Introduction – Caterpillars as Focal Study Organisms

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My cousin has great changes coming
Someday he'll wake with wings…
(Cousin Caterpillar (Mike Heron),
The Incredible String Band: The Big Huge, 1968)

Caterpillars are truly in the middle, ecologically speaking. They are both major consumers of plants and critical food for predators. Plants take the sun's energy and atmospheric carbon dioxide and use it to make sugars and oxygen, so they serve as the primary producers in most ecosystems (Jensen and Salisbury 1972). Herbivores (Crawley 1983), including caterpillars, eat plants, obtaining energy and building blocks for their bodies from the organic compounds composed of carbon, nitrogen, and other important molecules and essential elements from plant bodies; herbivores are therefore termed primary consumers. As the famously hungry (Carle 1969) larval stage of butterflies and moths, caterpillars make plant energy and nutrients available to predators by concentrating the essentials in their tissues as they feed and grow. But it is the consumed caterpillars that mediate the transfer of untold amounts of energy and nutrients from plants to carnivores. Many species of predators and parasitoids, termed secondary consumers, attack and eat caterpillars. The populations of these natural enemies depend on an abundance of caterpillars. Caterpillars are therefore at the center of food webs in terrestrial ecosystems, powering their life-supporting properties around the world.

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Evolution rewards the caterpillars that survive to become adult moths and butterflies and ultimately reproduce. Accordingly, caterpillars have evolved many fascinating behavioral and physiological traits to feed on plants despite the fluctuating availability of host plant material and the many defenses (chemical, physical, nutritional, phenological, and biotic) that plants have evolved in response to their herbivores. This coevolution between caterpillars and plants has been going on for millions of years. The diverse traits of plants are the bottom-up forces affecting caterpillar populations. At the same time, caterpillars have evolved myriad defenses in response to predation pressure from their many natural enemies, top-down forces that control caterpillar populations. Sandwiched as they are between the bottom-up and top-down forces that affect their survival, caterpillars have collectively evolved a staggering diversity of traits. Their lifestyle is a compromise wrought by the selective forces represented by the first and third trophic levels. The wide diversity in caterpillar form and behavior, which contributes in great part to their attraction for study, is the result of these evolutionary forces. This diversity is showcased in the 150,000 species of Lepidoptera known to science, with more still to be described. We are only beginning to catalogue this diversity, let alone understand the evolutionary forces driving the diversification of caterpillars. Within the pages of this volume, the reader will find our collective current understanding of caterpillars as components of food webs.

In this introduction we consider the discovery of connections between caterpillars and adult forms, the documentation of their natural history, the study of their development and physiology, and the significance of holometaboly. We will briefly recount and pay homage to the large body of work that laid the foundation for our understanding of the ecology and evolution of plant/insect/natural enemy interactions that have given rise to the contributions in this collection, *Caterpillars in the Middle*. In inviting the group of researchers represented in the pages of this book, we have sought to include insights from various levels of study, with the intention of providing a well-rounded look at advances in caterpillar biology, ecology, and evolution. Biologists may study organisms at any position of the food chain/web and often deal with the effects of one level on another; some even put all levels together and consider the effects of abiotic factors on their organisms of interest. In the chapters of this volume, you will find all these approaches, and we intend that this work will serve to inspire more research on caterpillars in all directions.

Who first recognized that caterpillars are immature stages of butterflies and moths? It is likely that early humans first noticed the beauty of flying adults, watching their movements with awe as the Lepidoptera visited flowers and landed on vegetation, some with their colors as beautiful and bright as flowers, others flying only at night and drawn to fire and lights as were the people who made those things. And while some ate caterpillars as an important source of protein (e.g., mopane worm, the larva of the emperor moth *Imbrasia belina*) (Baiyegunhi et al. 2016; Stack et al. 2003), did they connect the two life stages as parts of a single organism?

This realization may have taken place before written history, but the earliest recorded considerations of the phenomenon appear in the (384–322 BCE) writings of Aristotle (1942 translation; Ryan 2011). He described the caterpillar as a continuation of embryonic life, "a soft egg" that preceded the ultimate goal of adult butterfly. Aristotle was mistaken, however, that metamorphosis transpired despite lack of fertilization, seeing it as a process involved in the spontaneous generation of life (Reynolds 2019). He proposed that the eggs of holometabolous insects hatched "before their time," thus necessitating the extra stages of development outside the egg that preceded the perfect adult organism. Aristotle saw sperm as the agent that transformed the egg to another state, just as heat can cook an egg or curdle milk. These changes were necessary for the organism to achieve its "perfect" form, meaning the stage that could be used to determine its species or identity, the adult form. In the seventeenth century, scientists pursued their endeavors in the light of Aristotle's influence, and though his ideas have fallen out of favor in current understanding of the phenomena of fertilization and development, it is useful to consider the precedent to today's knowledge (Reynolds 2019).

We can find insight into the natural history of Lepidoptera in some of the artwork of early observers of nature. Maria Sibylla Merian's detailed illustrations of European insects and plants (Fig. 1) provided some of the earliest documentation of the life cycles of numerous Lepidoptera. In the seventeenth century, when women were not formally trained or educated and unusual interests led to suspicion and even accusations of witchcraft, this young German girl loved to draw insects (Sidman 2018). Merian, a craftsperson and the daughter of a tradesman (Todd 2007), lived from 1647 to 1717 and described and depicted what she observed around her, the first important step of scientific endeavor. She has been called one of

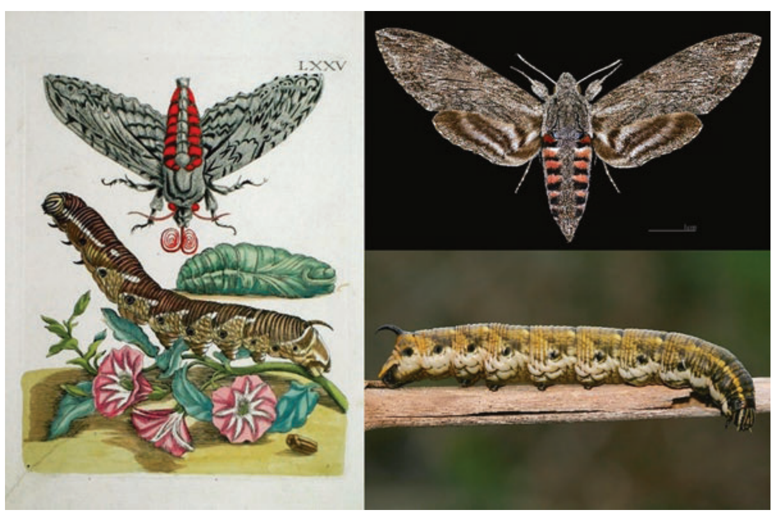

Fig. 1 Realistic depiction of moth life history including hostplant juxtaposed with high quality digital photographs of the twenty-first century. Left image – Maria Sibylla Merian's hawkmoth on morning glory – note all life history stages, even the shape of the frass produced by the large caterpillar. Upper right – *Agrius convolvuli* (L.) female dorsal view, photo by Didier Descouens (CC BY-SA 4.0); Lower right – *Agrius convolvuli korseby* caterpillar, photo by Kristian Peters (GNU Free Document License)

the first ecologists (Etheridge 2011), as unlike other artists of that time, she sought to show in her work the plants with which the insects were associated, putting the subjects in the context of their natural world. Using direct observation both in the wild and rearing insects in her home, focusing on the interactions between plants and animals, her work was foundational for modern-day ecology, the field of many authors in this book. In her quest to describe in her art the metamorphosis of butterflies and moths (as well as other animals), she raised many species from eggs and larvae, carefully recording all the stages of their life cycles. While people had long recognized that silk moths produced eggs that hatched into caterpillars that eventually made silken cocoons from which silk thread were obtained, not many had wondered about the origins of other beautiful moths and butterflies of all colors, sizes, and shapes. In her lifetime she illuminated the life cycles of European Lepidoptera and other insects in two major works of several volumes each (*Neues Blumenbuch*, New Book of Flowers, Merian 1675-1680; and *Der Raupen wunderbare Verwandelung, und sonderbare Blumen-nahrung*, The Wondrous Transformation of Caterpillars and Their Particular Nourishment from Flowers, Merian 1679, 1683, and 1718). Before Darwin, Humboldt, and Audubon, Merian traveled at the turn of the eighteenth century (1699) with her daughter on a voyage of discovery to Surinam to see and learn about neotropical Lepidoptera, after which she wrote *Metamorphosis insectorum Surinamensium*, The metamorphosis of the insects of Surinam, 1705, Amsterdam: G. Valck. Her work inspired many subsequent naturalists and artists, including Mark Catesby who pioneered depicting birds in their natural settings (Etheridge and Pieters 2015), the "Colonial Audubon" (Frick and Stearns 1961).

Scientific investigation continued with observation and illustration to investigations of physiology and development. In the mid-twentieth century, Wigglesworth (1934) discovered that hormones control transformation from larva to pupa to adult. Through his continued work (Wigglesworth 1954) and that of many others, we now know that transformation in all insects is regulated by the interplay of two hormones: ecdysone and juvenile hormone (Rolff et al. 2019). Some insects are hemimetabolous, developing through larval stages very similar in morphology to adults (e.g., Orthoptera) only lacking wings; others are holometabolous, with larvae of entirely different morphology than the adults (e.g., Diptera, Hymenoptera, and Lepidoptera). Why do these extreme changes in form exist within the life history of a single organism? Darwin postulated, in *The Origin of the Species by Means of Natural Selection* (1866), that the significance of holometaboly was that the different stages of development had different lifestyles and occupied different ecological niches; this idea was reiterated by Williams (1952) and reviewed by Wilbur (1980). Perhaps the most satisfying explanation is that complete metamorphosis is an adaptation permitting the decoupling of growth and differentiation (Rolff et al. 2019). This can be advantageous when food is sporadically available. Rapid growth is advantageous as the larva is a vulnerable stage, reducing the period of time it may be killed by predators, pathogens, and parasitoids. Plants can thwart herbivorous larvae through a variety of defenses: biotic, chemical, mechanical, and phenological. *It is this position of caterpillars in the middle of the top-down and bottom-up forces that provides the content of this volume.*

Many young ecologists of a generation ago were inspired by the influential volume *Coevolution of Animals and Plants* (Gilbert and Raven 1975) and by other volumes in which experts on different topics contributed chapters (Chapman and Bernays 1978; Futuyma and Slatkin 1983; Price et al. 1991). There have been many important books published in the last few decades about multitrophic interactions, many with a focus on arthropod/plant interactions. *Insects on Plants* (Strong et al. 1984) brought these interactions into more prominence in community ecology, and *Herbivory* (Crawley 1983) examined animal effects on plants at many levels. *Trophic Cascades* (Terborgh and Estes 2010) emphasized tri-trophic interactions involving vertebrate herbivores and vertebrate predators. An edited volume (Barbosa and Letourneau 1988) focused on mediation of complex interactions by plant allelochemicals, including their effects on higher trophic levels, while Rosenthal and Berenbaum (1991) focused on the effects of plant chemicals on herbivores. The multi-volume series published by CRC press, *Insect-Plant Interactions* (1979–1984), was made up of five volumes of contributed chapters, edited by Elizabeth Bernays. Two other edited volumes brought together the work of scientists examining plant-insect-enemy interactions, including *Multitrophic Interactions in Terrestrial Systems* (Gange and Brown 1997) and *Herbivores: Between Plants and Predators* (Olff et al. 1999). A volume entitled *Multitrophic Level Interactions* (Tscharntke and Hawkins 2002) included bottom-up and top-down effects in both above-ground and below-ground food webs. Some scholarly works have focused more on the first trophic level, plants (Fritz and Simms 1992); some on the second trophic level, herbivores (Tilmon 2008); and others on the third trophic level, predators and parasitoids (Hajek 2004; Hawkins 1994; Rico-Gray and Oliveira 2007; Wäckers et al. 2005). Still more were overviews of numerous kinds of interactions and how they have coevolved (Abrahamson 1989; Thompson 1982, 1994, 1997, 2005; Jolivet 1998; Schoonhoven et al. 2005; Herrera and Pellmyr 2002), some with a particular focus on global change (Kareiva et al. 1993; Post 2013; Tylianakis et al. 2008).

While caterpillars as herbivores were included in most of the abovementioned works and other books have focused on either identification (e.g., Wagner 2005) or the biology of particular groups (Tuskes et al. 1996; Tuttle 2007; Conner 2009), it was nearly 30 years ago when the first and only book on the ecology and evolution of caterpillars was published. That volume, edited by Nancy Stamp and Tim Casey (1993), became a treasured classic, bringing together the perspectives of a diverse and international group of researchers. Although the title suggested the focus was only caterpillar foraging ecology, its coverage included effects of abiotic and biotic forces on caterpillars, examination of interesting lifestyles, and how caterpillar feeding and associations varied in space and time. It is time for a new look at the ecological and evolutionary forces that affect larval Lepidoptera and to consider the effects of a changing planet on their continued existence. We are fortunate to have some contributors to the earlier caterpillar book (Stamp and Casey 1993) authoring chapters in this book. We have invited contributions from scientists whose interests and expertise range widely, from simple natural history to experiments and analyses that provide some insights that were not possible at an earlier time.

The idea for this book came from organizing a symposium for the Entomological Society of America meetings held in St. Louis in the Fall of 2019, and most of the participants in that symposium have contributed to this book. We were glad that other renowned scientists also agreed to contribute to this new compendium of research on caterpillars, their hostplants, and natural enemies, reflecting a variety of approaches and expertise. As this work is written in the early part of the twenty-first century, a time when we are well aware that human activity on the earth has changed the climate of our home planet, we attempted to include consideration of these forces in every contribution. We now present this book entitled *Caterpillars in the Middle: Tritrophic Interactions in a Changing World*, hoping it has something for everyone and may serve to inspire future research on and appreciation of caterpillars.

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