Contributions

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History of Ecological Sciences, Part 41: Victorian Naturalists in Amazonia—Wallace, Bates, Spruce

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Amazonia contains the world's greatest river system, most diverse ecosystem, and greatest diversity of plants and animals (Lord and Bell 2002, Rojas and Prieto 2009). Amazonia covers 3.7 million km^2 (1.4 million square miles), extending from the Andes to the Atlantic, with a homogeneous, moist, warm climate that supports a tropical rain forest bordered to the north and south by drier grasslands. The Amazon River contains almost a fifth of the freshwater flowing into the oceans, five times more than the Congo and 12 times more than the Mississippi. Three Victorian naturalists provided the first detailed surveys of its biotic resources and ecosystem. They were preceded in Brazil, however, by Munich zoologist Johann von Spix (1781–1826) and botanist Karl von Martius (1794–1868), who arrived in Rio de Janeiro in 1817 and traveled north by 1820 to the Amazon, before returning home to publish a volume of memoirs (1823) and enrich the Munich museum and botanic garden with their specimens (Sanders 1974, 1975, Juniper 2002:13–23). After Spix's death, Maartius published two more volumes of memoirs of their expedition (1828–1831).

Alfred Russel Wallace (1823–1913) and Henry Walter Bates (1825–1892) were evolutionary ecologists, in the Darwinian sense, and Richard Spruce (1817–1893) was a plant explorer like André and François André Michaux and Thomas Nuttall. Unlike Darwin, these explorers were not university educated, with wealth and connections that could lead to their becoming naturalists on naval vessels. Nevertheless, they made lasting contributions to our understanding of the ecology of the Amazon Basin (von Hagen 1948:213–263, Beddall 1969, Goodman 1972:284–295, Maslow 1996:87–120, Raby 1996:75–123, Rice 1999:260–289, McCalman 2009:221–250). Bates collected 14,712 species of animals, over 8000 of which were new to science—a record that "has probably not been equaled by a field naturalist before or since" (Usinger 1962:vii, Raffles 2002:136). Spruce collected over 7000 species of plants, many previously unknown to science (von Hagen 1945:230–296, Desmond 1975,

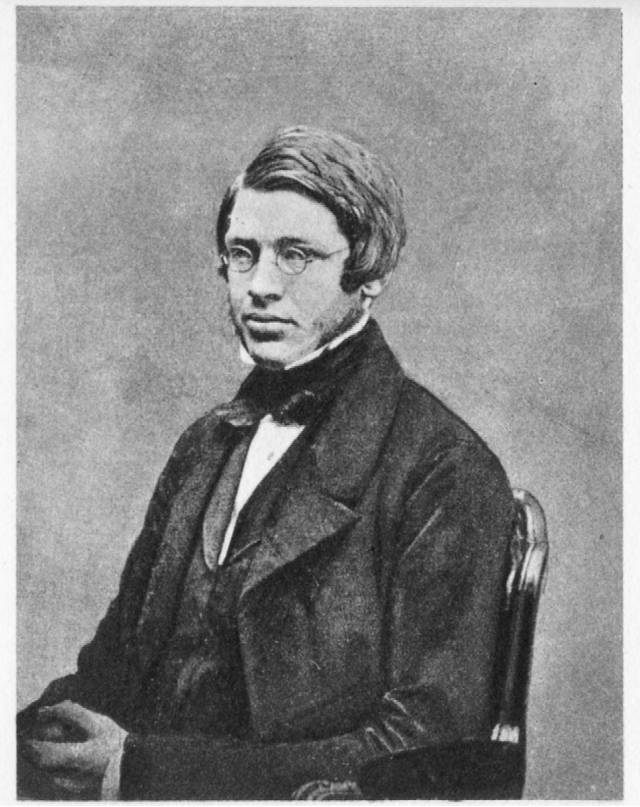


Fig. 1. Alfred Russel Wallace in 1848, age 24. Wallace 1905, I: facing 264.

Seaward 1996*a*:8). Wallace also made important collections of animals, though only two early shipments reached England; the rest sank with the ship that was taking him home (George 1979:504).

Wallace was educated until age 14, but was an avid reader who continued self-education after moving to London to live with a brother (Wallace 1905, I:20–228, George 1964, McKinney 1976, Wilson 2000, Raby 2001, Fichman 2004, Slotten 2004, Smith 2004). In 1837 another brother taught him surveying, which gave him an opportunity to observe different plants and geological strata in the countryside. Bates' father was a hosiery manufacturer in Leicester who, despite his son's academic talents, apprenticed him at age 13 to another hosiery manufacturer (Sharp 1892, Woodcock 1969, McKinney 1970, Moon 1976, O'Hara 1995, Bown 2002:198–226, Naylor 2004, Dickenson 2004). Bates also continued self-education by constant reading, and attending evening classes at the Leicester Mechanics' Institute (Bates 1892:246). He became a dedicated collector of insects, emulating a neighbor, Edwin Brown. His first publication was a brief article on beetles published in the first issue of *Zoologist* (Bates 1843), followed by another in 1848.

Spruce was the son of a schoolmaster in a village near York, and he followed in his father's footsteps until his school closed in summer 1844 (Wallace 1908, Pearson 1996, Boulger and Locke 2004, Raby 2004, Short 2004:285–294). By then he was already a prominent amateur botanist and an authority on mosses, and William Jackson Hooker, Director of the Royal Botanical Garden, Kew, suggested that he become a plant collector in the Pyrenees Mountains along the French–Spanish border. Spruce did so, successfully, from April 1845 to April 1846, during which he also learned to speak French and Spanish. Besides the collection of plants that paid for his trip, he published papers on the botany of the Pyrenees in general and on the mosses in particular (listed in Spruce 1908, I:xlix–l).

In 1844 Wallace obtained a teaching job in Leicester, and he and Bates met in the Leicester public library and discovered their mutual interest in natural history (Wallace 1905, I:237). They were both interested in the travel books by Humboldt and Charles Darwin, and in Charles Lyell's *Principles of Geology* (1830–1833), but they were enticed away from Lyell's opposition to Lamarck's theory of evolution by reading *Vestiges of the Natural History of Creation* (Anonymous 1844 [by Robert Chambers]; McKinney 1972:4–5). Wallace read *Voyage up the River Amazon* (Edwards 1847) by the American collector of birds and butterflies, William Henry Edwards (1822–1909), who later published *The Butterflies*

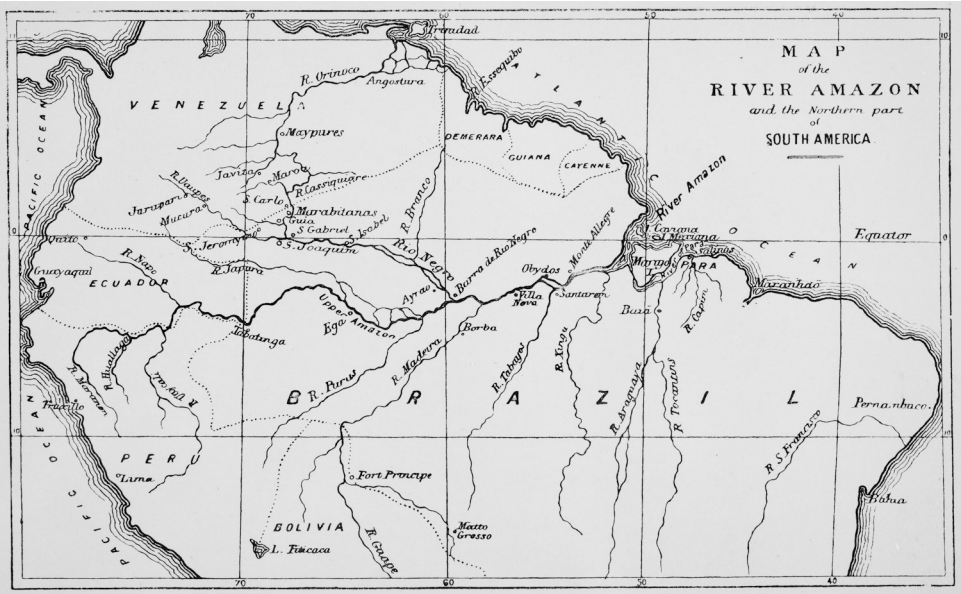


Fig. 2. Northern South America. Wallace 1890: facing 1.

of North America (three volumes, 1872–1897), and Wallace suggested to Bates that they travel to the tropics to collect biological specimens to sell and also gather facts "with a view to the theory of the origin of species" (Wallace 1905, I:256–257). Edwards was in London in 1848 and advised them to go to the Amazon and gave them letters of introduction to foreign merchants in Pará.

These "scientific entrepreneurs" (Raby 1996:79) left Liverpool on 26 April 1848 and reached Pará (= Belem) on the Pará River, which flows south of and parallel to the Amazon (Fig. 2), on 28 May (Bates 1864:1–65, Wallace 1905, I:267–268).

They found the tropical vegetation and, after learning how to find them, animals there very appealing. After two months they sent to England a collection of 553 species of Lepidoptera, 450 of beetles, and 400 of other species, many undescribed (Wallace 1890:34). They remained together for about five months (Raby 2000:44–45). From 26 August 1848 until 30 September, they traveled up the Tocantins River and back (Bates 1864:66–89, Wallace 1890:35–56). In June 1849, Bates again ascended the Tocantins to Cametá, its largest town, and stayed until 16 July (Bates 1864:89–100). In August 1849, Wallace traveled up the Amazon to Manaus, and in September, Bates followed. Wallace stayed there into December.

Because Wallace and Bates were being successful in their efforts to support themselves as collectors of biological specimens, several other botanists joined Hooker in sponsoring Spruce as a collector in the Amazon basin. Spruce, like Wallace and Bates, had been inspired by reading Charles Darwin's *Journal of Researches* to collect in the tropics (von Hagen 1945:233). He and an assistant, Robert King, sailed from Liverpool on 7 June 1849, on the ship with Herbert Wallace, who was going to join his older brother, Alfred. They reached Pará on 12 July, and Spruce and King stayed there for three months,

Fig. 3. A stream in the Amazon rain forest. Wallace 1890: facing 199.

during which Spruce began to master Portuguese.

Since Wallace, Bates, and Spruce soon mounted separate expeditions, their experiences and observations will be discussed separately, in the order in which their South American memoirs were published. Wallace only remained in South America for four years, and his *Travels* (Wallace 1853*a*) is much briefer than the two-volume memoirs by Bates (1863), who stayed 11 years, and Spruce (1908), who stayed 15 years.

In October 1848, Wallace posed a rhetorical question that was beyond the scope of his *Travels* to answer (Wallace 1890:59)

> *What birds can have their bills more peculiarly formed than the ibis, the spoonbill, and the heron? Yet they may be seen side by side, picking up the same food from the shallow water on the beach; and on opening their stomachs, we find the same little crustacean and shell-fish in them all. Then among the fruit-eating birds, there are pigeons, parrots, toucans, and chatterers—families as distinct and widely separated as possible—which yet may be often seen feeding all together on the same tree; for in the forests of South America, certain fruits are favourites with almost every kind of fruit-eating bird. It has been assumed by some writers on Natural History, that every wild fruit is the food of some bird or animal, and that the varied forms and structure of their mouths may be necessitated by the peculiar character of the fruits they are to feed on; but there is more of imagination than fact in this statement: the number of wild fruits furnishing food for birds is very limited, and birds of the most varied structure and of every size will be found visiting the same tree.*

The next month, as he walked over "an extensive plain," he contrasted in his mind life there with life in the rain forest (Wallace 1890:71)

> *...the abundance of every kind of animal life crowded into a small space was here very striking, compared with the sparing manner in which it is scattered in the virgin forests. It seems to force us to the conclusion, that the luxuriance of tropical vegetation is not favourable to the production and support of animal life. The plains are always more thickly peopled than the forest; and a temperate zone, as has been pointed out by Mr. Darwin, seems better adapted to the support of large land-animals than the tropics.*

Neither Wallace nor Darwin had seen vast herds of large wild mammals in tropical Africa, yet both knew that herds of domestic cattle and horses did quite well on South America's tropical grasslands. However, tropical forests seemed to them more extensive than tropical grasslands.

In May 1850, Wallace observed what he called "a most singular feature" of the Amazon (Wallace 1890:120–121)

> *The river was now so high that a great portion of the lowlands between the Rio Negro and the Amazon was flooded, being what is called "Gapó." This is one of the most singular features of the Amazon. It extends from a little above Santarem up to the confines of Peru—a distance of about seventeen hundred miles—and varies in width on each side of the river from one to ten or twenty miles. From Santarem to Coarí, a little town on the Solimòes, a person may go by canoe in the wet season without once entering into the main river. He will pass through small streams, lakes, and swamps, and everywhere around him will stretch out an illimitable waste of waters, but all covered with a lofty virgin forest. For days he will travel through this forest, scraping against tree-trunks, and stooping to pass beneath the leaves of prickly palms, now level with the water, though raised on stems forty feet high...In the Gapó peculiar animals are found, attracted by the fruits of trees which grow only there. In fact, the Indians assert that every tree that grows in the Gapó is distinct from all those found in other districts; and when we consider the extraordinary conditions under which these plants exist, being submerged for six months of the year till they are sufficiently lofty to rise above the highest water-level, it does not seem improbable that such may be the case.*

The igapó (as now spelled) does indeed have a unique flora (Goulding 1989:21) and the white bald uakari monkey is found only there (Goulding 1989:19). Besides igapó, the Amazonian forest includes two other types: várzea, or flood plain, and terra firme, which lacks standing water (Wallace 1854:254, Pires 1984:594).

After Wallace left Barra (Manaus) on 31 August 1850, he traveled up the Rio Negro to its Falls, which he reached on 19 October. He found it easy to procure fish there and made a collection of 200 drawings (Fig. 4). At San Carlos in February 1851 he watched Indians pulverize roots of timbo (*Paullini pinnate*) and prepare poison for a stream. The fish floated to the surface where they were caught. Wallace drew them before they were eaten (Wallace 1890:169). Bates (1864:242–243) also witnessed natives poisoning fish with timbo. By April Wallace had drawn and described 160 species from Rio Negro and estimated it and its tributaries contained 500–600 species (Wallace 1890:187). Most of those species lived also in the Amazon, which is now estimated to have 1000–3000 species (Géry 1984:353). Much of this diversity is related to fish having evolved in the annual inundation forests (Goulding 1980:28–29, 252, 1985). Wallace included six of his drawings and descriptions, identified by Tate Regan, in *My Life* (Wallace 1905, I:285–287). He gave the drawings to the Natural History Museum, London, and they are now published (Knapp 1999, Ragazzo 2002.

Wallace devoted 13 chapters (279 pages) to a narrative of his travels, with the last 4 chapters (82 pages) on geography and geology, vegetation, zoology, and aborigines. The waters in the different rivers in Amazonia were clear or blue, yellow or olive, and black. He attributed the clear water to rocky or

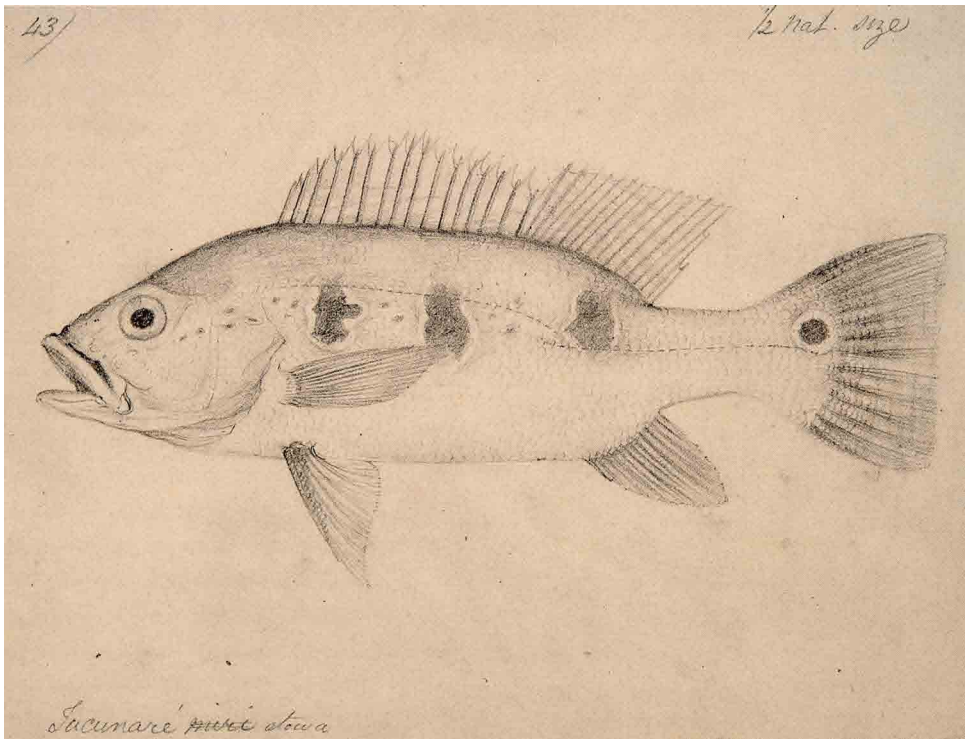


Fig. 4. Drawing Wallace labeled Tucuranéatowa (*Cichla orinocensis*). The Natural History Museum, London, UK. Knapp 1999:36.

sandy country, yellow to alluvial or clayey country, and the black water of the Rio Negro to decaying leaves, roots, and other vegetable matter (Wallace 1890:282–283). His threefold classification of Amazonian river waters is still considered valid and ecologically important (Goulding et al.1996:5–7). The Amazon's freshwater flowed 150 miles out into the Atlantic before mixing with ocean water, and yet tides affected the level of water for 500 miles up the river, because the river basin was very flat. He thought Rio Pará was not part of the Amazon, though connected to it by a channel, as Rio Orinoco and Rio Negro were connected (Wallace 1890:286–287). The rivers began to rise in December or January, at the beginning of the rainy season, and began to fall about 21 June, with the start of the dry season. In a discussion of climate, Wallace provided two charts, one contrasting the mean monthly temperatures of Pará and London, and the other, the mean atmospheric pressure and rainfall at Pará (Wallace 1890:297–299).

He believed the Amazon forest to be the most extensive in the world, but (Wallace 1890:302)

> *Instead of extensive tracts covered with pines, or oaks, or beeches, we scarcely ever see two individuals of the same species together, except in certain cases, principally among the Palms. A great extent of flooded land about the mouth of the Amazon, is covered with the Mirití Palms (*Mauritia flexuosa *and* M. vinifera*), and in many places the Assaí (*Euterpe edulis*) is almost equally abundant.*

Generally, however, the same species of tree is repeated only at distant intervals.

Although Wallace described the charms of tropical vegetation as seen from a roadside, he devoted most of his chapter on vegetation to economically important species. His zoology chapter described mammals (10 pages), birds (2 pages), reptiles and fishes (4 pages), and insects (1 page)—little more than a brief inventory, though he also published a detailed article on Amazonian butterflies (Wallace 1854)—before ending the chapter with a discussion on geographical distribution of animals. Although having similar climates, continents can have very different species, as Europe and North America, and even more so Africa, South America, and Australia. Oceans are formidable barriers, but rivers usually are not. However, the Amazon and its larger tributaries, such as Rio Negro, are barriers for monkeys, but less so for birds, though the three species of *Psophia* were an exception. Two species of similar butterflies, *Callithea sapphire* and *C. Leprieuri*, were found on opposite banks of the Amazon. On the other hand, the Cock of the Rock (*Rupicola crocea*) was circumscribed by geological formation and physical character of the country (Wallace 1890:326–330). In an article "On the monkeys of the Amazon" (Wallace 1852), Wallace divided their distributions into the four provinces of Guiana, Ecuador, Peru, and Brazil, separated by the rivers Amazon, Negro, and Madeira. His experiences with rivers as barriers to distribution convinced him that museum specimen labels reading "found along X river" were too vague, and he made his location notes as precise as possible.

By July 1852, Wallace had a collection of live animals that he decided needed his personal care for transportation to England (Wallace 1890:211). He loaded his cargo, both alive and preserved, onto the brig *Helen* and they left Pará on 12 July. On 6 August, the ship burned in the

Fig. 5. *Desmoncus macroacanthus*. Wallace 1853*b*: facing 73.

Atlantic, and Wallace was only able to save his papers, including drawings. They were rescued by a passing ship on 15 August, but it was an old, leaky ship that only reached England on 1 October (Wallace 1890:271–277, 1905, I:302–311). Fortunately, his London agent, Samuel Stevens, had insured his specimens, and therefore Wallace received £150 for loss of a collection valued at £500 (George 1979:504). That money enabled him to live 17 months in London, during which he published two books and six articles (Wallace 1905, I:313–332, Marchant 1916:477–478, Smith 1991:475, Camerini 1996:49, Raby 2001:83–92). His *Narrative of Travels* (Wallace 1853*a*) has

been described earlier; his other book was *Palm Trees of the Amazon and Their Uses* (Wallace 1853*b*), which discussed 48 species, with his drawings of each species and indications of the places in which he found them (Fig. 5). Since he relied on drawings and memory to describe the species, his accounts were better on uses than on botanical details. He thought 13 species were new, though 8 were not (Henderson 1996:193). His Amazon experiences had prepared his mind to later conceive a theory of evolution (Quammen 1996:58–75).

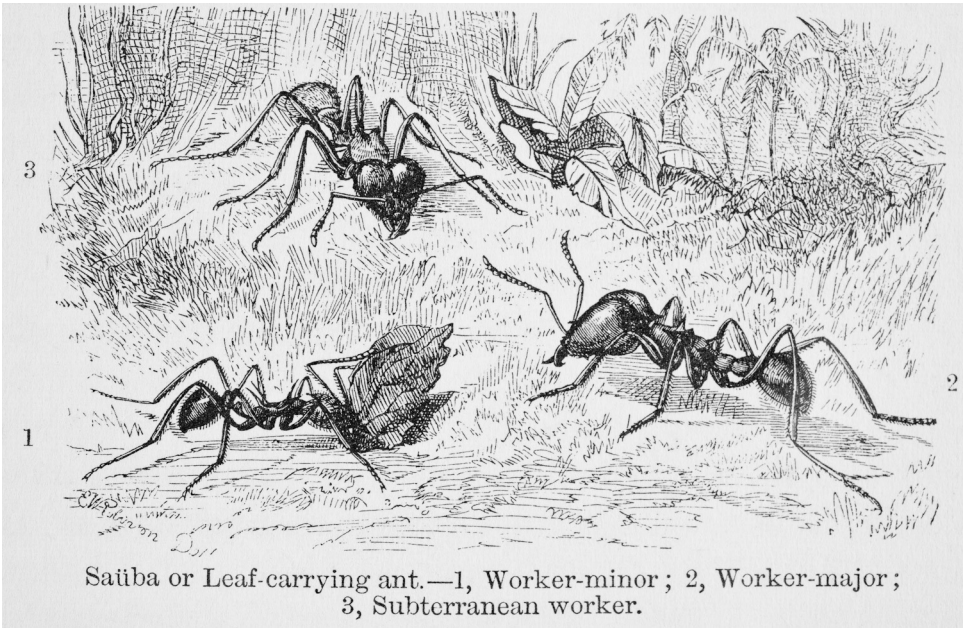
Bates' main interest was in insects, and Brazil has a spectacular insect fauna—well illustrated by *Life* editors and Lincoln Barnett (1960:40–59). However, Bates' collection of specimens and his *Naturalist on the River Amazons* show his interest in broad aspects of natural history, and he could not have supported himself if he had not collected, besides insects, birds, mammals, and a few reptiles and fish. Yet his memoir is especially noteworthy for its detailed accounts of insects. Entomologists Réaumur and de Geer had set high standards in the 1700s (Egerton 2006, 2008), and Bates was a worthy successor in quality, if not quantity. Furthermore, they had studied European insects "at home," whereas Bates studied insects in the field during a foreign expedition. Both Wallace and Bates devoted most of their memoirs to a narrative of their journeys, followed by a summary account of animals. However, Bates' chapter 12 is an account of animals seen and collected only at Ega (Tefé), where he spent 4.5 years. He also spent about 1.5 years in Pará, and his accounts of ants are therefore divided between chapters 1 and 12.

Upon arriving in Pará, he was dazzled by the variety of insects, but he concentrated on the life history of the saüba, or leaf-carrying ant (*Oecodoma cephalotes*), which was a "great scourge to Brazilians" (Bates 1864:11–18), because it damaged the foliage of cultivated trees. Saüba's subterranean galleries were mounds 40 yards in circumference and two feet high, composed of minute granules, agglomerated without cement, and with small, numerous entrances leading down two feet into galleries 4–5 inches in diameter. Bates concluded they used leaves to thatch the domes which covered tunnel entrances, thus protecting young broods from the deluge of rains. However, about 1870, Thomas Belt in Nicaragua discovered that they used the leaves as compost on which to grow their food, the fungus *Rhozites gonglyophora* (Belt 1888 [1985]:71–84, Cutright 1940:300). The gardener at the Pará Botanic Garden attempted to extirpate Saübas by making fires over some entrances and blowing sulfur smoke into the tunnels with a bellows. Bates watched and saw smoke rising from other entrances, one of which was 70 yards from where the bellows was used. Saüba were most active at night, when they invaded homes, and the hordes carried off grain and meal, which happened to Bates. His servant said they could carry off two bushels in a night. Many ant species have males, females, and workers, but Saüba had three kinds of workers (Fig. 6a).

Another formidable scourge was the fire-ant, which actually drove the residents of Aveyros from their village for several years (Bates 1864:250–251). Fortunately, it had a restricted distribution.

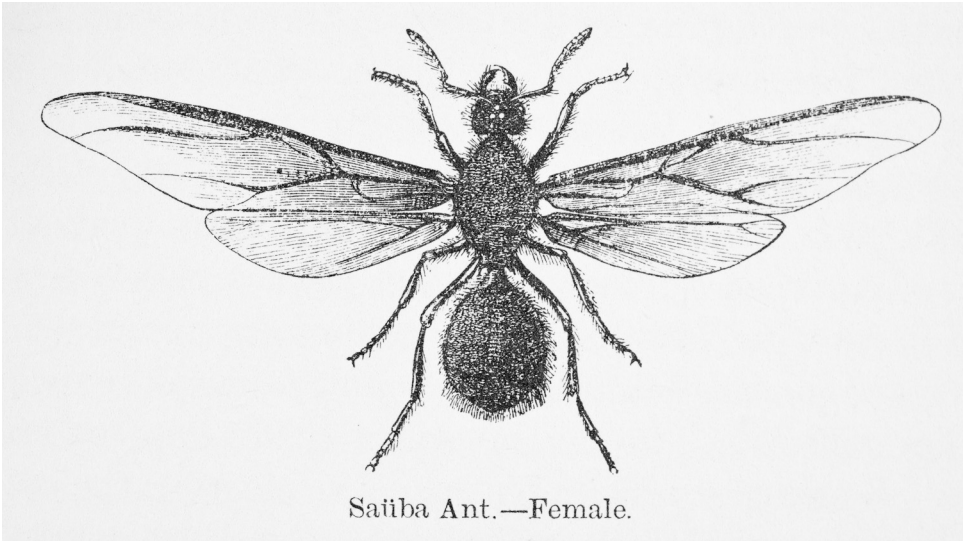
Foraging army ants of South America, *Eciton*, had similar habits to African driver ants, but their anatomies showed they were not closely related. The 10 species of *Eciton* that Bates studied (eight of which were new to science) seemed to have no permanent nest. Each species hunted in large organized bodies, but each in its own distinctive way (Bates 1864:415–425). Their processions were sometimes 60–70 yards long. Bates found correlations between anatomy and behavior in eight species. In some species

a



Saüba or Leaf-carrying ant.—1, Worker-minor; 2, Worker-major; 3, Subterranean worker.

b



Saüba Ant.—Female.

Fig. 6. (a) Saüba, or leaf-carrying ants (*Oecodoma caphalotes*): 1, worker-minor; 2, worker-major; and 3, subterranean worker. (b) A female saüba. Bates 1864:11, 17.

workers were clearly divided into large-headed and small-headed workers with different functions; in other species there were gradations between large and small workers, and all could participate in common tasks. Some species never climbed trees, others did. Two species had no eyes and moved along covered roads that they built as they proceeded.

A burrowing legless lizard, *Amphisbaenae*, little more than a foot long, lived in the saüba chambers,

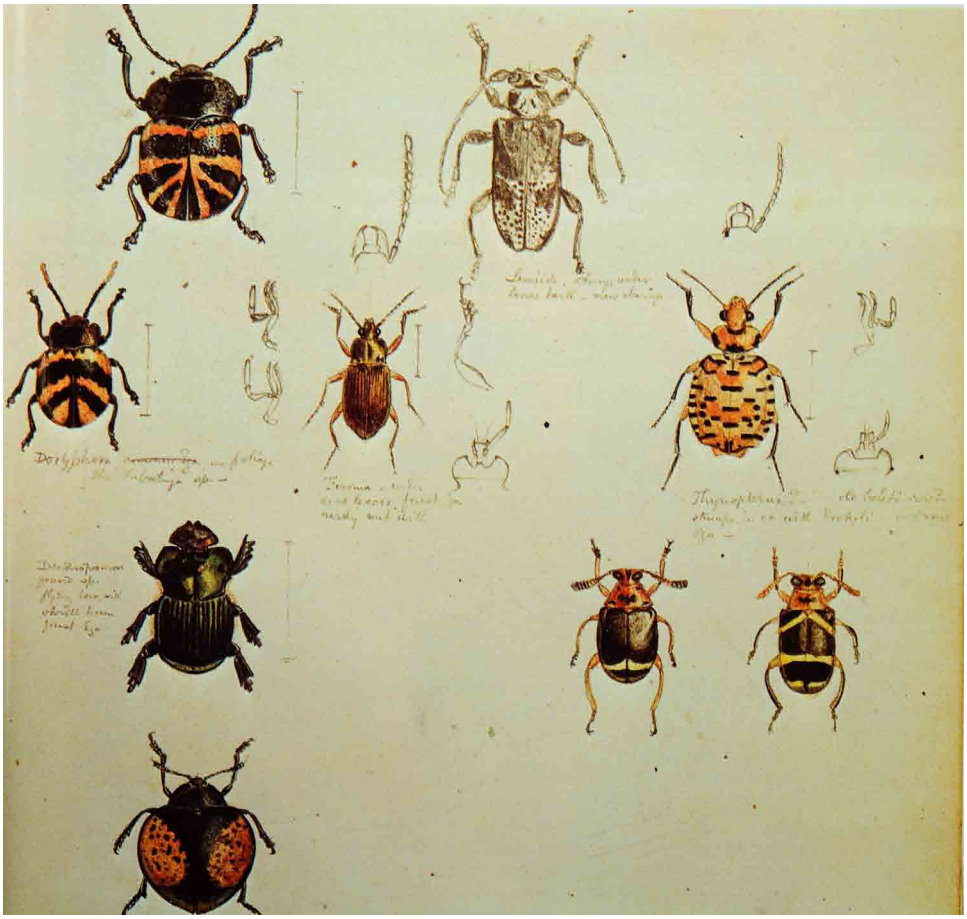


Fig. 7. Amazonian beetles. Collected and drawn by Henry Walter Bates. The Natural History Museum, London. Sterling 1973:123.

and Bates found ant remains in the stomach of one lizard. "Anomalous" beetles also lived there. The tamanduâ, or ant-eater (*Myrmecophaga jubata*), was common in some areas, but not in gapó regions, inundated for months. It was terrestrial, but three related species were arboreal (Bates 1864:109–113).

In general, beetles seemed scarce, partly because they could not survive the direct heat of the sun, and probably because numerous ants and termites destroy their larvae (Bates 1864:61–62). Many species of carnivorous beetles were arboreal. At Caripí, where Bates collected 1200 species of insects, vegetarian beetles were very numerous (Bates 1864:128–129).

Bates watched different species of wasps build nests for their eggs. A pale green sand wasp *Bembex ciliata* was common near Mapirí Bay. Females excavated tunnels 2–3 inches into river banks and each inserted a fly benumbed by its sting, on which she lay an egg before closing the tunnel. A larger species, *Monedula signata*, excavated tunnels in a sandbank in mid-river, then flew at least a half-mile to catch motúca flies *Hadrus lepidotus* to provision her nest. She would "take a few turns in the air around the place before starting" (Bates 1864:222), to fix in her memory the location. Kingfishers also nested in

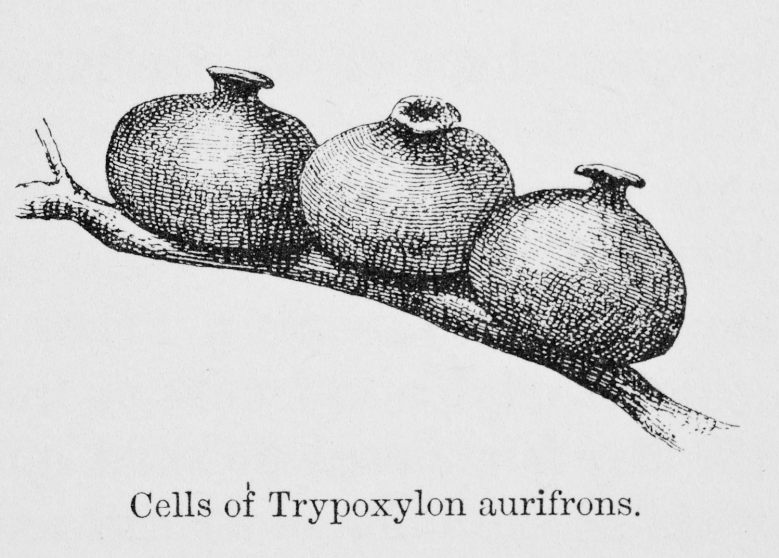


Fig. 8. (a) *Pelopaeus fistularis* female building a clay pouch on a stem. (b) *Trypoxylon aurifrons* nests on a branch. Bates 1864:226, 227, 1962.

clay cliffs, and, by contrast, sometimes flew 3–4 miles to fish. A large yellow and black wasp, *Pelopaeus fistularis*, did not excavate sandbank tunnels, building instead pouches out of clay pellets on the side of a branch or stem (Fig. 8a), 2 inches deep, in which it inserted with its egg a *Gastracantha* spider. *Tryporylon* wasps built nests of clay pellets on branches, but of a different shape (Fig. 8b). Two species, *T. albitarse* and *T.* nova sp., provisioned their eggs with spiders, whereas *T. aurifrons* inserted with its eggs small caterpillars. A stingless, biting honey bee, *Meliponae fasciculate* (Bates 1864: illustrated, 228), used clay as an outer wall for its hive in the crevice of tree trunks, but made the interior of wax.

Bates became an outstanding entomologist, as seen in a collection of some of his entomological papers (Bates 1978). It took the sharp eye of a close observer to make his most famous discovery, which he called "mimetic analogies" (Bates 1862:502–508), and now called "Batesian mimicry" (when one species mimics another) (Kimler 1983, Ruxton et al. 2004:139). He also discussed "imitative resemblances" (Bates 1862:508–509), now called "protective coloration," when a species mimics an aspect of its environment. He presented evidence for both phenomena in the midst of a long systematic article on Amazonian Heliconidae butterflies. He wrote it after he had read Darwin's *Origin* and had become a convert.

He cited three articles from the entomological literature in which examples of protective mimicry and coloration had previously been described (Bates 1862:508–509), but Bates was first to see such phenomena as evolutionary strategies, illustrating Darwin's theory (Blaisdell 1992:63–139). Heliconidae

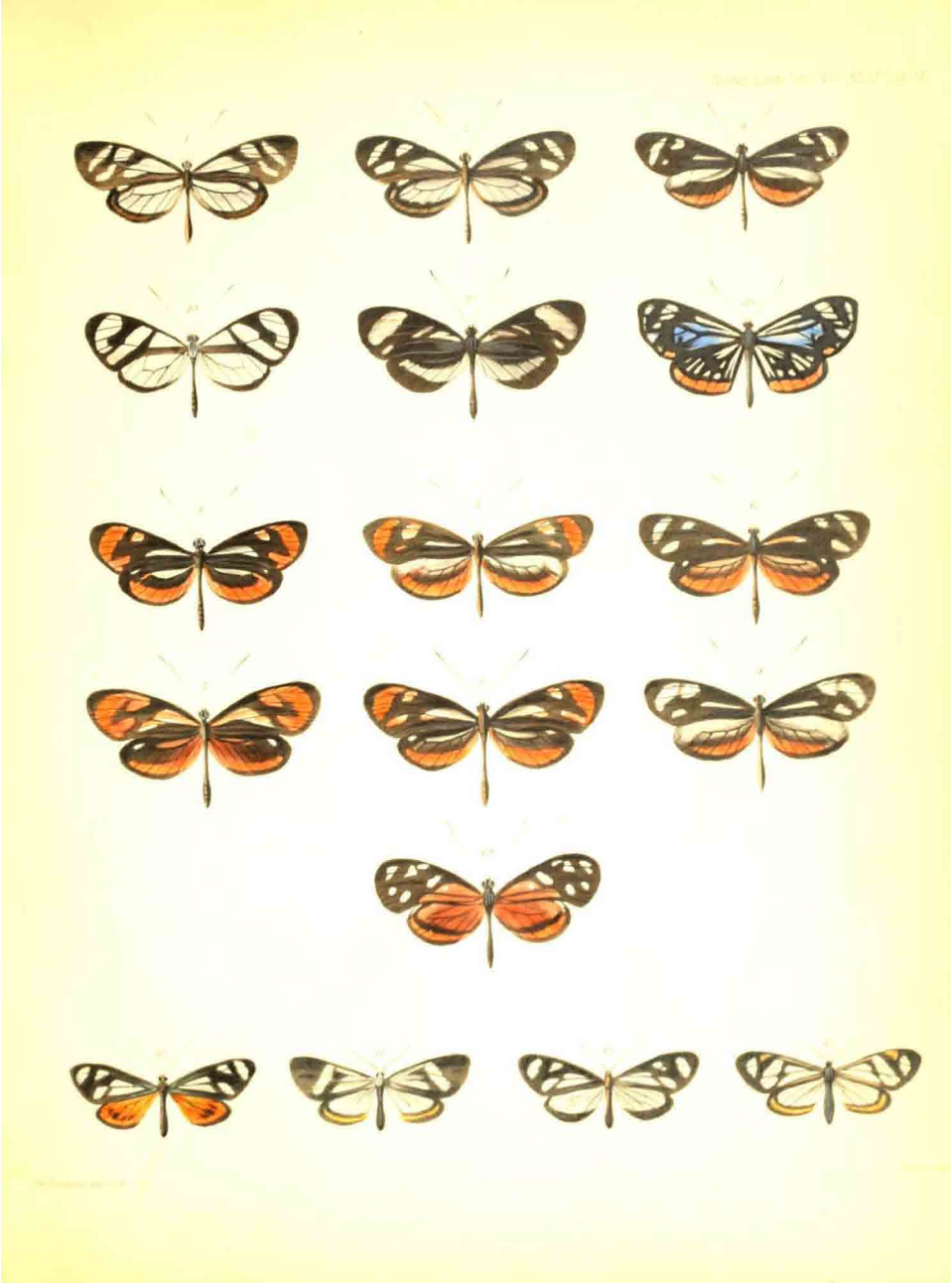


Fig. 9. Batesian mimicry. Figs. 4–8 are *Leptalis* species; Figs. 5a, 6a, 7a, and 8a are mimic species. Bates 1862: part of Plate 56.

were numerous and seemed to be unpalatable to predators, and thus it was advantageous for other species to imitate them (Bates 1862:510–511). Darwin was delighted and wrote to Bates on 20 November 1862 (Darwin 1997:539–540)

I have just finished, after several reads, your Paper. In my opinion it is one of the most remarkable & admirable papers I ever read in my life. The mimetic cases are truly marvelous & you connect

excellently a host of analogous facts. The illustrations are beautiful & seem very well chosen…I rejoice that I passed over the whole subject in the Origin*, for I should have made a precious mess of it.*

In his last comment, Darwin was referring only to mimicry, since he had discussed protective coloration in the *Origin* (Darwin 1859:84)

> *When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that these tints are of service to these birds and insects in preserving them from danger.*

Darwin feared that Bates' important discovery might be overlooked in an article whose title did not mention it, and therefore he published a five-page review of it (Darwin 1863). Darwin surely understood that this was the most dramatic support for his theory published by someone else, and summarized some of the evidence in his review (Darwin 1977:88)

> *The mockers and mocked always inhabit the same region; we never find an imitator living remote from the form which it counterfeits. The mockers are almost invariably rare insects; the mocked in almost every case abound in swarms.*

He added a summary of Bates' article to the fourth edition of the *Origin* (Darwin 1864:506, Peckham 1959:666), and his own discussion of it. Darwin found another article on protective mimicry that Bates had missed (Murray 1860), and in fact, there were many other references to protective coloration and some to mimicry in the literature, going back to Aristotle and including Darwin's grandfather, Erasmus Darwin (Evans 1965:211–212, Blaisdell 1982). In 1864, Wallace

Fig. 10. Bates collecting a Curl-crested Toucan, *Pteroglossus Beauharnaisii*, while being scolded by members of its flock. Bates 1864: 409.

also read a paper on mimicry at the Linnean Society, on Malayan butterflies, to be discussed in Part 42 of this history. Recently, Bates' *Heliconius* butterflies have been further studied, and it is now know that the gene for wing color is inherited with the gene for mate selection, enabling zoologists to understand speciation within that genus (Forbes 2011:83).

Bates did not push his concept of mimicry beyond its validity. Hummingbirds were American novelties, attractive to European collectors.

There were also hummingbird moths, found in the Old and New Worlds, which were functionally, and superficially, even anatomically similar (Bates 1864:114–115, illustrated). Both collected nectar from flowers while hovering before them. Bates saw this as a case of parallel evolution; no mimicry was involved.

Bates' skill at relating anatomy to function is seen in his explanation of the large beak of toucans (Bates 1864:404–412). Of the 37 toucan species, all in Latin America, five resided around Ega. The beaks of some species reached 7 inches long and 2 inches wide. The flowers and fruits on many large trees grew at the end of slender twigs that would not bear the weight of such large birds. Monkeys reach these flowers and fruits with long arms, and toucans with long beaks.

Bates' experiences with natives collecting turtles and their eggs on the Amazon were more extensive, intimate, and of longer duration than Humboldt's observations on the Orinoco of natives only collecting eggs (Egerton 2009:259–260). At Ega, turtles were treated almost like livestock (Bates 1864:321)

> *We lived at Ega during most part of the year, on turtle. The great fresh-water turtle of the Amazons grows on the upper river to an immense size, a full-grown one measuring nearly three feet in length by two in breadth, and is a load for the strongest Indian. Every house has a little pond, called a curral (pen), in the back-yard to hold a stock of the animals through the season of dearth—the wet months; those who have a number of Indians in their employ send them out for a month when the waters are low, to collect a stock, and those who have not, purchasing their supply…*

Although it was a valuable food, Bates longed for more variety (Bates 1864:322).

> *The flesh is very tender, palatable, and wholesome; but is very cloying: every one ends, sooner or later, by becoming thoroughly surfeited. I became so sick of turtle in the course of two years that I could not bear the smell of it, although at the same time nothing else was to be had…*

Bates was uncharacteristically vague about turtle names. The large species he described was clearly Humboldt's arrau, *Podocnemis expansa*, but Bates also discussed two smaller species that he identified only by their vernacular names, one of which was probably Humboldt's *P. dumerilliana*, but Bates never used that name. When he did mention *P. expansa* in a footnote (Bates 1864:349), he did not make clear to which species it referred. One smaller species, tracajá (Bates 1864:322)

> *Lays its eggs a month earlier than the large species, is of less utility to the inhabitants although its flesh is superior, on account of the difficulty of keeping it alive; it survives captivity but a very few days, although placed in the same ponds in which the large turtle keeps well for two or three years.*

The third species, aiyussá, when newly hatched, was distinguishable from the other two "by the edges of the breast-plate being raised on each side, so that in crawling it scores two parallel lines on the sand" (Bates 1864:372). Bates calculated that the people of Ega collected every year 48,000,000 turtle eggs from several islands, but he thought there were also vast numbers of eggs that went undetected, which were enough to maintain the population if the people did not also catch the young when they hatched (Bates 1864:365). Four side-necked Pelomedusidae species dominate the turtle fauna in Amazonia,

and since Bates wrote, their populations have plummeted from egg collecting and over-hunting (Best 1984:386–391). Turtle farming has been attempted, with little success, and conservationists have recommend hatcheries to save these species from extinction (Goulding et al.1996:66–69).

Bates was an outstanding naturalist whom Darwin urged to write an account of his travels. Fortunately, he did, and revealed a talent for narration. Darwin gushed (Darwin 1999:326–327)

> *...it is the best book of Natural History Travels ever published in England. Your style seems to me admirable. Nothing can be better than the discussion on the struggle for existence & nothing better than the descriptions on the Forest scenery. It is a grand book, & whether or not it sells quickly it will last. You have spoken out boldly on Species; & boldness on this subject seems to get rarer & rarer.—How beautifully illustrated it is.*

Darwin's opinion is echoed by a modern historian of the Amazon River (Furneaux 1969:118)

> *Bates's book,* The Naturalist on the River Amazons*, is the finest ever written on the area. He had a mystic communion with the forest, of a kind more normally associated with the desert or the sea, and he is able to transfer enough of his feelings on to paper to make his the best of all descriptions of the Amazon Jungle. The passages telling us of the habits of the insects are masterly, but although he specialized in this branch his touch is as certain when he writes about toucan, alligators, turtles, or monkeys.*

Both Wallace and Bates had knowledgeable discussions of Amazonian plants and vegetation in their memoirs, but since they collected animals, their discussions of animals were more detailed. Spruce was a botanist who discussed animals in his memoirs, but he discussed plants and vegetation in so much detail that his memoir, posthumously edited by Wallace, may have attracted few nonbotanist readers. He did publish an important article on animal migrations (Spruce 1867) that Wallace, who reprinted it in Spruce's memoirs (Spruce 1908, II:353–383), explained that it also contained "an admirable sketch of the broader aspects of the vegetation of the Greater Amazon Valley and adjacent regions." Spruce provides a detailed overview of Amazon vegetation in Volume I, pages 4–48—covering shallow roots with buttresses, aerial roots, lianas, epiphytes,

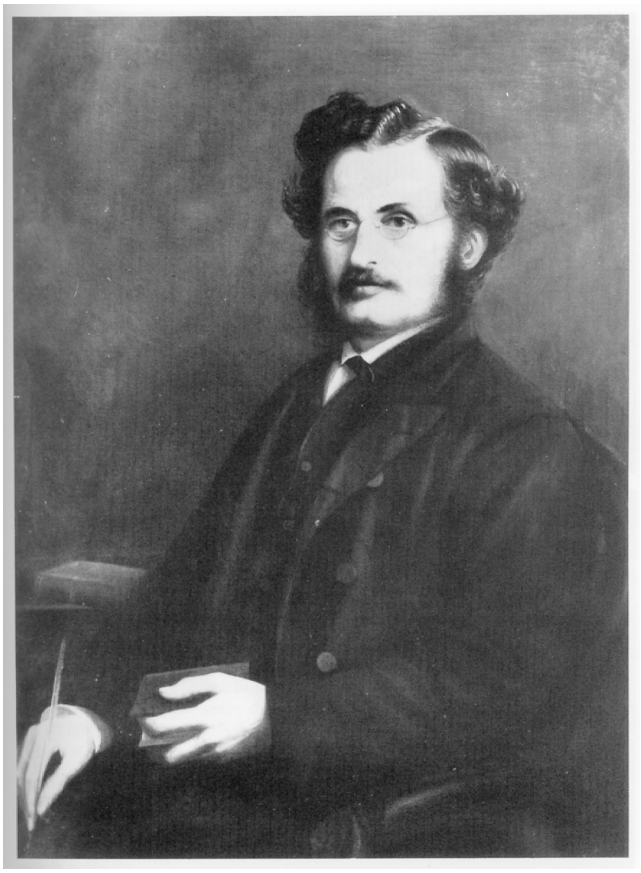


Fig. 11. Henry Walter Bates after his return to England. Royal Geographical Society, London, UK.

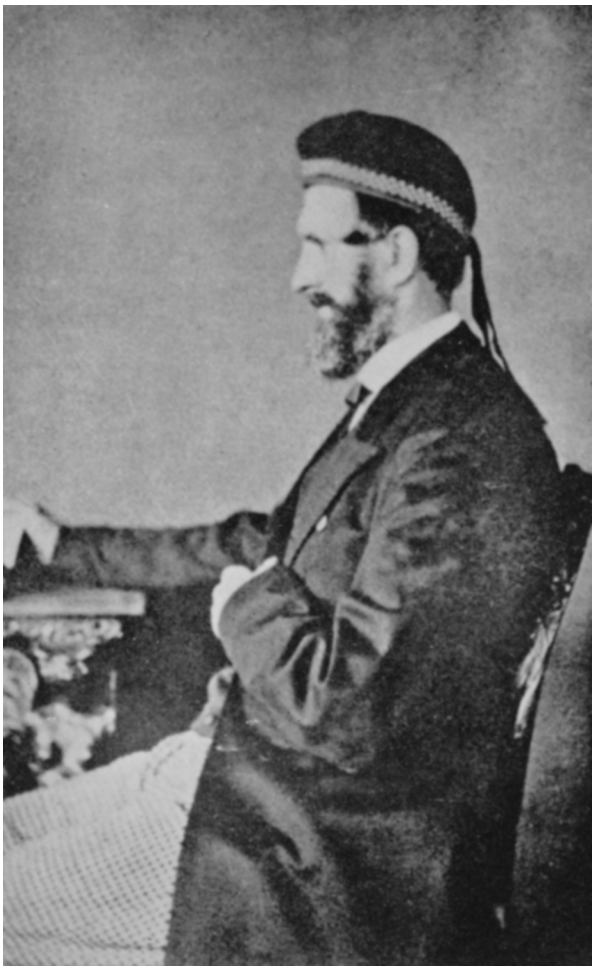


Fig. 12. Richard Spruce on his 47th birthday, 10 September 1864. Von Hagen 1945: facing page 236.

parasitic plants, palms, fern valleys, and much more—and a summary overview in Volume II, pages 354–362. His detailed botanic survey from place to place is interspersed within his travelogue. A botanist recently retraced many of Spruce's routes and found much of the vegetation still as he saw it (Prance 1996). For modern surveys of Amazonian vegetation, see four articles in Prance and Lovejoy (1985:109–206).

All three explorers made clear in their memoirs that, although the Amazon had the greatest expanse of forests in the world, that there was not a uniform vegetation across Amazonia. Spruce, however, went into far greater detail in describing the varieties of that vegetation. Mangroves were common along the banks of the Pará River from Pará down to the coast, but they declined upstream as freshwater replaced brackish water (Spruce 1908, I:4). Many characteristics of vegetation related to wet and dry seasons. During the rainy season, large islands of grass floated down the Amazon (Spruce 1908, I:108–112). Spruce first saw them when he lived at Santarem, where they sometimes clogged its port.

They were compact masses of live grass from 50 yards in diameter to several acres in extent. Recent examples are sometimes over a kilometer long (Goulding 1989:100). They originated in quiet Amazon bays or in lakes that drained into the Amazon during the wet season. The rain and rising water washed the dirt or mud away from the grass roots and the whole mass was then swept away. They consisted mainly of two kinds, bastard cane or canna-rana (*Echinochloae* sp.) and piri-membéca or brittle-grass *Raspalum pyramidale*, which grew only in "white" water that had muddy sediments. Spruce measured a *R. pyramidale* stem, which was 45 inches long, with 78 nodes. These islands were 20–30 feet thick, and all the grass nodes, except three or four at the top that extended above the water, grew rootlets, and the stems had vigorous panicles of flowers. Floating within these grass islands were several minute plants—*Azolla*, two Salviniae, a pistia, and frogbit (*Hydrocharella chaetospora*)—and several small mollusks. These islands floated in the current at 4–5 miles per hour, and they sometimes carried away anchored boats. Efforts to cut free the boats revealed manatees and snakes living within or below these islands. Spruce speculated that the immense quantities of grass washed out to sea every year probably decomposed in the tides and salt water, but he suspected that some of the logs from the eastern slopes of the Andes carried in the

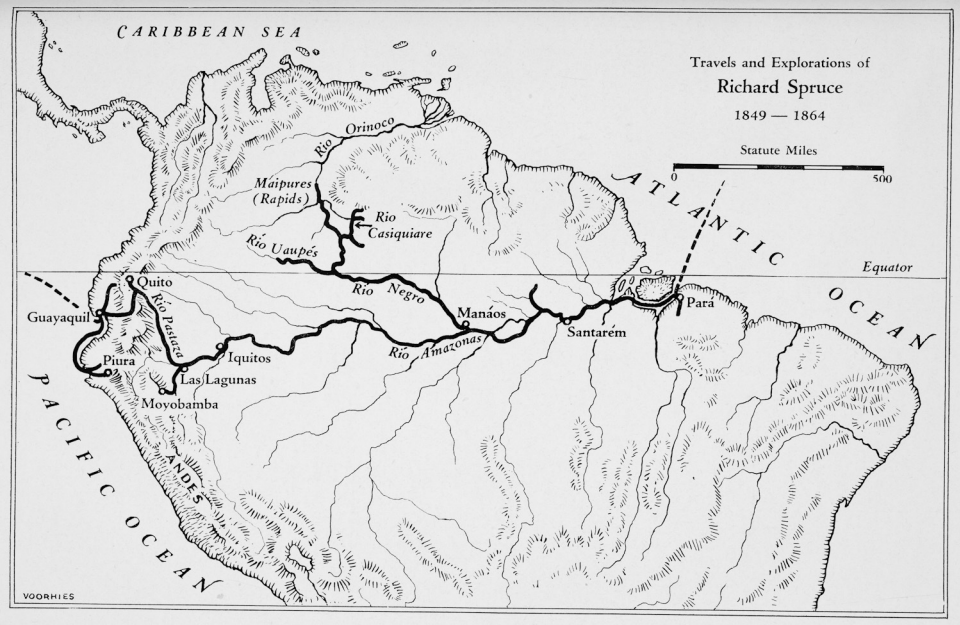


Fig. 13. Richard Spruce's travels, 1849–1864. Von Hagen 1945: facing page 296.

grass islands might be carried in the Gulf Stream to the coasts of Ireland, Norway, and Spitzbergen. Bates, returning from Pará to England on 6 June 59, 400 miles from the mouth of the Amazon, reported seeing numerous dense patches of grass, containing tree trunks and Ubussú palm fruit (Bates1864:461, Edition 2, one volume). Growth rates of these aquatics are quite high, and studies are being made on their agricultural uses (Junk and Howard-Williams 1984).

Grass islands were torn free by rains and rising waters, but floating trees were undermined and fell into the rivers during the receding of the waters. Rising waters loosened the soil, but it remained in place until receding waters pulled soil away, undermining trees (Spruce 1908, I:505–506).

Wallace's book on Amazon palms was an attractive introduction, but little more. There was already a substantial literature on South American palms, with which Wallace did not deal. He met Spruce for a second time around 15 September 1851, on returning from the Rio Negro to Manaus, and he showed Spruce his palm drawings. Spruce suggested they collaborate on a book on palms, but Wallace declined. He apparently sent Spruce a copy of his *Palm Trees of the Amazon*, for Spruce complained to William Hooker on 5 January 1855 (quoted in Henderson 1996:193)

> *The most striking fault of nearly all the fig*^{s} *of the larger species is that the stem is much too thick compared with the length of the fronds, and that the latter has only half as many pinnae as they ought to have. The descriptions are worse than nothing, in many cases not mentioning a single circumstance that a botanist would desire to know; but the accounts of the uses are good.*

Spruce collected about 90 species in seven locations, describing as new 47, of which 10 are currently

accepted (Henderson 1996:189–194). Spruce's long article on palms (Spruce 1869) is still valuable, especially for his discussion of geographic distribution of species.

Steamships ascended the Amazon in 1853, and an important port for them was Manaus. On 15 March 1855, Spruce left there by steamship, traveling 1500 miles in 18 days up the Amazon (Solimoes) to Nauta, 50 miles above Iquitos (Fig. 13). From there he took a canoe up Rio Huallaga to Chasuta, thence overland to Tarapoto (Spruce 1908, II: map facing page 100), which he reached on 21 June. Tarapoto, elevation 1500 feet, was pleasant, and he stayed for two years, until he received a British government request for him to collect cinchona tree seedlings in Ecuador for shipment to India, so that its quinine extract could combat malaria there (von Hagen 1945:280–281).

On his trip fromTarapoto to Ecuador, he descended from Mount Guayrapurima to a clear stream, Caraná, which had "the richest bit of fern ground I had seen in the world" (Spruce 1908, II:92). Despite declining health, Spruce faithfully carried out this difficult assignment. He learned more about *Cinchona* than had ever been known, collected about 100,000 seeds, and sent both seeds and seedlings to India, where they arrived in good shape (Brockway 1979:113–114, Drew 1996, Naranjo 1996). His own health continued to decline and he lost his funds in the collapse of a bank in Guayaquil. He left for England in early May 1864.

In his 1867 article on animal migrations (Spruce 1867), Spruce commented that probably no other large portion of the earth had as high a portion of its animals that were vegetarian as did the Amazon and Orinoco basins, with even the carnivores occasionally eating plants (Spruce 1908, II:362–363). He thought that the only animals which could inhabit a continent from sea to sea were a few general feeders and their parasites, and the larger predators and scavengers, such as vultures and termites. Lepidoptera distribution rarely corresponded to the main features of vegetation because caterpillars rarely ate foliage of dominant trees, but rather soft-leaved under-shrubs and low trees which grow (1) in forest shade, with restricted ranges, or (2) where primeval forest was destroyed, and waste places near human habitations. Of some 2000 tall trees Spruce had cut down for flowers and fruits, very few were infested with caterpillars. A tall leguminous tree or liana or a bombaceous species sometimes had caterpillars, and more rarely a laurel or nutmeg, but never a fig or guttifer. Many trees and lianas excluded caterpillars with strongly resinous or acrid or poisonous juices, and many more had leathery leaves, inedible except for minute caterpillars that ate galleries into the parenchyma. He listed the orders of plants on which caterpillars did feed.

Spruce observed several butterfly migrations; those east of the Andes were southward; those west of the Andes were westward (Spruce 1908, II:367–369). Many perished in the Amazon or the Pacific since they did not know how wide were bodies of water they attempted to cross. He assumed they sought a suitable place to lay eggs, although he admitted that Bates had reported migrations of only males. Darwin and Richard Schomburgk had also reported vast butterfly migrations in South America (Cutright 1940:319–320). Spruce also observed *Eciton* foraging ants which apparently had no settled habitation, since they carried pupae that seemed to be their own (Spruce 190, II:371–373). When they invaded a house, they could be driven out by sprinkling water on them, but house residents often waited until they had cleared out other insects and mice before acting.

Fig. 14. Tarapoto, with Mount Guayrapurima, where Spruce collected plants northeast of town, in the background. Drawn by Spruce in 1856. Spruce 1908, II:41, 1970.

The most remarkable migrations Spruce watched were of Wood Ibis, *Tantalus loculator*, between Rio Amazon and Rio Orinoco, only 300–500 miles apart in a straight line, but 1000 or more miles along the rivers (Spruce 1908, II:373–376). These birds timed their migrations to when the river they sought was low, with sandy beaches exposed, which favored their fishing. He saw them migrate north in November and south in May, with stops on islands near the mouth of Rio Casiquiari. Turbid Casiquiari water pouring into Rio Negro diminished its transparency, making it easier for the ibis to fish, which they did at dawn and dusk. Whereas butterflies were guided by instinct, Spruce thought these birds were probably guided by elders more than by instinct. On the western slope of the Andes, near Quito, immense flocks of parrots ascended by day to 8000–9000 feet to ravage fields of maize or other grains, and later descended to wooded valleys at 2000–4000 feet to roost (Spruce 1908, II:378).

Many mammals wandered to find food. Gregarious species, including wild pigs and some monkeys, had, for certain times of year, known feeding places when particular fruit ripened there (Spruce 1908, II:376–377). All animals, including jaguars, were fond of alligator pear *Persea gratissima*. Monkeys sometimes moved along river banks, their rate of progress depending on the abundance of food. Charro or barrigudo monkeys, which live on hot plains, sometimes ascended slopes of the Andes 5000–6000 feet, apparently to eat walnuts (*Juglans* species), but seemed not to spend the night.

Fish were abundant in white waters and scarce in black waters, which correlated with luxuriant littoral vegetation along the former and its scarcity along the latter (Spruce 1908, II:379–381). Rio Negro had few aquatic and no shore grasses, in contrast to the Amazon's floating and rooted vegetation. In Rio Negro, the main fish food was the fruit of riparian trees, especially *Caraipa laurifolia*.

Spruce wrote an article, "Ants as modifiers of plant-structure," which he sent to Darwin to critique.

Spruce believed that ants modified the leaves of a few species of bushes, mainly *Tococa* species of Melastomes, and that the leaf sacs they created became hereditary in these plants. Darwin responded on 1 April 1869 (in Spruce 1908, II:385)

> *The facts which you state are extraordinary, and quite new to me. If you can prove that the effects produced by ants are really inherited, it would be a most remarkable fact, and would open up quite a new field of inquiry.*

Darwin recommended that experiments be undertaken with these plants in hothouses. Darwin had the paper read to the Linnean Society of London on 15 April, after which the society's Council asked Spruce to obtain further supporting evidence before it could be considered for publication. He never obtained further evidence, and Wallace first published it when editing Spruce's memoirs (Spruce 1908, II:388–408). Spruce's most substantial publication was on liverworts, *Hepaticae Amazonicae et Andinae* (Spruce 1884–1885), of 600 pages in the 1885 separate publication, which remains "the most important reference on tropical South American hepatics" (Gradstein 1996:142).

Ecologists, however, find this conclusion to his 1867 article especially interesting (Spruce 1908, II:382)

> *...the modifications that have been and are still in progress among vegetable forms must have some correspondence with those that take place in animals; for all the realms of Nature act and react on each other. The atmosphere and the earth (with its productions, animal and vegetable) are continually giving and taking; and as their actual relations to each other vary more widely at different points along the equatorial belt than elsewhere on the earth's surface, it is plain that what seems equilibrium is either oscillation or progress, in some direction.*

This statement shows Spruce as an evolutionary ecologist, along with Darwin, Wallace, and Bates. Wallace's 54-titled bibliography of Spruce (Spruce 1908), is now superseded by Stafleu and Cowan (1976–1988, V:816–820) and Seaward (1996). No book-length study of Spruce appeared after his memoirs (1908) until 1996, when Seaward and Fitzgerald (1996) edited a commemorative volume.

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