

From Darwin's Treasure Chest: *Rhinoderma*

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Translated from German by AJ Gutman

In 1831, as Charles Darwin began his five-year voyage around the world aboard the HMS *Beagle*, he could hardly have imagined that the impressions he was about to collect would profoundly and permanently change the world. Compared to the later influence of his evolutionary theory, Darwin's other talents, as a natural scientist with universal interests, as a best-selling author of travelogues and natural history reports, and as a collector who dispatched and brought back to Europe a wealth of material, are easily overlooked. Herpetology also benefited from his discoveries. Among Darwin's collections were countless species previously unknown to science. Evaluation of this material was entrusted to Thomas Bell, a task he found somewhat overtaxing. Thus a portion of the work was passed on to the Natural History Museum of Paris, where Bell's friend Gabriel Bibron, along with colleague André Marie Constant Dumèril, described a number of species from Darwin's collection. Among these, in 1841, was a very special frog that the French researchers named in honor of its discoverer: *Rhinoderma darwini*.



Charles Darwin shortly after returning from his voyage on the H.M.S. *Beagle*.

Darwin's Frogs

In February 1835, the *Beagle* anchored in Valdivia, Chile. There, in the temperate rainforest, Darwin discovered some remarkable little frogs. Particularly impressed by these little mites, he recorded atypically detailed observations in his zoological notes. Among other things, he noted their variety of colors and their unusual appearance ("very pretty & curious").

Darwin's original observations on what was to become known as *Rhinoderma darwini* included the following paraphrased descriptions of several specimens:

Under side [of] throat, breast & cheeks rich chestnut brown, with snow-white marks; thighs of hind legs blackish with no marks. Legs yellowish also with no marks.— Upper side, pale iron-rust color, with posterior parts of body, thighs & anterior marks (one triangular & other transverse) beautiful bright green.— Iris rust color. Pupil black.— Eyes small.— Appearance very pretty & curious.— Nose finely pointed.— Jumps like a frog. Inhabits thick & gloomy forest. Is^d of Lemuy.

This species is excessively common in the forest of Valdivia. Seems subject in its colors to remarkable variation.— Undersurface posteriorly jet black & snow white marks, anteriorly rich chestnut brown; above cream color, with triangular slightly darker shades & small marks of green.— There is a point in all at joint of hind legs.— Iris of all is rusty red.

Above cream-colored, without shade of green. Hind legs yellow; beneath all black with different shaped marks of white.

Another, beneath anteriorly the brown is replaced by bright yellow.— Upper surface instead of cream color, rusty red — with darker triangular shading.— All die soon in confinement.

The unusual nature of these frogs did not become evident until much later. The genus *Rhinoderma*, as currently recognized, comprises two species: Darwin's Frog (*R. darwini*) and the more northerly distributed *R. rufum*. Conventional systematics views these two species as the only representatives of the family Rhinodermatidae, although Frost et al. (2006) no longer recognized this family, instead placing *Rhinoderma* in the family Cycloramphidae.

Darwin's Frog reaches 3–5 cm in length. Notable are the various and highly variable skin flaps, including the nasal protrusion for which the genus is named. These structures generally are interpreted to mimic leaves, allowing the frog to blend effectively with the plants and organic debris of its leaf litter habitat. Camouflage is further enhanced by the species' variable color, which ranges from the brown of dried leaves to the bright green of new growth. The ventral side is marbled black and white and is highly variable from



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The Valdivian forests of southern Chile are home to Darwin's Frogs.

one frog to another, so much so that individuals can be uniquely identified by their ventral pattern.

Darwin's Frogs inhabit the Valdivian rainforest in southern Chile and adjacent regions of Argentina. The species' distribution extends from around the level of the Chilean city of Concepción into northern Aysén Province. The extent of its southern distribution is unknown. This area is characterized by temperate rainforests. The average summer temperature is ~15 °C (Puerto Montt) and precipitation is ~2,000–3,000 mm/year, but may exceed 5,000 mm/year in some regions. Rain falls throughout the year, with a record at one locality of 360 rainy days in one year. Characteristic tree species include *Araucaria*, Southern Beech (*Nothofagus*), and Alerce (Patagonian Cypress, *Fitzroya* — named after the captain of the Beagle). Within the forest, frogs are diurnally active and generally inhabit more open areas with heavy ground cover.

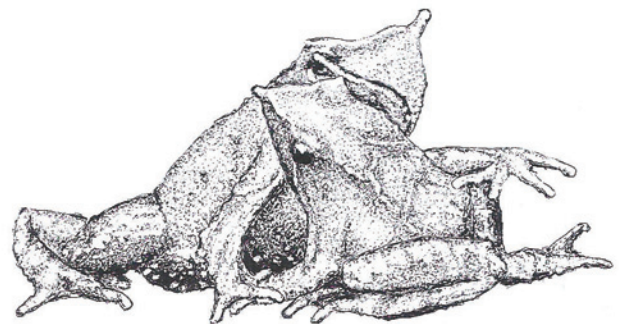
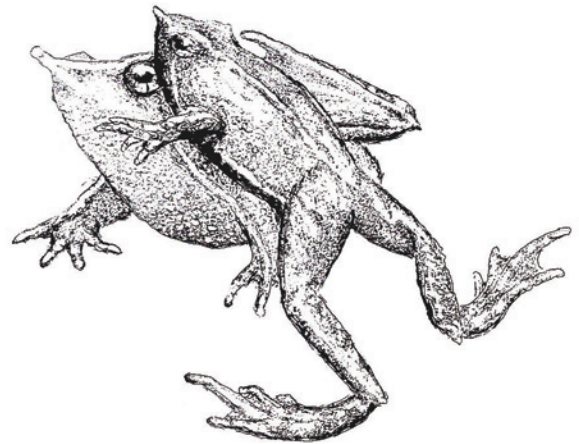
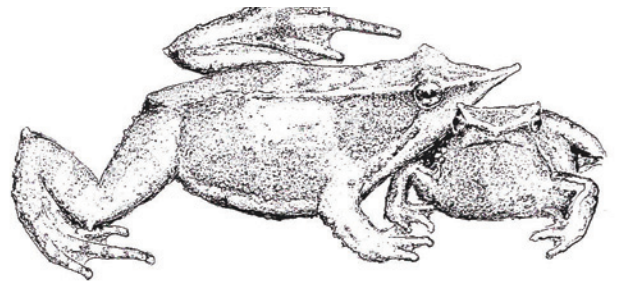
Reproductive Biology

Darwin's Frogs are notable for their unusual reproductive biology. Males employ a singular means of oral incubation in which the hatching tadpoles are collected in the vocal pouch, where they remain until metamorphosis. The newly metamorphosed froglets are then expelled. Mouthbrooding is unique among amphibians and has been known since the latter half of the 19th Century. However, many interesting details of this reproductive behavior have been described only recently from two decades of observa-

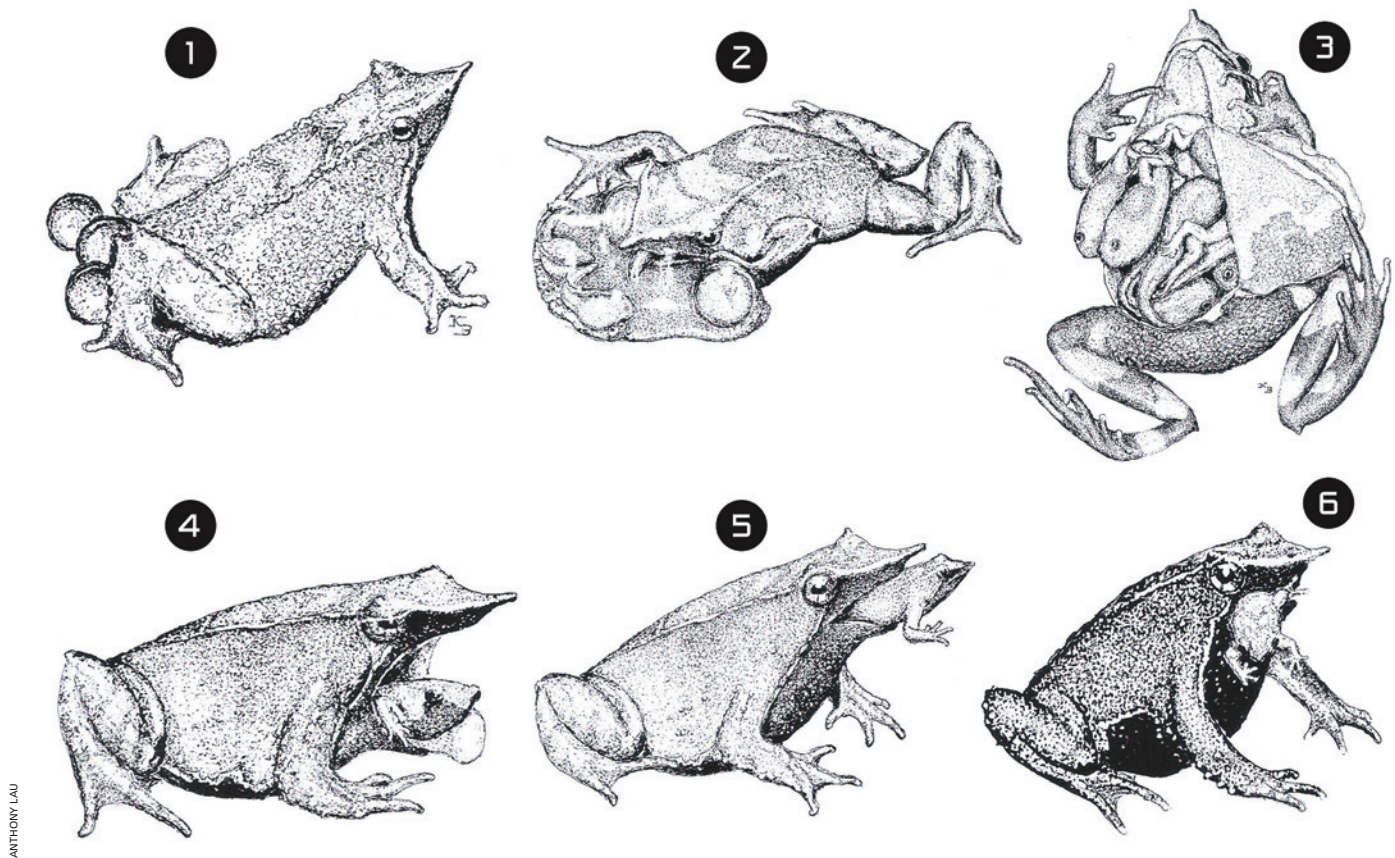


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The natural habitat of *Rhinoderma darwinii* in the Araucarian forests in Southern Chile.



Mating behavior can extend for extensive periods. (1) The larger female approaches a male immediately after chasing another male away, (2) responds to the male's embrace, and (3) reciprocates in kind. Drawings by K. Busse from a videotaped encounter.



ANTHONY LAU

Mating behavior continues with ovideposition. (1) The pair was disturbed and the male had just jumped away. (2) The male “swallows” the hatching tadpoles in the eggmass. (3) Male with tadpoles in his vocal sac (diagrammatic). (4) Male “spitting out” the metamorphs. Expulsion is triggered by contractions of the lower body combined with gaping. (5) A metamorph emerges, only to be caught by the male’s closing mouth. (6) The male holds the froglet by a hindlimb just before final release. Drawings by K. Busse from a videotaped encounter.

tion and research of captive specimens by Klaus Busse (2002) at the Koenig Museum in Bonn, Germany.

Males call (a bird-like sequence of 3–5 whistling tones) from in or in front of a retreat during the damp, cool weather from spring until at least late summer. When a female is ready to spawn, she will



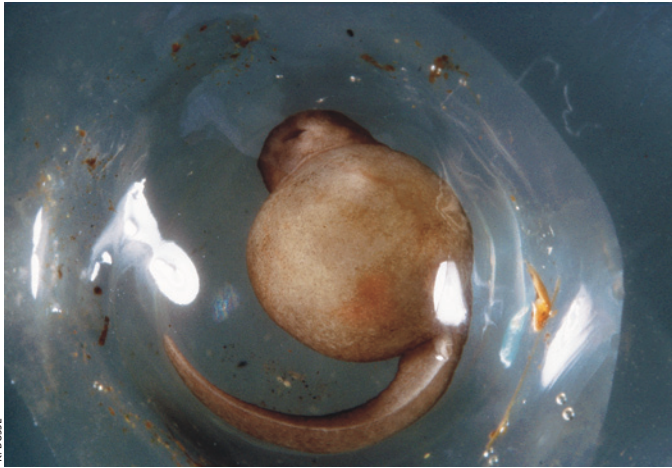
P. ULMER

More gut than frog: A male with vocal sacs filled with tadpoles.

approach, using the calls to navigate what for them is dense, visually impenetrable terrain. Once the two have found each other, the female often will react with a rather impertinent gesture, hurling the male away from her with a powerful kick of her hind legs. Hardly deterred, the male approaches again. Busse hypothesized that this “jumping-onto-kick-off behavior” serves a useful purpose. Since the male is exclusively responsible for raising the larvae, simply fertilizing her eggs is insufficient. Instead, she is seeking to enhance the likelihood of her progeny’s survival by identifying the strongest possible male, one who is capable of the demanding task ahead, both genetically and physically. To put it simply, the farther the male flies when he’s kicked, the punier and less suitable he is for raising her tadpoles. This highly unusual method of assessing suitability for fatherhood seems to be exclusive to Darwin’s Frogs.

Once, however, the female is satisfied with his flight characteristics and potential for caregiving, she will follow the male into a small, damp depression in the soil or leaf litter. There, after extensive mutual stimulation, including continuous calling, mutual embracing, and caressing, oviposition and fertilization take place. Due to the high ambient humidity, the eggs and larvae do not require open water. Eventually, both parents withdraw. Males do not guard the egg clutch, which develops for about 20 days.

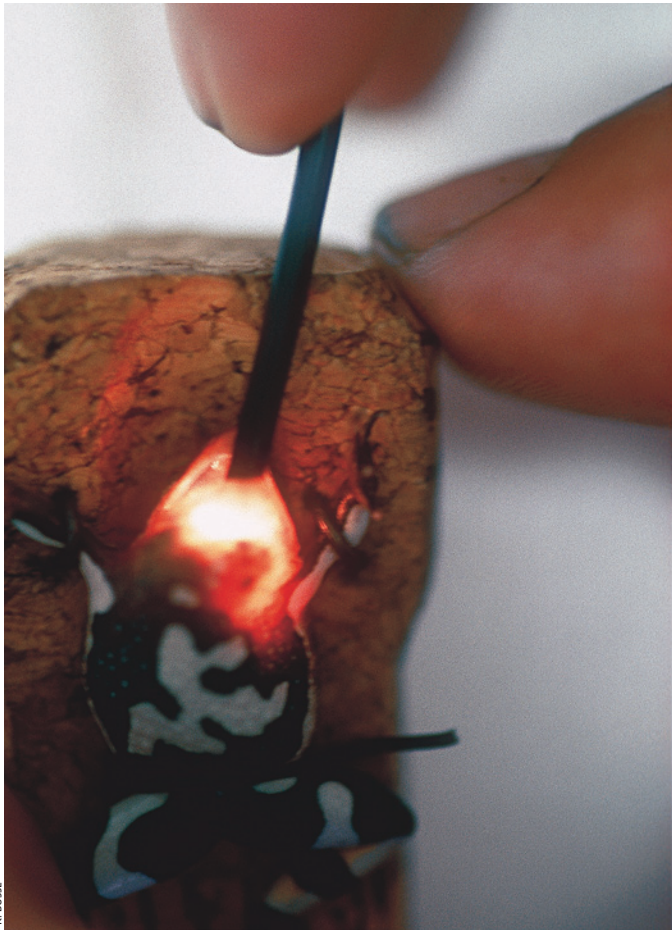
Just as the egg membranes dissolve and the tadpoles hatch, the male returns. Since the time interval until hatching can be quite variable depending, for example, upon temperature, the punctual



K. BUSSE

Tadpole in the egg a few days before hatching and being relocated into the male's vocal sac.

associated with purely aquatic animals) obviously does not apply here. Instead, the larvae thrash about vigorously, and the constant light-dark color change seems to produce a flashing signal that motivates the male. He picks up each individual tadpole with his mouth and they slide down into his vocal pouch where they continue to develop for 1–2 months (depending on environmental conditions). Nutrition of the tadpoles has yet to be clarified, although they likely are dependant on the unusually large yolk sacks that they retain after hatching. In addition, the inner epithelial layers of the male's



K. BUSSE

“Candling” the vocal sac of a “pregnant” male reveals the tadpoles contained within.



K. BUSSE

Freshly laid eggs in captivity.

arrival of the father is amazing, particularly in the apparent absence of any obvious regulating factors. The hatching tadpoles might summon the male by sending some kind of chemical signal, but we do not know for sure what triggers his response.

Similar to many other species of frogs, the tadpoles are dark on the back and lighter on the underside, although any protection provided by this countershading (a protective coloration usually



K. BUSSE

Adult Darwin's Frog with metamorph.



J. BOURNE

Darwin's Frog in nature.



M. SOLE



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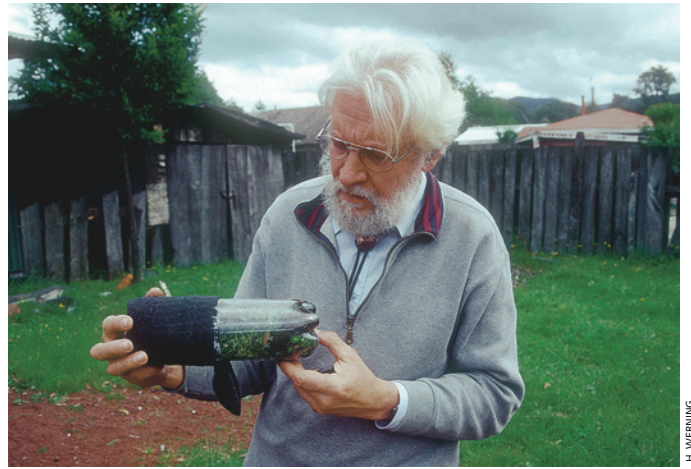
Darwin noted the considerable variation in color among individuals.

vocal pouch are believed to produce a substance that might provide additional nutrition. This substance is presumably absorbed through the skin of the larvae. Whether oral intake also takes place is unknown. In any case, this form of direct nutrition of the tadpoles through the father (patrotrophy) is so far unique among frogs. Also, the question of an oxygen supply for the larvae remains to be addressed. Busse (2002) suspected that an internal “foam nest” provides a direct oxygen supply via the circulatory system of the father. The male continues to feed during the incubation period, apparently uninfluenced by his “pregnancy.”

Once the larvae have metamorphosed, the male spits out his progeny over a period lasting from minutes to hours. The young frogs, although somewhat abruptly expelled into the light of day, are nevertheless fully functional. Quickly recovering from their startling change of scenery, they hop off to lead their independent lives.

The Mysterious Second Species

Philippi (1902) described a *Rhinoderma*-like species under the name of *Heminectes rufus*. This name fell more or less into disuse, as subsequent authors regarded it as a synonym for *R. darwinii*. The two species actually are relatively easy to distinguish. Darwin’s Frogs have barely any webbing on their hind feet, whereas the webbing on the hind feet of *R. rufum* is very well developed. The calls of the two species also are easily differentiated. Definitive proof of their status as separate species was provided by studies of reproductive biology



Dr. Klaus Busse of the Alexander Koenig Museum in Bonn with a container for transporting freshly collected Darwin’s Frogs.



The type locality of *Rhinoderma rufum* is now a pine “desert” (top); forest monocultures have replaced the natural habitat of the species.



Map showing the approximate ranges of *Rhinoderma darwinii* (green) and *R. rufum* (brown).

during the 1970s. The webbing is a strong indicator, with *R. rufum* much more strongly tied to bodies of water than its more famous relative. The male of this species also takes the hatching tadpoles into its vocal pouch but, after a stay of about two weeks, the young are released into small streams. Consequently, the reproductive biology of *R. rufum* represents a link between the more “normal” mode of many frogs and the highly specialized brood care of *R. darwinii*.

The distribution of *R. rufum* lies to the north of that of *R. darwini*, although the two species overlap in the area around Concepción. Historical type localities indicate a distribution as far as Zapallar, about 100 km north of Santiago in central Chile, a region characterized by dry, hot summers.

The habitat of *R. rufum* clearly differs from that of *R. darwini*, with the former restricted to drier forest types within the rainforest and also occupying sclerophyllous vegetation in areas with a Mediterranean climate. In those situations, moisture adequate for reproduction is restricted to riparian zones that often are enclosed by arroyos with dramatically steep walls. Dense layers of shade-producing vegetation within the arroyos create suitable microhabitats amid the dry heat of the surrounding areas. The notably cooler and damper Mediterranean conditions allow frogs to remain active throughout the year.

An Extinct and an Endangered Species

Since the studies on its reproductive biology, *R. rufum* seems to have vanished without a trace. Because it had long been considered to be conspecific with *R. darwini*, it had been largely ignored. Also, its occurrence in limited microhabitats (even within a large distri-



Klaus Busse and the author in 2003 searching for *Rhinoderma rufum*.



Eighty percent of the world's combined museum collections of *Rhinoderma rufum*; the larger pile on the left is from the Zoological Institute in Hamburg and that on the right from the Alexander Koenig Museum in Bonn. Additional specimens are in Valdivia, Chile.



A brown-mottled morph in nature.



Terraria for breeding Darwin's Frogs at the Alexander Koenig Museum in Bonn.

bution range) ensured that it was unlikely ever to be found in great numbers. During a 2001 conference in Santiago de Chile, to which Klaus Busse and I had been invited as speakers, Busse reported on his many years of experience working with *R. darwini* and expressed the wish to carry out comparative studies with *R. rufum*. The conference participants and all of the herpetologists and concerned lay people that were questioned later assured him that the species had not been seen in years — and yet, had anyone actually gone out purposefully seeking the tiny things? Consequently, we (representatives of the German edition of the magazine *Reptilia*, the Zoologische Forschungsmuseum Alexander Koenig, and the Zoological Society for the Protection of Species and Populations), in close cooperation with the Chilean Ministry of Agriculture, established a conservation and research project for these frogs. Among the most important financial supporters, aside from the many private contributors among the readers and authors of *Reptilia*, were the Amphibian Decline Task Force, the North of England Zoological Society, and the Zoos of Leipzig and Chester. We had many reasons for concern. The Valdivian Rainforest fell outside the global focus on tropical rainforests and was subject to substantial economic use and rapid destruction. Habitat for *R. darwini* continues to shrink each year, and *R. rufum* was presumed to be extinct.

We undertook an extensive search to find any extant *R. rufum*. We sought the frogs ourselves, we integrated local Chilean colleagues into our search parties, and we sent in renowned international herpetologists. We played back recordings of the species' mating calls, but they went unanswered. We thrashed through blackberry hedges and pinewood plantations; we combed through the vegetation belts, at times only a few meters wide between the streams and forests; we fished for tadpoles. We searched all of the known historical localities and every other spot that seemed suitable during our several-months-long excursions from 2003 to 2006 — all for naught. Given the size of its potential distribution area, hope remains that *R. rufum* still survives somewhere to this day. Our activities in Chile raised awareness and countless local park rangers, conservationists, and zoologists have taken up the search; nevertheless, no *R. rufum* has yet been sighted, and we are inclined to suspect the worst.

Since 2006 we have concentrated increasingly on *R. darwini*, and we found several new populations in recent years. Many questions about this species remain to be answered. Of concern, although not yet investigated and scientifically verified, are disturbing reports from local park rangers and conservationists that the number of Darwin's Frogs have decreased in recent years. Is it possible that an entire unique and spectacular genus of frogs is becoming extinct before our very eyes?

With further financial support from the zoos in Chester and Leipzig, we have outlined a doctoral study that should help to col-



The containers are in place, but the holding pens are still vacant.

lect important data over a five-year period on the ecology of *R. darwini*. Chilean herpetologist Johara Bourke, with support from the universities of Bonn (Germany) and Concepción (Chile), has been working on this project since the end of 2006. This long-term study, focusing on population monitoring, is supported in large part by our project (as well as by the Deutsche Akademische Austauschdienst). Initial findings on the ecology of *R. darwini* will be published in the near future.



Color can vary from brown to green — or some combination of the two.



An informal ceremony as the research and breeding facility became functional. Prof. Juan Ortíz is on the left; third from the left is Dr. Alexander Gutsche of the Humboldt University in Berlin.

A Breeding and Research Station

Another part of the project involves the *ex situ* breeding of *R. darwini*, initially planned at the Chester Zoo. In 2007, we imported 30 Darwin's Frogs from Chile to Europe for this purpose. The frogs were first kept in a quarantine station in Berlin, supervised by the veterinary specialist Frank Mutschmann. In so doing, we found evidence that the frogs were infected with the chytrid fungus, *Batrachochytrium dendrobatidis* — the first Chilean report of the fungus, which is implicated in the global decline of amphibians. Despite expert treatment, all of the frogs died within a few days to weeks after arrival.

Following this setback, we decided, in cooperation with the University of Concepción and financed largely by the Leipzig Zoo, to build a research and breeding station in the frogs' natural habitat. The University of Concepción provided us with a location on their property and construction (financed by the Leipzig Zoo) took place in the first half of 2009. The station, consisting of two laboratory and office containers and several generously proportioned outdoor enclosures, opened in May. While dedicated largely to the research and breeding of *Rhinoderma*, the station also is open to other herpetological work. Prof. Juan Ortíz directs the team of Chilean scientists, with Johara Bourke as a scientific consultant. At the invitation of the University of Concepción, Klaus Busse, currently the most experienced keeper of these frogs, traveled to Concepción at the end

of 2009 to assist with establishing the population of Darwin's Frogs at the station.

Other projects are currently underway in Chile. One, in cooperation with the Atlanta Botanical Garden and Zoo and the University of Santiago, will attempt to establish a captive population within a sterile "frog container" at the Santiago Zoo. Another research group in Chile is addressing the chytrid fungus. All of these projects will be working closely together as part of a "Rhinoderma Task Force."

The problems are multifold. We do not know how far the chytrid fungus has spread among populations of Darwin's Frogs in nature. Investigations from the summer of 2009 at our research and breeding station in Concepción have confirmed further incidents of infection in the wild. We also do not know if the existing populations of Darwin's Frogs are declining or stable in the face of ongoing habitat destruction from clearcutting and dam construction. We also still do not know what happened to *R. rufum*. The future of these singular frogs, first discovered by Darwin during his historic voyage around the world, in this International Year of Darwin, seems more uncertain than ever.

Acknowledgements

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Species of snakes that feed on skinks (such as the Oriental Whip Snake, *Ahaetulla prasina*) have independently evolved specialized mechanisms for grasping and holding them. These features include hinged maxillary teeth and gaps in tooth rows in which the skink's body is trapped.