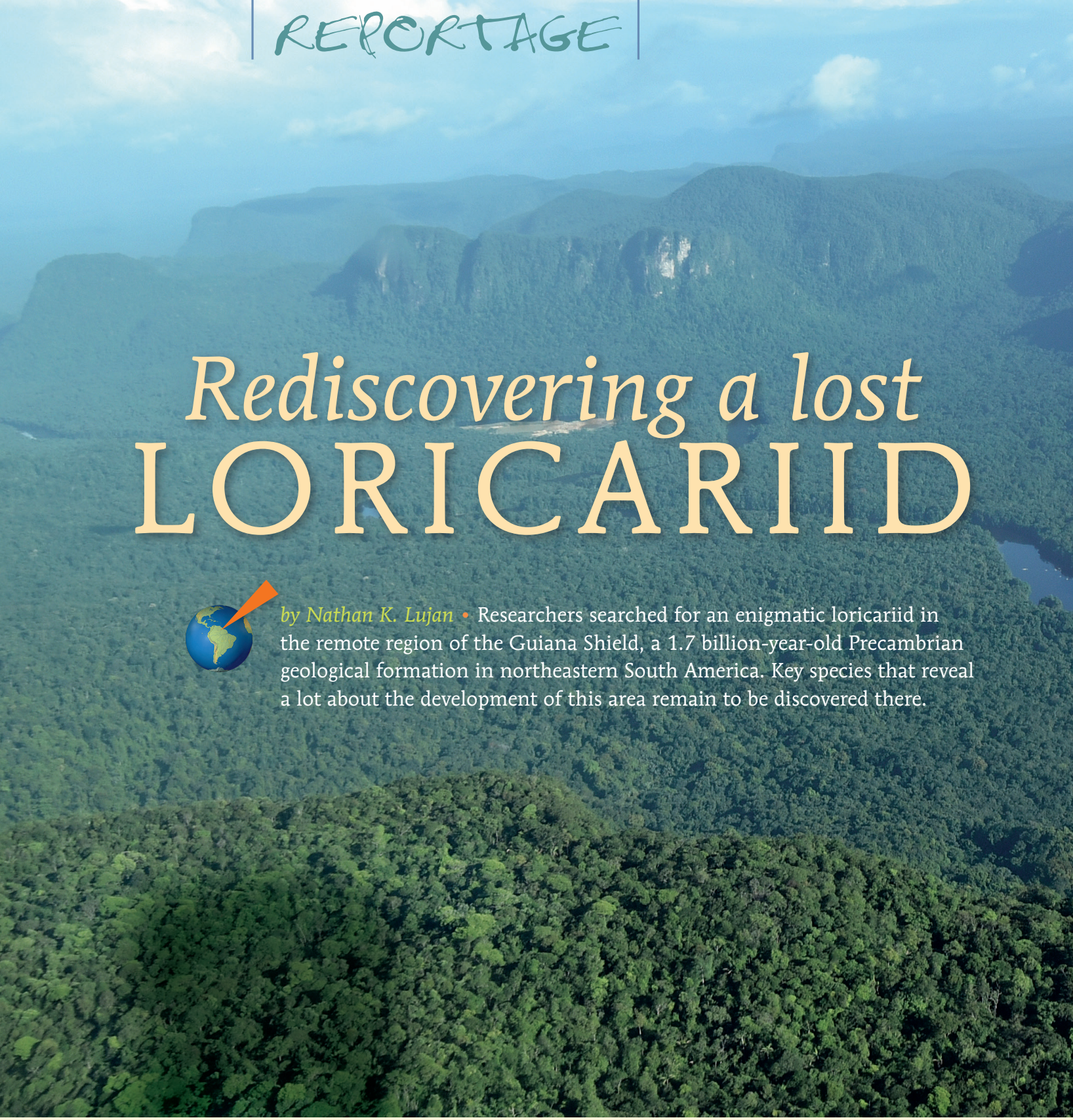

Rediscovering a lost LORICARIID

by Nathan K. Lujan • Researchers searched for an enigmatic loricariid in the remote region of the Guiana Shield, a 1.7 billion-year-old Precambrian geological formation in northeastern South America. Key species that reveal a lot about the development of this area remain to be discovered there.

The Guiana Shield underlies one of the most stunning landscapes on Earth. With its myriad waterfalls, mist-shrouded *tepuis* (mesas or table mountains), and crystalline geologic formations, this remote mountainous region could easily pass for a peculiar planet in one of James Cameron's sci-fi epics. British author Arthur Conan Doyle recognized this exoticism when he populated the Guiana Shield with apemen and pterodactyls in his 1912 novel *The Lost World*. Although Doyle's work was fiction, ongoing ichthyological discoveries by others (including myself) suggest that truth can indeed be stranger than fiction. We have yet to find apemen there, but the Shield is one of the regions of highest biodiversity in the world and is home to many endemic species. Current estimates of the ages of many lineages of fishes found there date back to the Cretaceous age of dinosaurs (more than 66 million years ago), and it is becoming increasingly clear that ancient rivers in the region served as the cradle for much

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The Guiana Shield is a font of biodiversity and one of the most impressive and unspoiled landscapes on Earth.

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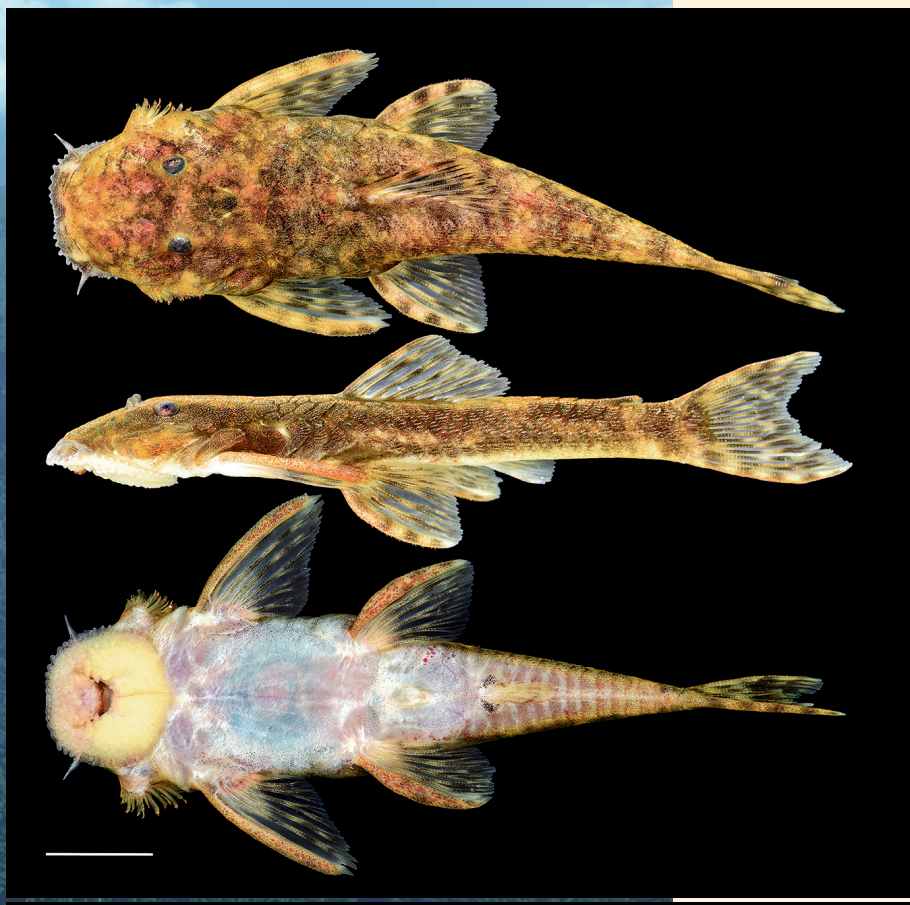
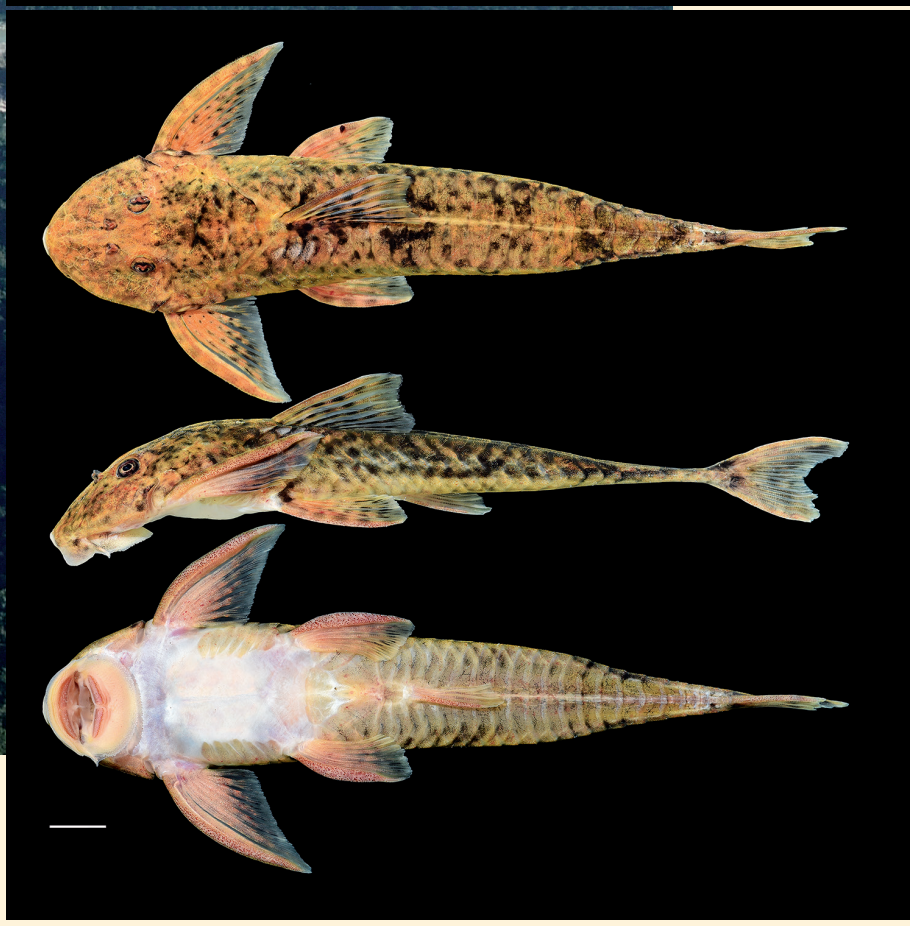




Top: One of the reasons for the expedition: *Lithoxus bovallii*. Note: The white bar in each photo represents 1 cm of length.

Bottom: *Cteniloricaria* sp. "Ireng."

of the fish diversity in the modern Amazon and Orinoco river basins, the most biodiverse freshwater ecosystems on Earth.

Legend has it that the name "Guiana" is derived from an Amerindian word for water, which is appropriate, given the abundance of rivers in the region and the central role that they played in the formation of the modern Amazon, Orinoco, and Essequibo Rivers. Although the Amazon, which bisects

The Ireng River forms the border between Brazil (bottom left) and Guyana (upper right). The fish is *Moenkhausia browni* from the Ireng.

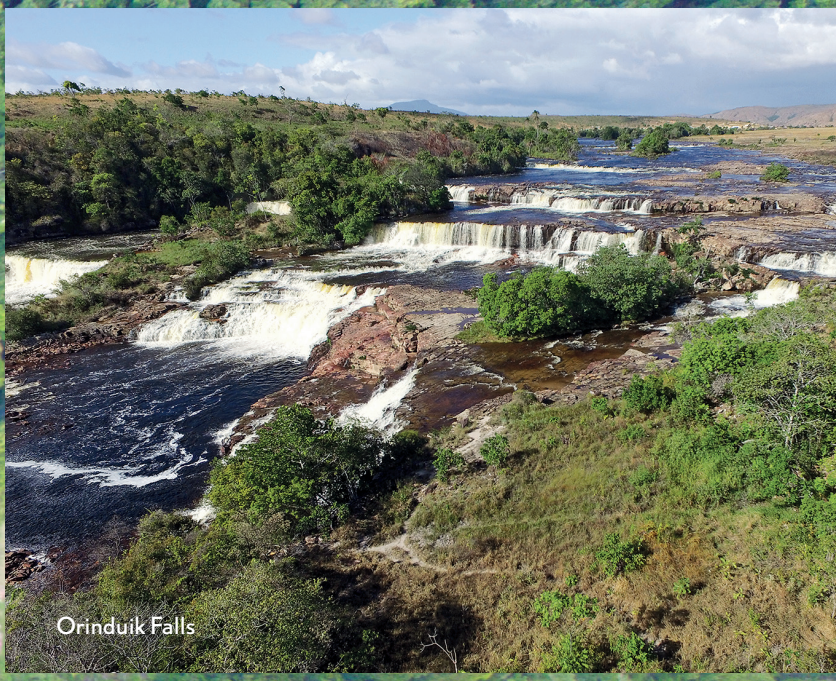
Inset: The author photographing live specimens of collected fishes.

the continent in an east-to-west direction, is now one of South America's most recognizable features, this drainage pattern was a result of the relatively recent tectonic uplift of the Andes Mountains about 11 million years ago. Prior to that event, the western tributaries of the Amazon flowed north into a delta in western Venezuela, and the headwaters of the northern Amazon's mighty Negro and Branco tributaries curved east around the southern Guiana Shield and out the eastern coast of modern-day Guyana, instead of south into modern-day Brazil, as they do now.

Reconstructing the ancient hydrologic history of South America is a fascinating exercise that is essential to understanding how the Amazon

TOP AND MIDDLE: NATHAN K. LUJAN; BOTTOM: K. ZYSKOWSKI

basin became as biodiverse as it is today. The Guiana Shield's distinctive geologic history, which primarily consisted of episodic vertical uplift followed by widespread but incomplete erosion, not only created awe-inspiring table mountains but also preserved innumerable clues to the origins of South America's rivers and their fish fauna. One of the challenges to understanding the history of life anywhere on Earth is that species are constantly evolving in response to competition and ecological stressors, among other evolutionary drivers. Aside from an incomplete fossil record, we have few opportunities to see what life was like at different points in the past. In the Guiana Shield, the repeated vertical uplifting of plateaus without major deformation of the geologic layers cut the headwaters of rivers off from the lowlands and created major escarpments and waterfalls. The result was that fish populations that had been living in the headwaters were isolated from the competitive ecological conditions and other factors that drove evolution in the lowlands, effectively preserving ancient freshwater fish species.



Orinduik Falls

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This new species of *Characidium* lives in the rapids of the Ireng.

We now know from geologic evidence, for example, that the vast Guiana Shield plateau, now approximately 1,300 feet (400 m) above sea level, was uplifted sometime in the Oligocene or Miocene geologic epoch, between 35 and 5 million years ago. In western Guyana, this uplift separated the upper Potaro River from the lower Potaro and appears to have isolated and helped preserve the endemic catfishes *Lithogenes villosus*, *Corymbophanes andersoni*, and *Corymbophanes kaiei* in the upper Potaro. Connecting the upper and lower Potaro is Guyana's most famous landmark, the thunderous Kaieteur Falls. Fossil-calibrated molecular phylogenies suggest that *Corymbophanes* separated from its closest relative elsewhere in South America approximately 18 million years ago, consistent with the geology-based date of the formation of Kaieteur Falls. *Lithogenes* appears to be even older.

Giant evolutionary puzzles

When I began my scientific career as a field biologist and taxonomist, my most exciting discoveries were of species that were new to science. I delighted in naming them after esteemed mentors, family members, and friends. As my methods have expanded to include molecular phylogenetics—the building of trees of life using evidence hidden in the DNA of the organisms themselves—my excitement about synthesizing my many years of field- and specimen-based data has grown. Phylogenies have allowed me to assemble my many observations of different species into a cohesive narrative about how the landscape formed. This process is gratifying—rather like putting together the pieces of a giant jigsaw puzzle to tell the story of life on Earth. After dozens of trips to the Guiana Shield, my colleagues and I have only recently begun to accumulate enough specimens and data to start putting the puzzle together.

Sometimes, a puzzle piece that was once present goes missing, and this is the case with the little-known loricariid species *Lithoxus bovallii* (unrelated to *Lithogenes*), described in 1906 by the eminent curator of the British Museum, C. Tate Regan. Regan named the species after its collector, Dr. Carl Bovallius, whom he referred to as "a Swedish gentleman." Unfortunately, the locality Regan published for this species—the "Kaat River," supposedly a tributary of the "Treng River"—does not appear on any modern map or gazetteer of Guyana. Thus, this has become a mystery in need of detective work. For a century, *Lithoxus bovallii* was known only from a handful of original type specimens, which had become bleached to a yellowish-white after over 100 years in alcohol. More important, no one knew for sure where the species lived or where to place it in the puzzle.

From the scant historical information that is available, we know that Bovallius travelled across the highlands of western Guyana in the late nineteenth century and even founded a small town on the upper Potaro River, upstream of Kaieteur Falls. Anyone scanning a mod-

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Top three: This large specimen of *Characidium crandelli* was collected in the same habitat as *Lithoxus bovallii*. Bottom three: *Neblinichthys* sp. "Kaibarupai" lives in the tumultuous currents below the uppermost waterfalls of the Ireng River.

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ern map of this region looking for the "Treng River" will immediately see the Ireng River, a south-flowing tributary of another river whose headwaters are very close to those of the Potaro—the Branco. Extensive recent surveys of the upper Potaro have shown that *Lithoxus bovallii* does not occur there; other ichthyologists and I have sampled the lower Ireng River without ever finding this species. It became increasingly clear that to solve this mystery, we had to plan an expedition to the headwaters of the Ireng River, where it begins to cascade out of the Guiana Highlands in a long series of rapids and waterfalls.

Landmark expedition

Luckily for us, one of the major waterfalls of the upper Ireng—Orinduik Falls—has become a moderately popular tourist destination, and a small airstrip has been built near it. After years of hoping to be among the first biologists to survey this area in more than a century, I finally had the chance to assemble an expedition to the upper Ireng in January 2016, thanks to a generous grant from the small New Orleans–based Coypu Foundation.

The excitement of being the first to survey an intact ecosystem is somewhat moderated by a sense of responsibility to survey the area thoroughly. I believe that it is vital for modern field biologists to collect as much information as possible about any area they survey in the event that a major environmental impact, like a dam or a gold-mining operation, negatively affects the ecosystem and its species. Unfortunately, such impacts are becoming increasingly common, even across the remote Guiana Shield.

With this in mind, I assembled a diverse team of seasoned field biologists, including two other ichthyologists from Auburn University (my former Ph.D. mentor, Jon Armbruster, and friend and collection manager Dave Werneke); Tim Colston, a herpetologist from the University of Mississippi; and Kristof Zyskowski, an ornithologist from Yale University. We were joined by two biologists from the University of Guyana (Mark Ram and Mahendra Doraisami) and an artist, David Brooks, who is also a skilled naturalist and a veteran of three of my previous expeditions to South America. Finally, since this expedition would be visiting territory belonging to the Amerindian Patamona people, we were also accompanied by my good friend Ovid Williams, a Patamona translator, guide, logistician, and employee of Guyana's Ministry of Indigenous Peoples' Affairs.

On January 2, after securing supplies and last-minute permits in Georgetown, this well-rounded crew boarded a charter flight to Orinduik Falls. Within hours of arriving at Orinduik's simple guest lodge, Jon, Dave, Mark, and I waded into the Ireng River's torrential habitats at Orinduik Falls to search for fishes. Within an hour of repeatedly setting a seine net and kicking rocks around, we had collected 10 fresh specimens of *Lithoxus bovallii* and solved the minor but longstanding ichthyological mystery surrounding this species. In the coming days, we would collect more specimens—not just this newly rediscovered loricariid, but also a new loricariid in the genus

Harttia and a new South American darter in the genus *Characidium*. After four days of sampling habitats in and around Orinduik Falls, we boated and portaged six hours upstream to the Patamona community of Kaibarupai, where the terrestrial habitat changed from Orinduik's arid savanna, characterized by few trees and sparse clumps of grass, to a closed canopy rainforest. Tim and Kristof were pleased by the various indicators of healthy, intact forest, including Bushmaster snakes (*Lachesis muta*), White Bellbirds (*Procnias albus*), and Guianan Cocks-of-the-Rock (*Rupicola rupicola*).

Fish discoveries

The touschou, or captain, of Kaibarupai, Kendall Salvatore, welcomed us and said that in the memory of the community, no other scientists had ever been there before. He and Kaibarupai's council allowed us to build a camp at the confluence of the Ireng River and a left bank tributary called Monkey Creek. From there, the team made daily excursions further up the Ireng River to a spectacular zone where the Ireng splits into three different channels as it exits a plateau 2,297 feet (700 m) above sea level. Each channel featured a waterfall at least 131 feet (40 m) high.

In the habitats above these waterfalls we discovered a new species of fast water–dwelling killifish (*Rivulus* sp.) and what is likely a new species of pencil catfish in the genus *Trichomycterus*. With the help of our Patamona guides, who already knew about a distinctive loricariid that only lives in the rapids below one of the waterfalls, we made one our most exciting discoveries: a new species of the loricariid genus *Neblinichthys*. The males of some members of this genus develop long external teeth on their snouts and heads, earning them the nickname "punk catfish." Unfortunately, the two specimens we collected were both females. The genus *Neblinichthys* comprises only six described species, all of them restricted to the uppermost reaches of rivers draining different sides of the Guiana Shield. This includes the headwaters of the Siapa, Caroni, and Paragua Rivers and the Mazaruni River. Like *Lithoxus*, which is also distributed across Guiana Shield headwaters, *Neblinichthys* seems to be an excellent example of the splitting, or vicariance, of once-contiguous populations that might have been caused by the uplifting of the Shield. It is inconceivable to most that these fishes could have distributed themselves across so many drainages, and across so many waterfalls, after the uplift—without leaving any remnants of a historically broader range in the lowlands.

To resolve these questions more definitively, and to fit these puzzle pieces into a phylogenetic picture that sheds

Andu waterfall in Guyana.

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Top: This new *Trichomycterus* species was distributed between Orinduik Falls and the upstream waterfalls at Kaibarupai.

Middle: A male *Pyrrhulina stoli* from the Ireng.

Bottom: The cichlid *Krobia potaroensis* is widely distributed in the Potaro drainage.

light on the early formation of the Guiana Shield, will require many more months of laboratory work and computationally intensive analyses. In the meantime, all the members of the 2016 expedition to the upper Ireng River take pleasure in having explored and documented an ecologically intact and biodiverse corner of the natural world. We relayed our observations to Guyana's Environmental Protection Agency and to our expedition partners, the World Wildlife Fund–Guianas and the Protected Areas Commission.

We hope that with the help of these outside partners and the continued diligence of the Patamona residents of Kaibarupai, this region will remain unspoiled so that scientists a century from now can visit, study, and make discoveries of their own.

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ONLINE

Author's website: https://www.loricariidae.org