Chapter 9
Tropical Caterpillar Addiction

Annette Aiello

It's tempting to begin this account with "It was a dark and stormy" journey to the Lepidoptera, but I will resist. It's true though that the path was a long and convoluted one, with plenty of possibilities unrecognized and opportunities missed.

I was born in 1941 in a large city, New York. We lived in Brooklyn, where the neighbors' yard held the only nearby representative of the natural world, a magnificent magnolia tree. The flowers and their perfume were the most wonderful things imaginable. I collected fallen petals in a shoe box and a few days later suffered a great disappointment when the petals turned brown.

My earliest encounter with nature was my grandmother's garden in Guilford, CT. It was simply gorgeous. On visits there, from toddler years on, I spent hours making the rounds of every plant in that garden. It had all the elements one might expect in a garden of that era: irises, lilies, roses, a rock garden with *Opuntia* cactus and *Portulaca*, *Gaillardia*, *Hosta*, love-in-a-mist *(Nigella damascena)*, mullein-pink *(Silene coronaria)*, snowberry *(Symphoricarpos albus)*, and nasturtium *(Tropaeolum majus)*; and of course, lots of butterflies. Children are naturally attracted to flowers and butterflies, and they feel a powerful urge to interact with them but don't know how. I remember that "Don't touch" frustration well (Fig. 9.1).

In 1948, my family moved to Killingworth, CT, a rural town where houses were few and far between, and where I attended a one-room schoolhouse. Now we were surrounded by nature. Killingworth then was mostly woodland, abandoned fields, small streams, swamps, and cranberry bogs, and I explored these at every opportunity, year round. I collected bird nests, shed snakeskins, rocks, and shells. And I raised and released baby birds that fell from their nests. In those days, before widespread light pollution and the rampant use of dichlorodiphenyltrichloroethane (DDT), the windows on summer evenings were teeming with insects, especially large colorful moths. As with the magnolia petals, I felt compelled to collect them. Having no guidance as to procedures or equipment, I dispatched them with carbon

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Fig. 9.1 Don't touch! The author conversing with flowers, July 1942, Guilford, CT

tetrachloride and displayed them in windowed handkerchief boxes lined with milkweed down. Of course, after a few years of labor by museum pests, the milkweed down was all that remained.

During my early teen years, a neighbor took me along on Connecticut Botanical Society field trips. They were wonderful, but I didn't know that one could study plants and animals in any formal way and make a career from something they liked to do. It took decades for me to figure that out. It was no help that high school biology was quite dull, except that I had a crush on the teacher. The course was taught entirely from a textbook with no laboratory sessions or field trips at all. If anyone had predicted then that I'd eventually do a PhD thesis in botany or go on to study insects, I would have said "Very funny." On top of that, the results of a "general interest" survey administered in our senior year (1959) were interpreted to suggest that I take up a career as a flower arranger.

I left home right after high school graduation and returned to New York City to study music. Once again I was severed from nature. I supported myself with a series of jobs: painting fingernails at a manikin factory in the garment district, working in a shoe factory in Greenwich Village, and coding questionnaires at the American Cancer Society.

Later, I moved to New Orleans for a few years and worked in a department store's accounting department and later was the jewelry-receiving clerk in Adler's jewelry store, a truly fun job as one never knew what wonders a package would hold. On the music side, I sang in the local orchestra chorus and the opera chorus. Throughout my years in New Orleans, I was intrigued by the plants, insects, and birds there,

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and though I passed the natural history museum on my bicycle ride to work every day, and though I thought of stopping in there to ask questions, I didn't do it. The museum opened after my working hours began and closed before they ended. Why didn't I call in sick and just go there? A combination of shyness and job responsibility most likely. Among the opportunities missed, that one perhaps was the most lamentable as it had the potential to point my life in the right direction almost instantly.

On my return to New York, I worked at the Diner's Club accounting office, then a feature news agency, and then Basic Systems Inc. (a now defunct subsidiary of the Xerox Corporation). Clearly, I needed to identify and focus on a meaningful career. But what? Why biology wasn't obvious I'll never know. A newspaper ad led me to the Germaine School of Photography, located in the basement of the Transportation Building in Lower Manhattan. The course was intensive, a 600-h curriculum covering every aspect of commercial black and white photography. Mainly we used large format studio cameras—with 5″ × 7″ sheet film. We lugged them and their huge tripods around on public transportation to reach our various field assignments, which included the construction sites of the World Trade Center and Lincoln Center. When the course ended in May 1967, I got my first camera, a Nikon single-lens reflex. It was spring, and instead of continuing exclusively in black-and-white format, I found myself taking hundreds of photographs of plants and insects. I photographed weeds in abandoned lots and railroad beds in the Brooklyn Bridge area, and wild flowers and insects all over the place in Connecticut where mother drove me around on weekends. A Killingworth neighbor invited me to go botanizing. She told me about a book called *Gray's Manual of Botany* that covered all the New England plants. I bought a copy and spent the next winter learning the terminology and trying to identify the plants in my photographs. It was beginning to sink in that biology could give my life meaning.

Finally, at the age of 28, I realized it was time to go to college. I majored in biology at Brooklyn College, and then went on to the Graduate School of Arts and Sciences at Harvard University. My doctoral thesis took me to Jamaica and Mexico, and it was in Jamaica that insects began to attract me greatly. I was especially intrigued by a treehopper (Membracidae) that had a colorful bubble-like projection which it threw off with a snapping sound when disturbed; I've never seen such a bizarre insect since. My guide in Jamaica was kind enough not to inform my Harvard advisor that I was collecting insects in addition to the thesis plants.

In 1976, as I was finishing the thesis, unexpected life events diverted me to Barro Colorado Island (BCI) Panama (Fig. 9.2) for 6 months a year to collaborate on a butterfly project with Robert Silberglied, a Harvard professor in entomology. Until his death in early 1982, we spent each March–August in Panama studying the two commonest butterflies in the neotropics, *Anartia fatima* of Mexico and Central America, and *Anartia amathea* of South America. We learned that they hybridize in Panama's Darien Province, towards the Colombian border (Fig. 9.3). Did they mate at random, or did they choose mates? What were the consequences of hybridization? Why didn't the two species spread into each other's ranges? To investigate those and other questions, we raised hundreds of butterflies for mate choice tests. Our waking hours were consumed with capturing females and harvesting eggs from

Fig. 9.2 Barro Colorado, Panama. *Upper left:* Approaching the dock from Gatun Lake. *Lower left:* Ascending the more than 100 steps from the dock to the Dining Hall and dormitory. *Upper right:* Barbour House, where we lived and conducted laboratory research. *Lower right:* The Herbarium, with a spider monkey and baby on roof

them, collecting caterpillar food plant, feeding caterpillars, separating pupae as they formed, marking adults individually as they emerged from their pupae, feeding adults, running the mate choice experiments, and keeping meticulous records of every individual for several generations. The caterpillar food plant was an abundant weed, *Blechum pyramidale* of the family Acanthaceae. To feed so many caterpillars, we had to travel off-island and collect huge amounts of *Blechum* along roadsides and waste areas, about a dozen garbage bags full per week. The project was intense

Fig. 9.3 *Anartia fatima (left), FA* hybrid *(middle), Anartia amathea (right)* (family Nymphalidae)

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and unrelenting, and we were slaves to it, 18 h per day, 7 days a week. As each generation of caterpillars grew to their largest size and approached pupation, they became voracious and we nearly went crazy trying to keep up with feeding them and cleaning their little cages, which were made from window screen cylinders with Petri dish bottoms and covers, and which held 25 caterpillars apiece. We sent 15 pounds of caterpillar fecula per week to a biologist in town, who used it as orchid fertilizer.

As the result of our efforts, we learned that the initial hybrids between the two species are healthy. We called them *AF* and *FA*. *AF* stands for an *amathea* female mating with a *fatima* male, and as you might guess, *FA* stands for a *fatima* female mating with an *amathea* male. Though the wing patterns of the two hybrids were more or less intermediate between the two species, they were not identical. Not only that, but their behaviors were quite different. Though *FA* females mated readily, *AF* females resisted mating with anyone, and even when they did mate, most of their offspring died as tiny hatchling caterpillars. Thus, genetic incompatibility helped keep the two species apart.

In addition to the initial hybrids, we did 12 other crosses between the two species, and that involved rearing the butterflies through three or sometimes four generations and obtaining the complete genealogy for each individual. With these crosses, we saw further breakdown in their ability to reproduce successfully. The 12 crosses were: four second-generation crosses among the hybrids: *AF*/*AF*, *AF*/*FA*, *FA*/*FA*, and *FA*/*AF*; and eight back-crosses between the hybrids and the original species: *A*/*AF*, *A*/*FA*, *AF*/*A*, *FA*/*A*, *F*/*AF*, *F*/*FA*, *AF*/*F*, and *FA*/*F*. The butterfly specimens from this study are housed in the collection of the Museum of Comparative Zoology at Harvard.

You have to be young and slightly nuts to undertake such a large rearing project, and I do not recommend it to anyone unless they already are quite mad and/or have lots of helpers. In spite of it all, I still enjoy seeing *Anartia fatima* fly by, and always I say a fond “Hello.”

The two main creatures on our walls in Barbour House on BCI were the large native forest gecko, *Thecadactylus rapicaudus*, and the common American roach, *Periplaneta americana*. Our first impulse was to squash the roaches, but, instead, we decided to put names on them. We painted white typewriter correction fluid on the large plate (pronotum) that covers the thorax, and when that dried, we used a fine technical pen to write names: Alice, Elmer, Harry, etc. It was quite a surprise to discover that there were only six individuals, not millions, and a further surprise to learn that once we thought of them as individuals, our attitude toward them changed completely. They came and went and we worried about them when one was absent for more than a few days. We put up two silly signs: “Please do not kill the roaches, the geckos eat them” and “Please do not kill the geckos, they eat the roaches.” Sometimes the roaches travelled to the habitation above, and there Alice was saved from certain death when Andrea Worthington, our upstairs neighbor, noticed the roach she was about to step on had a name. Weeks later, when our new upstairs neighbor was John Pickering, I was awakened one night by a scratching sound. Approaching cautiously with a flashlight, I discovered the source: a roach chewing the binding of a notebook. It had a name. Who was it? Closer now, I read "Hi Bob and Annette," and a smiley face. John had found an unmarked roach and had been waiting two weeks for us to see it. Luckily, I got that opportunity, because it was never seen again.

It was on BCI that I fell in love at first sight with tropical caterpillars in general. The botanical thesis did get finished and published, but caterpillars put an end to my formal connection to botany. The thesis wasn't wasted time and effort, however. My botanical knowledge served me well because, after all, caterpillars eat plants. BCI was a biologists' paradise. It was brimming with life and thanks to the forest guards, who patrol the island 24 h a day on foot and by boat, it was safe to wander the trails even at night to search for caterpillars or gather emergency food plant. Meals on BCI were, and still are, cafeteria style. There was no food shopping, cooking, or washing dishes. Back then, unlike now, there were no telephones on the island. And, of course, it was before e-mail or even computers. Life was simple: eat, sleep, work.

At that time, most tropical caterpillars had not yet been associated with their adults, and I quickly became addicted to rearing them to find out who they were and how they lived; quite reminiscent of opening packages at Adler's, only much more exciting. Dan Janzen and Winnie Hallwachs were just beginning their massive Lepidoptera rearings in Costa Rica, and Diomedes Quintero was starting the insect collection at the Universidad de Panamá. These were some of the best years of my life.

One of the first creatures to arouse my curiosity was not large or colorful. It was the maker of the small sand and silk cases (Fig. 9.4) that adorned the walls of the BCI buildings inside and out. They were half-inch long, spindle shaped, and flattened, and each contained a larva that stuck out one end and pulled the case behind it. I say "larva," not "caterpillar," because I didn't know what these little guys were, or what they were eating. Were they moths? Beetles? Flies? Some weird worm? Nobody on BCI could tell me. In Barbour House, where we stayed, there were lots of them in the bathroom, and I did a mark-recapture study of the cases in there to find out where individuals went, how far they moved, and when they were active. Liquid paper painted on a small area of each case provided a background to write individual numbers using a 000-pen. I captured larvae from the other buildings to study them in captivity and, as they developed, provided them with different colored particles (white sand, black sand, powdered red brick) to observe the case-making sequence. I could hardly sleep thinking up things to try with them. I installed windows by cutting a square hole in a few cases and gluing a piece of plastic wrap over the opening to see what went on inside. The larvae were most active at night. They were eating animal hair and dead insects, and turned out to be clothes moth relatives. I dubbed them "bathroom moths." They stacked their food neatly inside the case. They turned around inside the case by doubling back on themselves in the wide, center portion. I followed them from egg to adult, feeding them dead mosquitoes, which they liked very much, and I even managed to get a number of them through on a diet of my hair alone. I found that in order to be nutritious the hair had to be dirty, which meant going several months without washing my hair. The findings formed my first single-author entomology paper, *Life history*

Fig. 9.4 The bathroom moth (*Phereoeca allutella*, Tineidae). Clockwise from *upper left:* an accumulation of pupation cases in a corner; a case partially cut open to show the larva and its larder, my hair; the case of a larva that was provided with different colors of building materials during its development; two cases with windows; case number 23; an adult moth; a larva reaching out of its case to pull a mosquito inside

and behavior of the case-bearer Phereoeca allutella (Rebel, 1892) (Tineidae). It seems appropriate to end this account of the bathroom moth with its motto, "Hair today, guano tomorrow."

Anyone who has reared insects has experienced sleepless nights of anticipation prior to emergence of the adult of an unidentified species. For me, the most difficult waits occurred when I had some idea what the moth or butterfly might be. Those outcomes were a rewarding combination of confirmation and surprise. The anticipation was especially acute when rearing butterflies of the genus *Adelpha* Hübner, [1819] (Nymphalidae). *Adelpha* is special because, as I discovered, the keys to understanding the evolutionary relationships among its 85 species lie in the forms of the caterpillars and pupae. Their adult wing patterns do not reflect species relationships. Species with similar patterns often are unrelated, and related ones often look quite different from one another. It is not known why that is, but it is so.

Of the 36 species of *Adelpha* known in Panama, I have reared 14. Well, actually only 13. The 14th one fell into my hands on three occasions, in 1982, 1983, and 1985, and each time it died, twice as a caterpillar, and once as a pupa just a day before expected eclosion. Please, readers, would one of you find and rear this frustrating creature, which I have dubbed *Adelpha croaki*. It eats the leaves of a tree called *Heliocarpus* (family Malvaceae), and it belongs to the *Adelpha serpa* group.

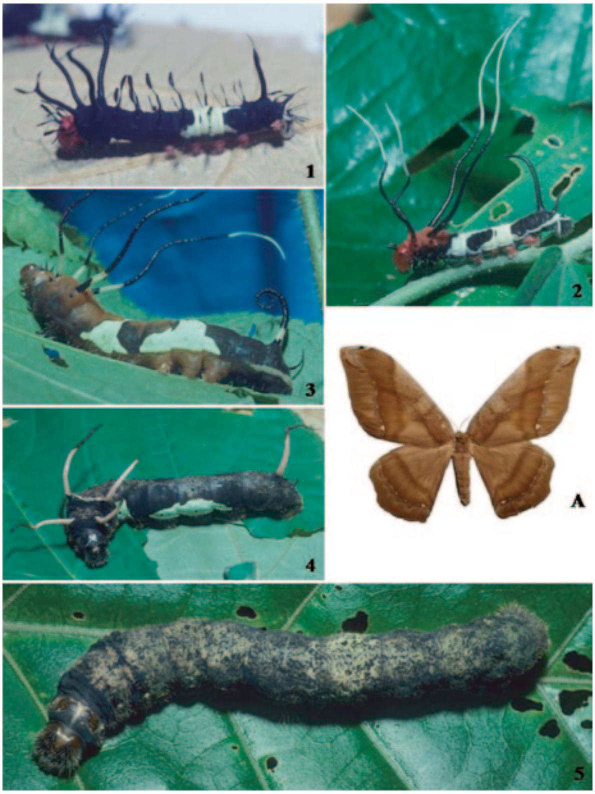

Fig. 9.5 *Arsenura batesii* (family Saturniidae). *Numbers* correspond to caterpillar stages *1–5*. *A* adult

There is reason to suspect that it will turn out to be *Adelpha radiata aiellae*, but we just don't know (Keith Willmott, personal communication).

Failed rearings are discouraging, but there is always hope for another opportunity, though sometimes it takes years to get an answer. It is amazing how the mind can accumulate hundreds of isolated observations and retain them for decades, ready to fit into place when a new observation or insight presents itself. As an example, because the caterpillars died because of a variety of mishaps, it took some time to realize that several rather different-looking ones (Fig. 9.5) represented different larval stadia of the same species, *Arsenura batesii*.

Over the years, I learned that many other species of Lepidoptera have caterpillars that change in form or pattern as they develop (Fig. 9.6). The butterfly *Dynastor darius* (Fig. 9.6D) has three different head forms during its life. When the caterpillar emerges from the egg, it is tiny; the body blends with the leaf, and the fuzzy head looks like a bit of mold. When it molts (sheds its skin), the intermediate stages have smooth heads protected by horns and have a complex pattern of triangles. In the final stage, the caterpillar has a brown head with black horns and black border. The pupa is spectacular; it resembles the head of a snake. I had a number of these pupae suspended in their little cages on my work table, and whenever the table

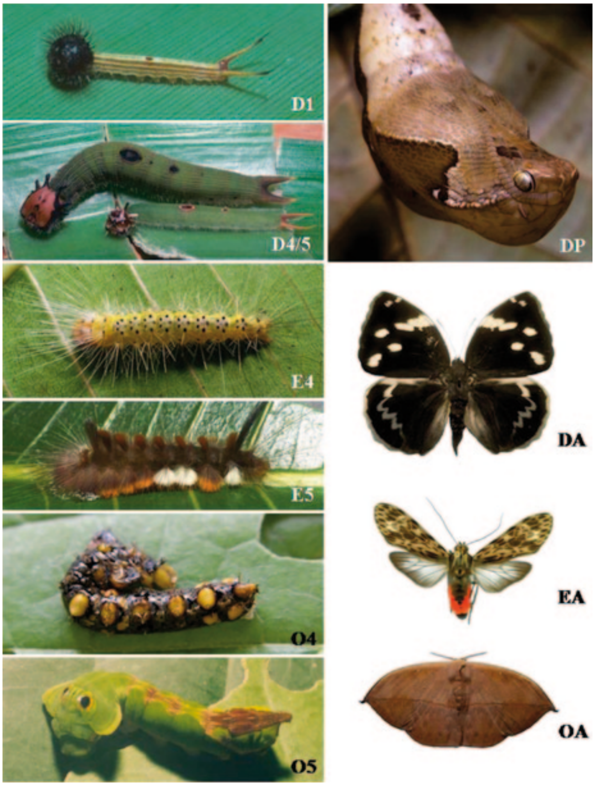

Fig. 9.6 Three species whose caterpillars change their appearance as they develop. *D* = *Dynastor darius* (family Nymphalidae); note that the pupa closely resembles the head of a snake. *E* = *Eucereon latifascia* (family Erebidae). *O* = *Oxytenis modestia* (family Saturniidae). Numbers correspond to caterpillar stages. *P* pupa. *A* adult

jiggled enough to disturb them, they thrashed side to side, triggering my adrenaline every time. Another example of change in appearance with development is the moth *Eucereon latifascia* (Fig. 9.6E). The caterpillar is yellow with tiny black spots and sparse beige setae (hairs), but when it molts to the final stage, its appearance changes dramatically. It bowled me over when it molted because I had collected both forms, never imagining that they pertained to the same little moth. An interesting twist to the complexity of caterpillar form is that there are many examples of totally unrelated species that are similar in form and/or color pattern (Fig. 9.7).

Evolution has produced myriad caterpillar defense strategies: concealment, camouflage, imitation of inedible objects, false threatening eyes, toxins, poisonous spines. Each of these strategies has endless variations and can change each time the caterpillar molts. It is such fun to be fooled and then discover that what you thought was inanimate really is a caterpillar. The moth *Oxytenis modestia* (Fig. 9.6O) had several surprises for me. The caterpillars rested curved on their food leaf and resembled bird droppings with seeds in them. But when they molted to their final stage, they were green or brown, and the thorax had false eyes that they could open and close by inflating or deflating the body using blood pressure. When disturbed, they opened the eyes and reared up, waving back and forth like a snake. The adults rested with the wings flat and spread to closely resemble dead leaves, and when

Fig. 9.7 Three pairs of unrelated caterpillars that have similar color patterns and/or forms. *Top row: left:* a moth, *Oxytenis naemia* (Oxytenidae), and *right:* a butterfly, *Adelpha phylaca pseudaethalia* (Nymphalidae). *Middle row: left:* a moth, *Pseudodirphia eupanamensis* (Saturniidae), and *right:* a butterfly, *Hamadryas iphthime* (Nymphalidae). *Bottom row:* two unrelated moths: *left: Mesoscia dumila* (Megalopygidae) and *right: Apatelodes paratima* (Apatelodidae)

touched, they wafted to the ground just like fallen leaves, never moving the wings at all.

Meanwhile, back at *Adelpha*, another rearing that took a stressful turn several days before the adult was to emerge had a happy ending. The USA invaded Panama and toppled the dictatorship, and the highway to the city was closed for 1 week. Without periodic ventilation and humidity monitoring, most of the pupae in my lab were doomed. The *Adelpha* was of particular concern because it belonged to a species I had not reared before and had only one individual of. Once the highway reopened, we made a beeline for the city. All of the pupae had failed, with one exception, the *Adelpha*. The adult had emerged flawlessly and died on the cage floor with the wings perfectly spread. It was *Adelpha messana messana*, known to me at that time as *Adelpha ixia leucas*, which was the name used in my publication about it.

Sometimes, caterpillars survive a series of misfortunes against all odds. Such was the case with a large owl butterfly caterpillar, *Caligo idomeneus*, that was brought to me with no food plant, with parasitic fly eggs stuck all over its head, and with an internal thoracic rupture incurred when it landed on someone's shoulder and suffered a reflexive whack. Not having any idea what this intriguing caterpillar was, I used forceps to remove the fly eggs—luckily not yet hatched—and offered it a salad of every plant around; it chose *Heliconia latispatha*. Being asymmetrical because of the rupture, the caterpillar did not attach well to its support, and it fell soon after pupation, while still soft. Now the pupa was flattened on one side and almost certainly done for. Incredibly, it endured and reached the adult stage, though the wings are noticeably larger on one side than the other.

Many biologists suffer spectacular accidents in the field, but I am sorry to disappoint the reader. Despite several close calls, I have had no serious falls or adventures and no broken bones, just two relatively minor, but miserable mishaps. The first was an attack by a female wandering spider, *Phoneutria boliviensis* (family Ctenidae) who, unknown to me, was guarding her egg sac a few feet away in the same tree I was collecting a leaf from. When I jiggled the branch, she rushed over, bit my right ring finger then dropped to the leaf litter and raced away. She was quite large; the fang marks were 8 mm apart. The pain was excruciating and lasted 12 h, during which time I was unable to work, or eat, or escape by sleeping. Wandering spiders are especially common in banana plantations and are the misnamed "tarantulas" of the "Banana Boat" song.

The other incident had to do with ticks. BCI is famous for ticks, and their removal is part of one's evening ritual. Ticks are not nearly as common in Arraiján, the little town where we now live, but there they do carry rickettsial diseases (mainly *Ehrlichia* and *Babesia*) that mostly affect cattle and doggies. In July 2003, I contracted *Ehrlichiosis* from a dog tick. The disease began to manifest itself a week or two later during visits to my family in Killingworth and the Smithsonian natural history museum in Washington, DC. Mild flu-like symptoms gradually worsened over a period of a week, giving way to nausea, chills, fever, extreme weakness and total loss of appetite, a horrible headache, and brown vision that made it impossible to see the paperwork I had to sign when admitted to a Washington hospital for four nights. Doxycycline put a stop to the infection, but it was another week before I gained enough strength to return to Panama. Do I now use repellant? Nope. The idea of years of daily chemical applications scares me lots more than a possible rickettsial incident that now I would recognize the symptoms of and seek earlier treatment for. Accidents and the threat of tropical diseases do not deter the field biologist. The allure of what wonders might lie over the next hill or around the next bend is just too strong. Biology is a way of life, not a job. It is an extension of one's self.

The reader who asks "What does any of this have to do with serious science or how does it help society?" has a valid question. Are not biologists just playing, especially when they actually enjoy their work? To understand why our activities are important, try and imagine that you and your family have just landed on an alien planet. You emerge from your spaceship and look around at the strange organisms surrounding you. What are they? Are any of them plants—organisms that derive their sustenance from a combination of earth, air, and energy from their sun? Which animals are dangerous? Which can be eaten? How do all these organisms interact with each other? In other words, you would have all the same questions we have been asking here on Earth for thousands of years. Whatever little details we can discover about life on Earth are important. What a single person contributes may seem like trivial anecdotes, but when woven into the total fabric of our knowledge, a big picture emerges, and it grows slowly but steadily to reveal the vast truth of how life began and perpetuated itself and how the web of life developed its almost unimaginable complexity, which now is being destroyed. And that includes ourselves because we are an intrinsic part of the web. Once our place in it becomes too overbearing, it will all tumble down. But, not to worry. Long after we have disappeared, Earth will recover, and the complexity will restore itself, though with plants and animals different from those we see today.

Annette Aiello is a staff scientist in entomology at the Smithsonian Tropical Research Institute in Ancon, Balboa, Panama, where she has been studying insect life histories for nearly 40 years. Her main focus has been the transformations of moths and butterflies, especially their caterpillars: their development, behavior, and defenses, as well as the clues that they and their host plants can contribute to our understanding of species relationships (classification). Her publications include other subjects as well: plants, beetles, leafhoppers, insect outbreaks, mimicry, and even sloth hair. Her early interests lay in botany, which she pursued on her own until at last entering college in her late 20s. She obtained her BA in biology, magna cum laude, at Brooklyn College in 1972, and an MA and a PhD in biology at Harvard University in 1975 and 1978 respectively. Her PhD thesis was in taxonomic botany: *A Reexamination of Portlandia (Rubiaceae) and Associated Taxa,* with Dr. Richard A. Howard as her advisor. She is a resident of Panama, and she and her Panamanian husband, Ricardo Cortez, live in a small town several miles west of the Panama Canal.

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