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Darwin, Evolution, and Galapagos
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The Evolutionary Significance of the Pink Iguana

Introduction:

In 1986, Galapagos park rangers patrolling the remote summit of Volcán Wolf reported a sighting of a Galapagos land iguana with an unusual characteristic: bright pink scales. While many dismissed the anomaly as a skin condition, Dr. Gabriele Gentile from the Tor Vergata University of Rome and his team began searching for the elusive pink iguana in 2005. The next year the team (which included Howard and Heidi Snell) successfully captured, measured, and drew samples from 32 iguanas displaying the unique phenotype. The population was nicknamed, “Rosada,” the Spanish word for pink.

The public was introduced to the iguana with the publication of a genetic analysis on January 13, 2009. The results published in this paper suggested that Rosada deserved recognition as a unique species due to its morphological, behavioral, and genetic differences from the two already recognized members of the genus *Conolophus*. On August 18, 2009 an official description of a new species, *Conolophus marthae*, was published in the taxonomical journal *Zootaxa*. While several research papers are pending, the information currently available challenges accepted theory regarding the evolution of the iguana in the Galapagos. The goals of this paper are to: (a.) introduce the reader to a distinctive new species of Galapagos Megafauna; (b.) analyze *marthae*'s significance in terms of current understanding of Galapagos Iguana evolution; (c.) suggest the probable route of colonization for the new species; and (d.) highlight the need for conservation and further research.¹

Meet Rosada:

Description:

Conolophus marthae's striking coloration, nuchal crest, and communicative signals distinguish the iguana from its genetic relatives, *subcristatus*, and *pallidus*.

Rosada is immediately recognizable by its namesake characteristic: a pink head followed by a pink body with black stripes and blotches that merge entirely in the lizard's black tail. The prominent nuchal crest adorning the iguana's head is, in contrast to other Galapagos land iguanas, essentially spineless. Caudal and dorsal crests are less evident than those of *subcristatus* and *pallidus* (Gentile-Aug. 2009:5).

Rosada is also differentiated by its unique pattern of head-bobbing. The head bob is evidenced in both Galapagos land and marine iguanas and is an important mechanism in establishing territory and attracting mates. By videotaping *marthae*'s head-bob and using a grid to compare it to that of other Galapagos iguanas, Gentile found that its nod is highly distinctive and, if anything, more similar to the bob of marine iguanas than that of other *Conolophus*.

Most other characteristics fall well within the norm for *marthae*'s genus. The holotype selected by Gentile measured 108 cm and weighed 5 kg, placing it firmly within the size range of other *Conolophus*. Its diet is strictly vegetarian and studies are currently analyzing the level of overlap between the plant DNA found in the stools of *marthae* and the synoptic *subcristatus* (Gentile-2009: email). Rosada also exhibits the elongated snout and non-recurved claws typical of land iguanas.



Connor Pierson *Conolophus Subcristatus*
North Seymour



Gabriele Gentile 2009. *Conolophus marthae*, Volcán Wolf

Population Data:

Conolophus marthae is endemic to Volcán Wolf which, at anywhere from 350,000 to 500,000 years old, is one of the geologically youngest and most active parts of the entire archipelago. Wolf is the highest of all Galapagos volcanoes reaching over 1700 meters and is home to a diverse population of reptiles, including several subspecies of Galapagos tortoise in addition to *subcristatus* and *marthae*. The latter is usually found basking in the sun anywhere from 900-1700 meters in altitude just above the lush vegetation resulting from the “garua”(De Roy-2009: 118).

It is suspected that Rosada’s population numbers less than one hundred iguanas. This estimate is based on the fact that the animal is immediately recognizable in the rocky calderas around which it resides and that only thirty-six iguanas were caught in the first two expeditions organized to search for it. Gentile’s team has suggested that *marthae* be placed on the “Red List” of the International Union for Conservation of Nature as a critically endangered species (Gentile-Jan. 2009: 509). Although an explanation for the small population has not yet been determined, two notable facts are worrisome. The first is that high levels of hemoparasites were found in the bloodstreams of the pink iguanas

tested. Another is that in three prolonged visits to the islands the team has never captured a single juvenile iguana (Gentile-2009: email).



Pierson. Dead juvenile iguana, North Seymour

The pink iguana population appears to be reproductively isolated. Inter-specific breeding pairs of *subcristatus* and *marthae* are likely an extremely rare occurrence and has never been documented. Genetic analysis (discussed further below) revealed no evidence of interbreeding in the Rosada population and only one case in which a *subcristatus* individual may have had a pink grandparent (Gentile-Jan. 2009: 509). The most obvious reproductive barrier is the aforementioned head-bob which likely arose as a result of character displacement.



Pierson. Male Marine Iguana in midst of “head-bob”
Fernandina Island

Genetic Analysis:

After confirming the existence of a small but definite population of unique iguanas, Gentile and his team set out to genotype the then unknown “Rosada.” The team took 141 DNA samples (See Figure 1.) from the land iguana populations in the western and central islands including from the isolated *rosada* and *pallidus* populations (Gentile-Jan. 2009: 507). In order to compare the mtDNA of land and marine iguanas, the group also sampled ten marine iguanas and drew upon information provided by Kornelia Rassmann who sampled over 150 marine iguanas in one several analyses regarding marine iguana evolution (Rassman-2004: 76).

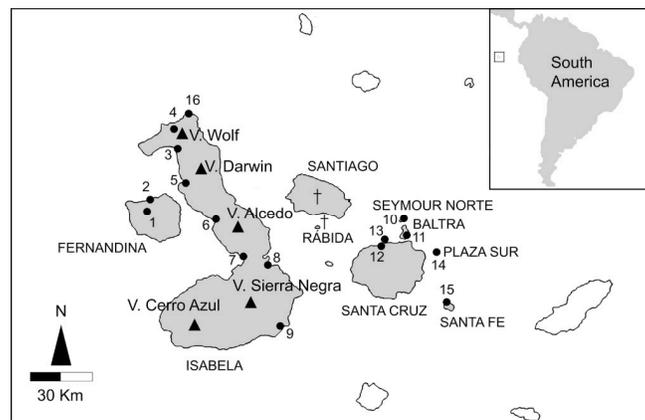


Figure 1.
Gentile *et. al* Jan. 2009
Sites 3 and 4 represent Rosada collection points.

Gentile and his team compared the mitochondrial regions of different iguana populations and were stunned by the results. A mitochondrial control region as well as the mtDNA region cytochrome b were compared across iguana populations for disparity in alleles. The amount of incongruence between the regions yielded a measure of genetic distance. The genetic distance between the established species *subcristatus* and *pallidus* was found to be 1.7 %, a figure close to that already established in the works of Andrew

Tzika and others (Tzika-2008). However, the genetic distance measured between Rosada and other populations of *Conolophus* was a whopping 7.4%. Recombination analysis using RDP3 software found no data to support the theory that Rosada resulted from a hybridization of marine and land iguanas. This result, coupled with the fact that pink and yellow land iguanas share a large percentage of alleles, suggests that Rosada represents a unique species within the genus *Conolophus* (Gentile-Jan. 2009- 509).

Most importantly, the significant genetic distance between *marthae* and the rest of the *Conolophus* clade suggests a time of divergence far earlier than not only that of the yellow land iguana species but of nearly all other related Galapagos species as well. By comparing the given genetic distance with that of species with known fossil records, the team estimated that pink and yellow land iguanas diverged roughly 5.7 mya, well before the existence of any of the archipelago's now present islands (Gentile-Jan. 2009-508).

Filling in the Gaps in Iguana Evolution:

Accepted phylogeny:

Recognizing *marthae*'s significance begins with an understanding of the colonization of the Galapagos by mainland iguanas. Galapagos marine and land iguanas are so radically different from one another morphologically that it seems hard to believe they are sister taxa. However, the work of Gentile (Jan, Aug, 2009), Kornelia Rassmann (2004) and Paul Higgins (Higgins 1978) all provide genetic evidence suggesting a much closer relationship between Galapagos marine and land Iguanas than either have with their mainland relatives.



Pierson. *Almblyrhynchus* and *Conolophus*. Sister Taxa
Fernandina and Santa Cruz

Although related, the differentiation present between the two species could only have occurred over an extended time period. Initial estimates by Dr. Vincent Sarich calculated that the species diverged 15-20 mya (Browne-1992). In 1997, Rassmann revisited the subject and argued that speciation could have commenced as recently as 10 mya (Rassmann-1995). This statistic is likely an underestimate because it relies on the rate of evolution in mitochondrial segments of ungulates, a rate that has been suggested to be faster than the same rate in cold-blooded reptiles (Rassmann-2004: 72). Rassmann's argument provided further support for the theory that speciation occurred on the islands after a single colonization event. At the time Rassmann published her findings, the oldest known seamount once thought to be part of the Galapagos was dated at 11 my, but some research suggested that the nazca plate had been churning up new islands as far back as 90 mya (Rassmann-2004: 72).

Given that there is no evidence of ancestral mainland populations of land or marine iguanas similar to those found in the Galapagos, it would seem logical to claim that the two genera are a product of now submerged islands lying within the Carnegie ridge. However, there was no other evidence to suggest that speciation out-dating the present archipelago was even possible. The only other known instance of Galapagos

iguana speciation was that between *subcristatus* and *pallidus*, a genetic distance much smaller than that of both species to the genus *Amblyrhynchus*. The Santa Fe population clearly began diverging from the more dispersed yellow land iguana well within the timeframe of the current archipelago.

The critical questions facing those trying to puzzle out Galapagos iguana evolutionary history were why radical speciation within the iguana clade began occurring millions of years before any of the present islands existed and why there had not been a single separate example of iguana speciation until the very recent divergence of the Santa Fe population. Relatively low levels of genetic isolation within the genus *Amblyrhynchus* is understandable as currents could sweep far-swimming marine iguanas to other islands and therefore minimize genetic divergence within those populations. However, land iguanas are generally isolated on their respective islands. The iguanas even lack the tortoises ability to float and their only natural means of migration is to accidentally raft from one island to another. If a pregnant female were swept to a new island upon one of these rafts, founder effect could rapidly lead to genetic divergence and, potentially, speciation. Rassmann, arguably the most prolific author considering Galapagos iguana evolution, struggled with the discrepancy she saw between iguanas and other Galapagos species. She writes, “[w]ith their old evolutionary ages and yet low levels of adaptive radiation, the iguanas differ decisively from, for example, Galapagos finches with a relatively young age but having thirteen species today”(Rassmann-2004: 83). The existence of such a seemingly unsolvable hurdle undermined the hypothesis that speciation occurred *in situ* rather than after multiple colonizations by different species.



Pierson. Swimming Marine Iguana. An explanation for why extensive speciation has not occurred within the genus *Amblyrhynchus*. Fernandina

Marthae's significance:

The discovery of a land iguana that diverged before the existence of the present archipelago is monumental. Rosada's existence supports a single colonization hypothesis in light of the lack of evidence of the emergence and extinction of three distinctive mainland iguana species. More importantly however, *marthae's* discovery proves that multiple instances of speciation have been occurring over the past several million years, and that the birth and death of Galapagos islands has likely been an active agent in speciation.

The relative inability of land iguanas to transport themselves from one island to another may explain the absence of more distinct species. However, the existence of an iguana population of ancient origin endemic to a geologically young area suggests that some fortunate iguanas from isolated species can overcome geologic activity of the Galapagos and experienced rapid genetic differentiation by moving from older to younger islands. The limited number of species of land iguana still appears to signal uncanny uniformity until the genetic divergence between different species populations is analyzed.

One needs to look no further than the scattered population of *subcristatus* to see how quickly population isolation leads to differentiation. Gentile found a genetic distance of 1.4% between populations in the western and central islands, a number comparable to that between the already defined species of yellow iguana. Tzika also highlights what she believes to be five specific land iguana “conservation units” of which she denotes two populations, Rosada and Plaza Sur, as deserving further recognition as genetically unique (Tzika-2008). One explanation for why further speciation has not occurred within the lifespan of the current archipelago is that during glaciations such as the Younger Dryas occurring little more than 10,000 years ago, the sea level dropped over one hundred meters to reveal previously submerged land masses. The emergence of so much land (See Figure 2) would have eased migration between islands and reduced the impact of founder effect wherever new genes were brought into growing populations. Such interaction can also explain why the unique Santa Fe population is perhaps not more differentiated from its near relative *subcristatus*.

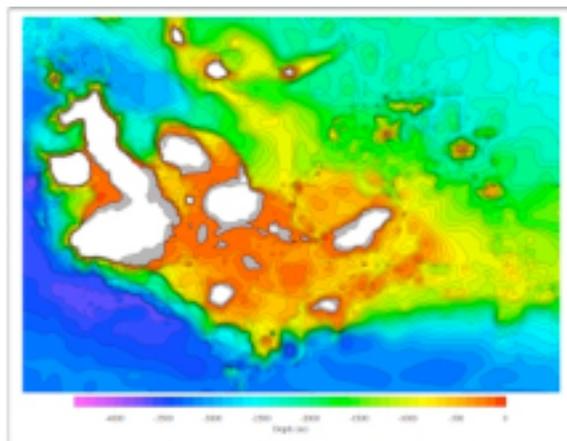


Figure 2. Tzika *et al.* 2008 Grey areas represent land that was above water during the last glacial period.

Divergence occurring due to the colonization of new landmasses even as the old landmasses began disappearing is not restricted to Galapagos iguanas. Support for this theory can also be found in the case of a much larger lizard, the Komodo Dragon whose genetic divergence within each population is extremely high given the fact that the islands it inhabits are only a few km apart. Individual populations were stranded as rising sea levels covered existing land bridges (Tzika-2008). In the archipelago, this phenomenon likely affected the speciation of smaller genera, including that of Galapagos weevils and geckos, with estimated divergence times predating the present archipelago (Sequeira-1999).

Colonization, Why and How:

A Stranded Population:

Volcán Wolf is the last place most would look for evidence of a basal split in the genus *Conolophus*. While the volcano does support a large variety of reptile life, (many different subspecies of tortoises were dumped there by passing ships) it makes little sense that such a young, isolated, and temperamental volcano would be the last refuge of an iguana species that began its journey to speciation on sunken islands over a hundred miles to the east. However, some fortuitous event may have led to the establishment of a *marthae* population while Wolf was still an island. The absence of other iguanas on the island at the time of establishment likely led to the founding colony's success.

Colonization method:

This colonization hypothesis rests on the theory that *marthae* has been out-competed by the more dominant *subcristatus*. It seems unlikely that the large discrepancy

between the areas colonized by the two species can be attributed to improved rafting ability by the yellow form. A more probable scenario is that where populations of the species overlapped, *Rosada* was driven to extinction by the synoptic yellow species. The members of Gentile's team are currently searching for overlap in the diets of the species (Gentile-2009: email).

The date of divergence given by Gentile (5.7 mya) places the initial act of separation as occurring on a submerged island relatively close to the current archipelago's oldest islands, which some estimates place at 4-5 myo (Rassmann-2004: 76). Isolating mechanisms must have arisen relatively early as both species "island hopped" and probably used some of the same stepping stones to move from the dying western islands to the central islands of the Galapagos. If not, perhaps many developing *marthae* populations were absorbed into *subcristatus* through hybridization and only those few that drifted to other islands retained genetic "integrity".

There is evidence to support the theory that *marthae* could have reached the central and, eventually, the far western islands in this fashion. Iguanas are extinct on both Santiago and Rabida. While the Santiago populations are believed to have gone extinct after the arrival of humans on the island (at which point the existence of living pink iguanas would likely have been recorded), fossils from Rabida's lava tubes provide evidence that iguanas on that island became extinct long before the arrival of humans. Gentile is currently collaborating with Dave Steadman of the University of Florida in order to analyze fossils from Rabida and other islands to test for the possibility of the presence of the *marthae* phenotype (Gentile-2009: email). A similar route of colonization

has been proposed to explain the distribution of tortoises around the islands (de Roy-2009: 120).

Although pink iguana founders likely landed on multiple western islands, Volcán Wolf proved to be a successful ecosystem because it was so isolated from populations of *subcristatus*. Even after the island became a part of Isabela, lava flows restricted to movement of iguanas between the volcanoes. The genetic analysis conducted in Rome by Gentile's team revealed no genetic divergence within the Rosada population (Gentile-Jan. 2009: 508). Therefore, the theory that Volcán Wolf was colonized by a limited number of individuals and that the population has remained in reproductive isolation is supported.

The Future of the Pink Iguana:

Our Impact:

The extinction of the pink iguana should not simply be accepted another event in the natural course of nature. The few hard facts currently available point to human involvement in the decline of the species. Although Volcán Wolf is rarely visited by humans, feral cat populations have adapted to the area. Unless there is an incredible preponderance of the Galapagos Hawk in the area, the introduction of cats and disappearance of both juvenile pink and yellow iguanas is not a likely coincidence. Once goats manage to maneuver the lava fields separating the surrounding volcanoes from Wolf they will likely become a pest as well. The Hepatozoon, the type of hemoparasite affecting the iguanas, is common in dogs and may have been introduced by domesticated animals.

Our Options:

The few remaining *Conolophus marthae* represent a population in danger of becoming the next Lonesome George. The pink iguana population is so small that Gentile actually set a taxonomical precedent by choosing to leave his holotype in the field in order to conserve the population, rather than place it in a museum collection. Due to diminished government funding, private donors and organization must step up to protect this iconic species before its impending extinction. Researchers currently have no means of conducting extended expeditions due to the lack of semi-permanent shelter (Gentile-2009: email). The continued survival of the species likely calls for a captive breeding program. Further funding could eventually help initiate such a program through the Charles Darwin Research Station. The discovery of such distinctive megafauna on the archipelago proves that the Galapagos' natural resources are far from exhausted. The pink iguana should become a symbol of hope inspiring conservation throughout Las Encantadas.

¹ I would like to express my gratitude to Dr. Gabriel Gentile for providing me with pre-published information and access to unique content.

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