BOOK REVIEWS

Perspectives on Royalty

Biology and Conservation of the Monarch Butterfly. STEPHEN B. MALCOLM and MYRON P. ZALUCKI, Eds. Natural History Museum of Los Angeles County, Los Angeles, CA, 1993. xii, 419 pp., illus. $90. Science Series, no. 38. From a conference, Los Angeles, Sept. 1986.

As an educated non-lepidopterist, what do you know about the monarch butterfly? You've probably heard that it is the distasteful model for the Batesian (edible) mimic appropriately known as the viceroy. You may know that it derives its unpalatability from the toxic chemicals (cardenolides) produced by its larval host plants, members of the milkweed family. And chances are you have seen spectacular pictures of its winter roosting aggregations, so you know it undergoes a regular seasonal migration, similar to that of birds, between summer breeding grounds in temperate North America and wintering grounds in central Mexico and on the southern and central coast of California. Chances are that's more natural history than you know about any other insect. If you have kids, they'll probably encounter all this lore before they reach high school. The monarch, which has been nominated as our national insect, has become one of the best organisms for engaging the imagination and interest of the general public with matters of ecology and conservation. The trouble with all of this is that none of the "knowledge" just itemized is exactly true. Nor is it exactly false. This remarkable book shows us that the more we learn about the monarch the less we "know" with confidence.

This is essentially a collection of papers presented at the Second International Conference on the Monarch Butterfly ("Moncon-2"), held in 1986 in Los Angeles. The long publication delay is unfortunate, but not catastrophic. Little that appears here has been "scooped" in journals or rendered obsolete. Some of the papers have been updated to include literature through 1990. This is a remarkably candid, heretical, and iconoclastic symposium, and nearly all the outrageous questions it raises remain unanswered in 1993.

Just how weakly founded has the pre-Moncon conventional wisdom been?

Is the monarch a Batesian model? Is the viceroy a Müllerian mimic? Yes and yes. The paper by Ritland and Brower on the situation in Florida (where there are monarchs alongside another putative model, the queen, and an endemic subspecies of the viceroy that looks much more queen-like than monarch-like) makes it abundantly clear that monarch mimicry is a game of permutations and combinations. Of the revisionist papers this is the least surprising, because a version of the story appeared in a journal in 1991. Even so, it will raise eyebrows.

Does the monarch use plant-derived cardenolides for defense against predators? Yes—but its ecological chemistry turns out to be much more complex than that. Lincoln Brower's famous cabbage-reared monarchs were reportedly feeble but palatable in the absence of cardenolides, and numerous subsequent studies have documented a "palatability spectrum" reflecting the cardenolide content of the milkweeds ingested. But as far back as 1978 Rothschild, Marsh, and Gardiner claimed the presence of autochthonous cardioactive substances in monarchs reared on cardenolide-free (indeed, leaf-free) lab diets. And in 1984 Rothschild, Moore, and Brown pointed out the potential role of pyrazines in the danaid "defensive odor." These leads remain to be explored in depth. A third group of relevant compounds, pyrrolizidine alkaloids, has generated a large and polemical literature. Danaids and some other unpalatable butterflies actively collect pyrrolizidines from plants that produce them; they turn out to be important in pheromonal communication but also, apparently, in anti-predator defense. The monarch is an atypical danaid in its nonchalance toward pyrrolizidines. It also has a derivatively simplified courtship and thus may not "need" pyrrolizidines in that context. Is this a cause-and-effect relationship, and if so, which is which?

The conventional interpretation of milkweed-monarch chemical ecology is the "ploy-counterploy model" of Fraenkel: cardenolides are an evolved anti-herbivore defense of milkweeds, surmounted by the danaids and then opportunistically used by them for their own defense. But systematist Phillip Ackery points out that from a cladist's standpoint virtually the whole apparatus of aposematism is in place before the lineage leading to the monarch "discovers" cardenolides. Indeed, only a minority of danaids may use cardenolides for defense, or even have access to them. Ackery speculates provocatively

"On 15 February 1987 the smoke of a nearby fire elicited this panic response from perhaps [several] million aggregated monarchs overwintering on Sierra Chincua in central Mexico. The response began suddenly and lasted for about 30 minutes, with approximately one-half the colony taking flight above the forest canopy. The remaining butterflies plummeted to the forest floor." [From *Biology and Conservation of the Monarch Butterfly*; photograph by John I. Glendinning]

that the acraeine, heliconiine, and danaine butterflies "may be pre-adapted to feed on toxic plants, rather than the larval hosts contributing significantly toward overall unpalatability." Indeed, dependence on host-derived cardenolides for defense may be a derived state in the monarch and its close relatives, with the autochthonous defenses posited by Rothschild *et al.* being the remnants of an ancestral system, latterly made redundant. But the whole concept of preadaptation is notoriously prickly, and Ackery does not press on to its full implications for mimicry theory.

Do monarchs at least migrate properly? Adrian Wenner (with Ann Harris) tries to convince us in his best iconoclastic style that they don't, at least in California. His local natural historicizing is immediately answered by Nagano *et al.*, who, using both pre- and post-Moncon data on recaptured tagged butterflies, effectively refute his claims. Cockrell, Malcolm, and Brower settle another controversy by demonstrating in several ways that eastern monarchs spread northward in generational waves, not all in one long reach. Lynch and Martin complement this by showing that the milkweeds used by the first arrivals on the Gulf Coast in spring are highly toxic and emetic and thus help to condition predators farther north to avoid monarchs. This is important, because most monarch reproduction in the north occurs on innocuous plant species and the butterflies are largely palatable.

So far so good for conventional wisdom. But now Ackery's systematist colleague Richard Vane-Wright raises the biggest controversy of all with what he calls—rather ostentatiously—the "Columbus hypothesis." In a nutshell, this claims that the monarch's seasonal mass migration is a recent phenomenon, an artifact of colonial and modern land-use patterns and concomitant vegetation changes in temperate North America. He notes provocatively that nearly all the aggressive colonization by the monarch beyond American shores (in the South Pacific and various Atlantic islands) occurred in a short time in the 19th century and there has been almost none since—a pattern not readily explained by the evolution of commerce. Moreover, the first reports of wintering clusters appear about the same time. Are both, then, epiphenomena of a huge population explosion triggered by deforestation?

Remarkably, historical data examined so far are of little help in testing Vane-Wright's idea. The Mexican wintering sites were only discovered by Fred Urquhart's group in the 1970s and seem to have little associated local tradition. The oldest (implied) notice of the Californian roosts is from the 1860s. None of the authors in this volume cites Boisduval's important *Lépidoptères de Californie* (1869), which incorporates notes from Lorquin's extensive lepidopterological journeys—but it doesn't mention the phenomenon anyway. Entomological resources have probably been exhausted, but there exists a wealth of narratives, published and unpublished, of Monterey, Santa Barbara, and other modern monarch wintering grounds as they were in Mission and early Californian times. There is at least some hope that such archival research may yield older descriptions of monarch roosting. Is anyone sufficiently motivated—and skilled—to look seriously?

Much of the conservation interest in the monarch revolves around migration as an allegedly "endangered phenomenon." Is it? If Vane-Wright is correct, it evolved very recently and indeed may not be biologically "necessary." Property owners and municipalities on the California coast have very tangible interests in this question. In fact, the antiquity, stability, plasticity, and necessity of monarch migration and roosting are far from purely academic questions. Several contributors to this volume discuss the life cycle of the monarch in Australia, where it arrived in the past century and where it has developed a degree of seasonal migration as well. The apparent plasticity of its biology in its range beyond the seas cautions us not to interpret its current behavior at home as necessarily eternal. At any rate, Pleistocene geography and climatology force us to assume that monarch migration has not been static for any very long time.

The South American monarch, which is questionably distinct at the species level from ours, appears to migrate as well—but once again the phenomenon is poorly understood. It breeds on milkweeds in northern and central Argentina and flies up above their altitudinal range in the altiplano of northwestern Argentina and nearby Bolivia. But what is it doing there, and where is it during the austral winter? My suspicion is that it will be found roosting somewhere in the Bolivian yungas, giving our ignorance an interhemispheric symmetry.

If it is unclear whether the North American, tropical, and South American monarchs are conspecific, is it clear who their closest relatives are or how long ago they differentiated? Of course not. Attempts to date divergence in this lineage by way of genetic differentiation are based on such generalized molecular-clock assumptions as to be essentially worthless, and despite some striking advances in danaid systematics by the use of cladistics and the incorporation of early-stage characters in the analysis, the phylogeny of the monarch is still a muddle. And given that the danaids are overwhelmingly an Old World tropical group, how did the monarch get here? Kitching, Ackery, and Vane-Wright are quite right when they detect an ideological element in the 19th-century tendency to derive *Danaus* (and a great deal else) from the Old World via the Bering land bridge, but that does not mean that interpretation must be wrong. It is true, as claimed elsewhere in this volume, that there are few danaid mimics in the Americas as compared with the Old World, but how does one test the "statistical significance" of that? The authors in this volume nearly miss noting the unambiguous monarch mimicry of the odd pierid *Neophasia terlootii* (which, contrary to what one might think from the discussion here, occurs not only in Arizona but rather widely in northwestern Mexico, where it is not uncommon) and do miss altogether the monarch-mimicking female form *eusemna* of the ancient Mexican relict *Baronia brevicornis*, which is involved in multiple mimicry associations.

There are more and more surprises—more Mexican overwintering sites, possible overwintering sites in interior California, all sorts of chemical and morphological delights—and I am struck by how useful this book will be to some historian of science several decades hence, who will undertake to use the study of the monarch as an exemplar of how science works. The book has no epigraph; may I suggest one? The 19th-century American humorist "Artemus Ward" (Charles Farrar Browne) wrote: "It ain't so much the things we don't know that get us in trouble. It's the things we know that ain't so."

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The Neuroglia Mystery

Astrocytes. Pharmacology and Function. SEAN MURPHY, Ed. Academic Press, San Diego, CA, 1993. xx, 457 pp., illus. $99.

Traditionally, introductory neurobiology textbooks begin with the statement that central nervous tissue contains two main types of cells: glial cells and neurons (nerve cells). After definitions are given and morphology is covered, glial cells are rarely mentioned again, with attention focusing on nerve cells. The reason is obvious: neurons produce electrical signals about which much is known, whereas glial cells are electrically silent. Yet, as is made clear in *Astrocytes*, this silence does not equal passivity. In the vivid, if mixed, metaphor of