calibrated divergences among major families as well as finer-scale relationships within Sphingidae and Saturniidae (Kawahara et al. 2009, 2019; Zwick et al. 2011; Hamilton et al. 2019; Rougerie et al. 2022). Studies focused on Bombycoidea and Lepidoptera more broadly consistently recover hawkmoths and silkmoths as sister lineages (Zwick et al. 2011; Hamilton et al. 2019; Kawahara et al. 2019) embedded within a broader bombycoid radiation, and provide strong branch support across hundreds of taxa. This phylogenetic resolution enables PCMs that explicitly test for the correlated evolution of flight-related traits, identify lineage-specific adaptations, and distinguish convergence from shared ancestry. Ongoing work continues to expand phylogenomic sampling and reinforce relationships within this group. These capabilities are often lacking in clades with fewer species or unresolved phylogenies.

Bombycoidea is a disparate clade that evolved multiple, distinct flight strategies

Bombycoidea is a disparate clade with flight-related trait variation demonstrated both between and within the major families. Hawkmoths (Sphingidae) and wild silkmoths (Saturniidae) are the two most speciose lineages within Bombycoidea, containing over 80% of the superfamily's diversity (Kitching et al. 2018). Despite likely being sister-families (Kawahara and Breinholt 2014; Breinholt et al. 2018; Kawahara et al. 2019), hawkmoths and silkmoths differ markedly in life-history strategies (Janzen 1984; Lemaire and Minet 1998) and flight behavior (Aiello et al. 2021a, 2021b; Janzen 1984) (Fig. 2). Hawkmoths are agile fliers that routinely engage in energetically demanding hover feeding and are capable of tracking rapidly oscillating flowers up to 14 Hz (Wasserthal 1993; Farina et al. 1994; Sprayberry and Daniel 2007; Sponberg et al. 2015; Stöckl et al. 2017). In contrast, silkmoths exhibit a characteristic bobbing or erratic flight style (Aiello et al. 2021a; Lewis et al. 1993; Sikandar et al. 2025), tracing unpredictable paths

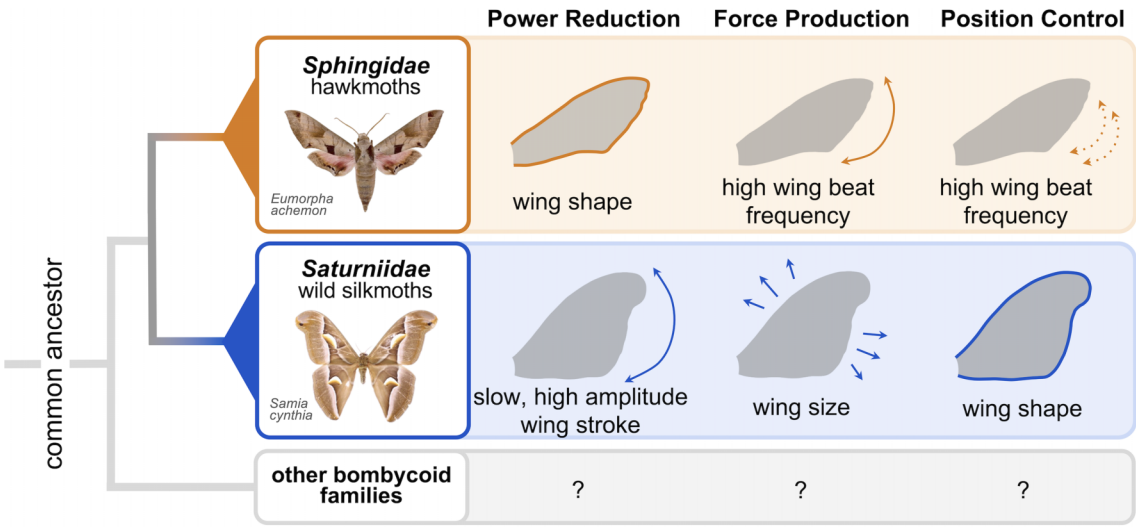

Fig. 3 A summary of the known flight strategies that evolved across Bombycoidea. Between hawkmoths and wild silkmoths, divergent flight strategies evolved where flight performance emerges from distinct combinations of wing size, shape, and movement in each clade. The power requirements of flight are reduced predominantly through wing morphology (e.g., high aspect ratio wings) in hawkmoths, while silkmoths rely on slow, high amplitude wing movements. Sufficient force production in the vertical direction is predominately achieved through the evolution of high-frequency wing movements in hawkmoths and the relatively large wing-to-body size ratio in silkmoths. Finally, positional flight control is likely achieved through the evolution of high wing beat frequencies and wing beat frequency modulation in hawkmoths while silkmoths have evolved wing shapes advantageous for flight control (see Aiello et al. 2021a, 2021b; Gau et al. 2021, 2022). Finally, while the neuromechanics of flight has received less attention in other bombycoid families, the phylogeny of these groups and the relationships of these groups to hawkmoths and silkmoths is well resolved providing a ripe opportunity to a broaden the understanding of flight across this clade. This is a modified figure from Aiello et al. 2021a.

to escape predators. Unlike most hawkmoths, most silkmoths lack functional adult mouthparts and therefore depend entirely on energy reserves accumulated during larval development to fuel their brief adult reproductive phase. These differences in adult energy acquisition strategies (and therefore energy balance) between silkmoths and most hawkmoths are likely a significant selective pressure driving interfamilial adaptations in traits impacting the power requirements of flight.

Hawkmoths and silkmoths have diverged in their flapping-flight strategies. Species in both families have markedly different wing shapes, sizes, and motions to achieve comparable mean force production and reductions in aerodynamic power requirements (Aiello et al. 2021a, 2021b) (Fig. 3). Hawkmoths produce sufficient aerodynamic force through the use of higher wingbeat frequencies and wings with a more distal distribution of area. In contrast, silkmoths rely primarily on larger wing size to body mass ratios than hawkmoths to achieve sufficient force production. To reduce power requirements, hawkmoths evolved high aspect ratio wings, a morphological trait, while silkmoths rely on the kinematic mechanism of slow, large amplitude wing strokes. Finally, we find that wing shape evolution favors maneuverability in silkmoths, but not in hawkmoths. Instead, the evolution of high wing beat frequencies in hawkmoths likely plays a significant role in flight control by allowing more opportunities per unit time to control and redirect their force vectors (Aiello et al. 2021a, 2021b; Gau et al. 2021).

While hawkmoths and silkmoths have diverged in flight morphology and wing movements, substantial interspecific trait variation also occurs within each family. Thus, each family occupies a distinct, yet broad region of flight morphospace. Indeed, wing shape, size, and kinematic parameters vary widely between species *within* each family (Aiello et al. 2021a, 2021b), reflecting diversification within each family that could be driven by a variety of different selective pressures related to ecology, behavior specialization, and predator–prey interactions. This hierarchical pattern of disparity within each family and even larger, minimally overlapping adaptive shifts in traits between families (Aiello et al. 2021a, 2021b; Janzen 1984) provides two opportunities. First, the adaptive shift in flight strategy and flight-related traits occurring in parallel with the divergence between the two major bombycoid families provides the opportunity to test how traits evolve relative to major evolutionary shifts associated with inter-familial shifts in life history, feeding strategy, and flight behavior. Second, the interspecific variation occurring within each family provides the opportunity to test how traits un-

dergo correlated evolution while accounting for confounding variables (e.g., life history, feeding strategy, flight behavior), which can help reveal influences of other species-specific selective pressures.

While most work on bombycoid flight focuses on the divergent flight strategies between and within hawkmoths and silkmoths, the study of neuromechanical diversity (e.g., correlated evolution of flight-related traits) in other bombycoid families also warrants attention, and may prove fruitful for testing additional hypotheses about the evolution of insect flight. One example of this is the presence of other "wild silkmoth-like" groups in Bombycoidea that exist outside of hawkmoths and silkmoths, such as Eupterotidae and some larger Endromidae (*Endromis*) (see Fig. 4 for exemplar images). Interestingly, while some species belonging to families outside hawkmoths and silkmoths possess morphology similar to that seen in wild silkmoths, wing morphology of many of these species is intermediate between that of hawkmoths and silkmoths (Aiello et al. 2021a). Thus, studying these lesser known groups could provide additional opportunities to examine morphologies that could be similar to the ancestral state of the most recent common ancestor of both hawkmoths and silkmoths which could help reveal how and why evolution of traits impacting flight performance (e.g., wing shape, size, and movement) diverged between the hawkmoths and wild silkmoths as well as help answer other questions such as whether the convergence in morphology between wild silkmoths and other bombycoid families is also associated with convergence in flight strategy.

Bombycoid moths thus display diversity among various physiological, morphological, and behavioral components of the flight system. The collection of work highlighted in this section demonstrates that in bombycoid moths, selective pressures can independently drive the evolution of morphology and/or movement to influence force production and power requirements, allowing each performance metric to be partially decoupled from any single trait. The ability to evolutionarily tune both wing morphology and wing movement to influence flight performance likely relaxes strict morphological and kinematic constraints, allowing for the evolution of diverse wing morphologies and movements across closely related taxa. This interspecific diversity in the traits contributing to flight performance makes the bombycoid moth superfamily a powerful model clade for studying insect flight.

Bombycoidea demonstrates convergence

Among the interspecific trait variation across the phylogeny, instances of convergent trait (or behavior) evolution is a particularly useful feature of a model clade (Jourjine and Hoekstra 2021). Convergence is the evolution of similar ecologies, behaviors, life history strategies, morphological and physiological traits, or other specializations or combinations thereof in separate groups of organisms that do not share recent common ancestry (e.g., Kronforst and Papa 2015; Aiello et al. 2017; Keiler et al. 2017; Demery and Burns 2023). Convergence manifests in myriad ways. By revealing instances in which similar traits evolve independently in distinct lineages, convergence allows hypotheses about the coupling between life history, flight behavior, morphology, and/or physiology to be tested repeatedly and independently within a shared evolutionary system (Jourjine and Hoekstra 2021). In particular, the extent to which changes in one trait are accompanied by predictable shifts in other traits like anatomy, kinematics, or energetics can be evaluated more rigorously when multiple independent evolutionary solutions are available for comparison. Therefore, convergent evolution provides a framework for understanding how flight-related traits evolve and for identifying general principles underlying insect flight.

Bombycoidea is a clade with multiple examples of convergent evolution across different traits. Despite the pronounced divergence in flight strategy, flight behavioral repertoire, and life-history between hawkmoths and silkmoths, species in both families have convergently evolved analogous traits. Notable examples include the convergent evolution of hindwing tails across silkmoths (Rubin et al. 2018, 2025; Hamilton et al. 2022), hindwing eye spots in multiple saturniid subfamilies and smerinthine hawkmoths (Lemaire and Minet 1998), and the convergent loss of functional adult mouthparts (and therefore feeding as an adult) in most silkmoth species and the smerinthines (Lemaire and Minet 1998).

Predation pressure, particularly from echolocating bats, appears to be a major driver of convergent hindwing tail evolution in silkmoths (Barber et al. 2015; Lee and Moss 2016; Rubin et al. 2018, 2025; Hamilton et al. 2022). Rapid diversification of hindwing shape, including the evolution of elongated and cupped hindwing tails, has been strongly linked to bat predation, as these structures reflect sonar echoes and divert a bat attack away from the vulnerable body. While the silkmoth forewing plays a critical role in generating the aerodynamic forces for flight (Jantzen and Eisner 2008), the aerodynamic consequences of the hindwing and its many elaborations (e.g., tails) remain less understood. Silkmoth hindwing tails appear to repeatedly evolve in similar locations along the hindwing span (Barber et al. 2015; Rubin et al. 2018, 2025; Aiello et al. 2021b). The repeated position of these tails raises questions about developmental and functional constraints,

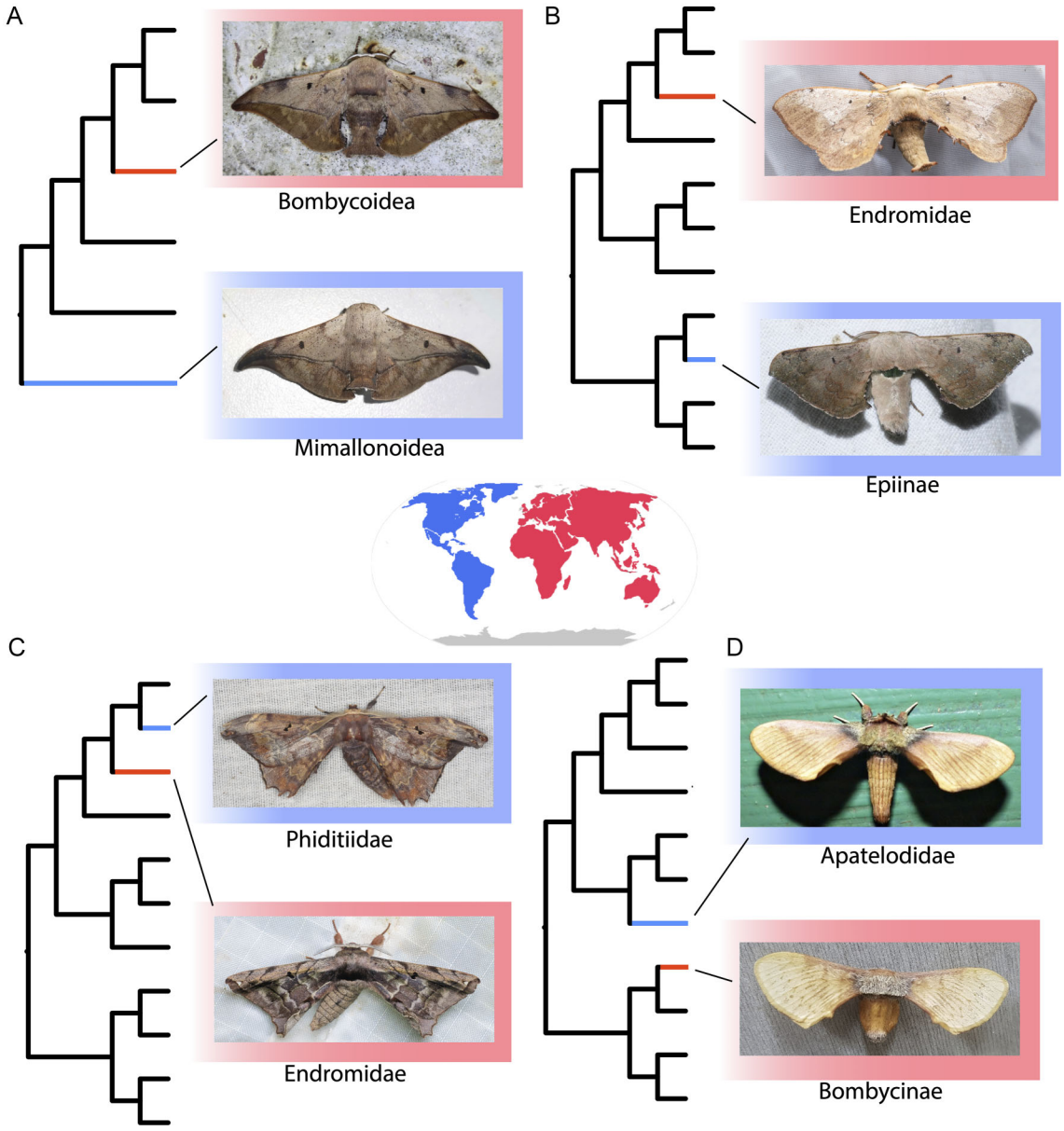

Fig. 4 Cases of extreme concomitant morphological and visual convergence in moths. Each lettered pair display externally highly similar species belonging to unrelated genera from either separate superfamilies or families, with one member of each pair being from the Old World and the other from the New World. This illustrates the multiple independent convergences of morphological syndromes across space and time in Bombycoidea. Parenthetical text refers to the specific bombycoid family in which a convergence occurs. Phylogenies illustrate nonmonophyly of each pair (relative relationships based on Kawahara et al. 2019 and Hamilton et al. 2019). (A) Mimallonoidea/Bombycoidea (Endromidae); (B) Bombycoidea (Endromidae/Epiinae); (C) Bombycoidea (Phiditiidae/Endromidae); (D) Bombycoidea (Apatelodidae/Bombycinae). New World species are represented by the bottom pair of the top panel and the top pair of the bottom panel. Images from iNaturalist (CreativeCommons, individual photographers given in Acknowledgements).

and whether correlated changes in forewing motion, morphology, and body dynamics occur with their evolution.

A second compelling example of convergence within Bombycoidea is the independent loss of functional adult mouthparts in most wild silkmoths and in the hawkmoth subclade Smerinthinae. In both cases, the inability to feed as adults imposes strict energy constraints, which likely favor flight adaptations that reduce power expenditure. Recent work finds that silkmoths exhibit within-wingstroke body oscillations that are features of a mechanism reducing aerodynamic

power requirements (Sikandar et al. 2025) distinct from the adaptations already discussed above. Whether similar energy-saving mechanisms have evolved in non-feeding smerinthine hawkmoths remains largely unexplored, presenting a valuable opportunity to test how consistently energetic constraints shape flight mechanics across lineages.

Bombycoidea contains model species

The bombycoid moth clade contains the Tobacco hornworm (*M. sexta)*, a species whose ease of laboratory rearing and agricultural pest status led to a long history as a model of insect development (e.g., Nijhout and Williams 1974; Booker and Truman 1987) and, more recently, as a model for understanding how insects achieve and control flight. In addition to *M. sexta*, other bombycoid species like *Macroglossum stellatarum*, *Daphnis nerii*, *Agrius convolvuli*, and *Hyles lineata* are also widely used as systems for studying insect flight and therefore represent other emerging model species within Bombycoidea. A model clade containing well-studied model species establishes points of reference when characterizing the neuromechanics of flight across other species of the clade, allowing researchers to build upon the extensive understanding of a specific trait which likely shares more affinity among closely related species (Jourjine and Hoekstra 2021; Mabry et al. 2024).

Studies on flight control in *M. sexta* and the other emerging bombycoid model species reveal flexible and precise mechanisms for maintaining position and orientation during flight that integrate multiple control factors (Hedrick and Daniel 2006; Sane 2016; Hedrick et al. 2024) to produce fine-tuned motor coordination (Ortega et al. 2019, 2023; Wood et al. 2024). Across these bombycoid model species, the kinematics and aerodynamics of hovering and forward flight have been well characterized, revealing the biomechanical principles underlying flight stability and maneuverability (e.g., Aiello et al. 2021a; Johnston and Levine 1996; Willmott and Ellington 1997; Bomphrey et al. 2005; Hedrick and Daniel 2006; Mountcastle and Daniel 2009; Zhao and Deng 2009; Cheng et al. 2011; Tubbs et al. 2011; Kim et al. 2015; Kihlstrom et al. 2021; Hedrick et al. 2024). Similarly, research on sensory-motor integration has further expanded our understanding on the connections between flight behavior and sensory processing, leading to the identification of neural circuits that directly link flight motor centers to sensory centers of olfaction (Willis and Arbas 1991; Raguso and Willis 2002; Bradley et al. 2016; Chapman et al. 2018), vision (Raguso and Willis 2002; Sprayberry and Daniel 2007; Sprayberry 2009; Windsor et al. 2014; Stöckl et al. 2016; Copley et al. 2018; Stöckl et al. 2019; Bigge et al. 2026), and mechanosensation from the proboscosis (Sponberg et al. 2015; Roth et al. 2016; Stöckl and Deora 2024), antenna (Sane et al. 2007; Grosse-Wilde et al. 2011; Dieudonné et al. 2014; Dahake et al. 2018; Chatterjee et al. 2022), and wings (Ando et al. 2011; Dickerson et al. 2014; Hinson and Morgansen 2015; Pratt et al. 2017; Dallmann et al. 2023). Together, this collective work offers insights into flight aerodynamics and control (Ellington et al. 1996; Willmott and Ellington 1997; Daniel and Combes 2002; Combes and Daniel 2003; Sane 2003; Bomphrey et al. 2005; Bomphrey et al. 2006; Hedrick and Daniel 2006; Mountcastle and Daniel 2009; Han et al. 2015; Kim et al. 2015; Greeter and Hedrick 2016; Taha et al. 2020;Aiello et al. 2021a; Wold et al. 2024a; Sikandar et al. 2025), energetics (Casey 1976), muscle mechanics (Stevenson and Josephson 1990; Tu and Daniel 2004; George and Daniel 2011; George et al. 2012; Sponberg and Daniel 2012; Wold et al. 2023), wing and body morphology and mechanics (Aiello et al. 2021a; Wold et al. 2024a; Rubin et al. 2018; Gau et al. 2019; 2021; 2022; 2023; Rubin et al. 2025), sensory-motor integration (Frye 2001a, 2001b; Hedrick and Daniel 2006; Sane et al. 2007; Wang et al. 2008; Sprayberry 2009; Fernández et al. 2012; Springthorpe et al. 2012; Dickerson et al. 2014; Hinson and Morgansen 2015; Roth et al. 2016; Pratt et al. 2017; Copley et al. 2018; Dahake et al. 2018; Dallmann et al. 2023; Stöckl and Deora 2024), and neural control strategies (Willis and Arbas 1991; Raguso and Willis 2002; Fernández et al. 2012; Springthorpe et al. 2012; Dieudonné et al. 2014; Bradley et al. 2016; Chapman et al. 2018; Fandino et al. 2019; Ortega et al. 2019; Sikandar et al. 2023; Tom et al. 2024).

Emerging experimental and computational methods have made it possible to examine insect flight and related traits in greater detail. For example, recent advances in neurophysiological techniques have made it possible to record large neuronal populations using multielectrode arrays as well as the recording of complete motor programs of wing motion (Metallo 2013; Ortega et al. 2019), offering comprehensive views of how muscles and neurons coordinate to produce stable, adaptive flight patterns (Tubbs et al. 2011; Ortega et al. 2019; Ortega et al. 2023). Wing and body morphology in *M. sexta* are well documented using both light photography to capture superficial external traits (Aiello et al. 2021b) as well as microcomputed tomography techniques to capture internal soft tissue structures (Baker et al. 2024). Internal hemolymph flow is well documented in hawkmoths and essential to energetics (Heinrich 1971; 2013), functional endothermy (Heinrich and Casey 1973; Heinrich 1974), antennae function (Puchalski et al. 2024), proboscis control

(Salamatin et al. 2021), and potentially body mechanics (Brasovs et al. 2023). Extensive aerodynamic models ranging from computational fluid dynamics simulations to 3D reconstructions of vortex flows have been developed for *M. sexta*, providing a detailed quantitative framework for understanding force production and airflow during complex flight behaviors (Van Den Berg and Ellington 1997; Willmott et al. 1997; Liu et al. 1998; Bomphrey et al. 2005; Bomphrey et al. 2006; Aono et al. 2009; Cheng et al. 2011; Nakata and Liu 2012; Johansson et al. 2013; Zheng et al. 2013; Sun 2014; Warfvinge et al. 2017; Matthews and Sponberg 2018; Xue et al. 2022). Further, the caterpillar stage reveals an entirely different morphology, biomechanics, and locomotion, serving as inspiration for soft-bodied robotic locomotion (Trimmer 2008; van Griethuijsen and Trimmer 2009; Lin and Trimmer 2010; Vaughan et al. 2018).

Finally, recent applications of CRISPR-Cas9 gene editing in *M. sexta* have expanded the genetic tools available for studying flight-related traits, allowing researchers to link specific genes to sensory perception, foraging, and pollination behaviors (Fandino et al. 2019; Tom et al. 2024). Because these tools have proven highly effective in *M. sexta* and the other emerging Bombycoidea model species, their application to other bombycoid species is expected to yield similarly robust insights, enabling comparative analyses across the clade using consistent methodological frameworks.

Recents insights to insect flight using the bombycoid moth clade

Bombycoid moths fulfill all the necessary and advantageous criteria for an ideal model clade. Even though we are still far from having a comprehensive understanding of all the patterns and processes that shape flight diversity in this clade, bombycoids have already been used in several recent studies to answer broad questions about insect flight.

Resonant mechanics of flapping flight

Most flying insects use indirect flight actuation (Gau et al. 2019), with thoracic muscles deforming an elastic exoskeleton that moves the wings rather than attaching at the hinge. This elasticity creates resonant dynamics through exchange of elastic and wing kinetic energy each stroke (Gau et al. 2019, 2022). By tuning wingbeat frequency to resonance, insects may maximize elastic energy exchange efficiency (Gau et al. 2021, 2022). However, operating at resonance limits rapid frequency modulation for control (Gau et al. 2021), because muscular work per cycle is small relative to total wingstroke energy, requiring many strokes to change frequency (Wold et al. 2024b). This efficiency–maneuverability tradeoff may constrain insect wingbeat frequency (Wold et al. 2025). Wold et al. used flight kinematic variation in Bombycoid moths to study how resonant properties vary as a function of clade and wingbeat frequency (Wold et al. 2024a). In accordance with the hypothesis of resonance tuning, moth resonant frequencies increased linearly with wingbeat frequency. These differences were primarily driven by differences in wing inertia rather than thoracic stiffness: faster flapping hawkmoths had smaller wing inertia which drove up their resonant frequency. However, hawkmoth species all flapped significantly faster than resonance, while silkmoths flapped nearly at resonance. By virtue of flapping faster than their resonant peak, hawkmoths experienced a deficit in efficiency, but may gain control advantages useful for hovering flight and nectar feeding. In contrast, silkmoths were close to optimally efficient. These results are consistent with agility requirements for hawkmoth hover-feeding and the likely limited energy balance in nonfeeding silkmoths.

Ecological drivers of neural investment

While model species such as Drosophila have enabled a wealth of knowledge around neuroanatomical structure, these species are divorced from the evolutionary contexts that actively shape these neural circuits. Neuroanatomical work across Bombycoids (often within hawkmoths) and comparisons across species (including model species) can be leveraged to help demonstrate how investment in neuroanatomical structures are driven by ecological needs. For instance, compared to Drosophila, *M. sexta* utilizes more giant descending axons to cope with sensorimotor demands (Wood et al. 2025). Further, the optic lobes of *H. lineata* contain more than twice the number of neurons in the *Drosophila* brain, despite the rest of the brain being otherwise comparable in number of neurons (Scheffer et al. 2020; Aksamit et al. 2024). This large neural investment in visual processing (Bigge et al. 2026) is likely driven by the nocturnal, visually guided flight niche of most hawkmoths. Comparative work across hawkmoths indicates that markedly different investment in olfactory and visual brain areas occurs depending on diel niche, the time of day at which moths display locomotor activity (Stöckl et al. 2016, 2017). Besides effects on size and internal structure, diel niche also influences connectivity of visual and olfactory circuits, as seen by the presence of ascending projections of motor information to the olfactory system being currently only found in nocturnal hawkmoths (Chapman et al. 2017). These results

cover only neuroanatomical diversity in hawkmoths, but there is great potential for future work targeting differences between the sister silkmoth and hawkmoth clades. Spurred by the frequent variation of diel niche across bombycoids (Hamilton et al. 2019), development of new datasets covering bulk neuroanatomy of silkmoths (Sehadová et al. 2023), and putative identified genetic markers connected to evolution of these niches (Sondhi et al. 2024), there are a wealth of opportunities to further understanding of how ecology drives neural structure. Indeed, these comparative neuroethological efforts will be aided through new molecular sequencing approaches enabling across-species analysis of neuroanatomy, usage of cell-specific markers, and quantification of gene expression levels at the cellular level (see Cicconardi et al. 2025).

Aerodynamic effects of wing-body coupling

In flapping flight, the wings do not act on a rigid body: every wingstroke produces time-varying aerodynamic and inertial forces that drive coupled wing-body dynamics (Taylor and Thomas 2002; Sun 2014). At low wingbeat frequencies (longer flapping periods), these periodic forces can strongly excite the body's pitching and vertical ("bobbing") oscillations during forward flight (Betts and Wootton 1988; Taylor and Thomas 2002; Sikandar et al. 2025). In wild silkmoths, with a flight strategy similar to butterflies, these oscillations are tightly linked to the wingbeat, so the body's orientation and motion influence the instantaneous wing kinematics relative to the airflow and, in turn, the aerodynamic forces and power required to maintain flight (Sikandar et al. 2025). These oscillations help keep wing inclination and angle of attack in useful ranges through the wingstroke, which supports weight and thrust while reducing drag (Sikandar et al. 2025). In addition, body oscillations may aid stability and their energetic advantage may be critical to adapting to adult silkmoths' limited energy budgets (Aiello et al. 2021a; Sikandar et al. 2025). Conversely, hawkmoth flight is more similar to hummingbirds and does not feature large body oscillations tuned to wingstroke kinematics (Aiello et al. 2021a; Cheng et al. 2016; Hightower et al. 2021). This contrast highlights an additional mechanism contributing to the divergent aerodynamic strategies between these two diverse sister families. Together, this combination of divergence within Bombycoidea and apparent convergence in some features with groups outside Bombycoidea (e.g., silkmoths and some species of butterflies) makes this model clade a strong comparative system for isolating how morphology and kinematics shape wing-body coupling.

Leveraging comparisons between bombycoid moths and other clades to reveal generalized principles of morphology, movement, and behavior

The comparison to other insect clades

While we have argued Bombycoidea is a particularly suitable model clade, other groups of insects provide complementary comparative insights. An advantage of the comparative model clade approach is that questions can be addressed hierarchically across different scales of phylogenetic diversity from a single genus like the drosophilids to the whole clade of flying insects. Specific examples of comparisons across different phylogenetic scales can be seen when comparing Bombycoidea to other lepidopteran clades or different insect orders.

Phenotypic convergence between bombycoidea and other clades within lepidoptera

Life is limited by a suite of evolutionary constraints, whether biotic or abiotic or some interaction of those; and these limits manifest both genotypically and phenotypically. Despite the diversity of life and the diversity of habitats on the planet, there are still a finite suite of physiological adaptations that are bounded by ancestral genomic constraints and more broadly, by the planet's physical parameters such as gravity and air density. Consequently, similar phenotypes do evolve convergently in broadly similar but nonoverlapping regions of the planet. In the context of wing morphology and flight performance, studying convergence in these characters in widely separated regions of the world in unrelated taxa offers opportunities to understand how millions of years of evolution directly translate to capacity to fly on Earth. Using broadly distributed model clades, and studying how flight evolved in members of those lineages, there is capacity to recognize the limits of biological solutions to earthly constraints of flight.

While numerous examples of convergence in wing shape and patterning exist across families within Bombycoidea (e.g., Endromidae and bombycine bombycids in Eurasia vs. Apatelodidae, Phiditiidae, and epiine bombycids in the Americas) (Fig. 4B–D), the strongest examples of wing shape, size, and even patterning convergence to morphologies observed in Bombycoidea occur outside the superfamily in the distantly related Mimallonoidea (Fig. 4A). Mimallonoidea is the sister group to Macroheterocera, of which Bombycoidea is part; but is vastly less diverse than Macroheterocera (∼350 species in Mimallonoidea vs. the 10,000+ of Macroheterocera) (Kawahara et al. 2019; St Laurent et al. 2021). The most recent common ancestor of Mimallonoidea and Bombycoidea is ∼100 Mya (Kawahara et

al. 2019), thus observed cases of morphological similarity in both groups may be considered convergent and less directly influenced by genomic controls evolved via more recent ancestry (e.g., aforementioned convergences *within* Bombycoidea). The Mimallonoidea are endemic to the Americas unlike the globally distributed Bombycoidea and have convergently evolved wing shape and patterns remarkably similar to the Old World endemic bombycoid family Endromidae. It appears as though the niche space occupied by Mimallonoidea in the Americas, where endromids are absent, is filled by Mimallonoidea, whereas in Eurasia where mimallonoids are absent, endromids fill this space. These complementary niche occupations provide one hypothesis for why these clades resulted in extreme examples of convergence that are so profound that the unrelated genera appear visually (and possibly functionally) identical. The clearest example of this is *Thaelia* (Mimallonoidea) and *Mustilizans* (Endromidae) (Fig. 4) (Herbin 2016). Another strong, but less dramatic example is *Psychocampa* (Mimallonoidea) and *Comparmustilia* (Endromidae). Quantification of environmental or ecological parameters thought to impact wing shape and patterning could therefore be empirically examined in these different geographic regions and directly related to evolution of these moths, which is an example of the type of broadscale developmental and evolutionary biology work that could be performed using model clades such as these. In sum, these cases of convergence across Lepidoptera, which include taxa remarkably similar to Bombycoidae in an unrelated superfamily, exemplify the wider relevance of studying Bombycoidea as a model clade and the insights their study can likely yield about other, less accessible, lepidopteran clades.

Comparisons across insect orders can yield further insight into the evolution of flight

Diptera is another insect clade that displays many of the features of a model clade for studying insect flight and comparisons between Diptera and Lepidoptera could provide insight into general principles of insect flight. Indeed, Diptera is a diverse, comprehensively sampled clade that also contains a model species, *D. melanogaster*. Across Diptera, variation exists in both locomotor behavior and associated locomotor morphology. However, given the wide range of forms and deep common ancestry, studies focused within the genus of Drosophila may serve as a more focal model clade. Thus, Diptera, and even subclades within Diptera (e.g., Drosophilidae), also possess many of the features of a model clade, and with further comparative work in these groups could serve as another emerging model clade for the study of insect flight enabling complementary insights into the neuromechanical processes governing flight.

Other groups of insects should also be cultivated into explicit model clades for comparative neuromechanics. While specific locust, cockroach, stick insect, and beetle species have served as essential models for movement and, in some cases flight control, there has been less broad comparative work across these groups than in Lepidoptera and Diptera (and specifically bombycoids and drosophids). The bee (Anthophila) serves as another possible model given the diversity of studies on both Bombus (bumblebee) and Apis (species) and the broad diversity, common association with flower foraging, and varying degrees of sociality.

Development of multiple model clades within insects will enable broader phylogenetic comparison. For example, while moths are synchronous fliers that pace the wingstrokes with their nervous system, both bees and flies exceed the frequency limits of this strategy by using asynchronous, or stretch-activated flight muscle. This stretch activation decouples the wingbeat frequency from the neural activation and allows for wingbeat frequencies in excess of 1000 Hz. Asynchronous flight is present in four major orders of insects, but a comparative phylogenetic analysis of muscle types across the whole insect phylogeny supports a single common origin for these stretch activation in these four orders (with many subsequent reverting and regaining transitions within orders) (Gau et al. 2023). This predicts that groups like bombycoids moths may be "secondarily synchronous" having evolved from an asynchronous ancestor. While phylogenetic reconstructions do not preclude the possibility of multiple origins, recent muscle physiology has shown that the stretch activation property necessary for asynchrony is still present in *M. sexta* flight muscle supporting this secondary loss. Leveraging in depth studies of multiple synchronous and asynchronous model clades, would help resolve if all asynchronous species share common molecular and physiological determinants of asynchrony and how there have been repeated transitions back and forth between the two strategies across the insect phylogeny.

Conclusion

Insect flight can emerge through the combination of a variety of underlying neuromechanical mechanisms that are each tuned to meet species specific demands. In this work we demonstrate that Bombycoidea meets all the requirements to be a model clade tractable for the study of insect flight. Bombycoidea possesses well-resolved phylogenies, extensive trait variation, convergence, several model species, and experimen-

tal tractability enabling the study of how morphology, physiology, neural control, and mechanics combine to produce diverse flight strategies. Studies within Bombycoidea reveal how closely related taxa can achieve similar aerodynamic outcomes through distinct combinations of traits impacting flight performance, and the comparison of findings across other insect orders will reveal constraints, general principles, and evolutionary lability underlying powered flight across insects.

Author contributions

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