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# History of Squamate Lizard Dactyloidae from the Eastern Caribbean Origins of Anolis from Martinique, Zandoli Matinik (*Dactyloa roquet*)

by

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**Summary** – The Anolis of Martinique, Zandoli (in Martinique), the species of reptile lizard *Dactyloa roquet* represents with the species of amphibian Hylode of Johnstonei, *Eleutherodactylus johnstonei*, the two species of herpetofauna endemic to the eastern Caribbean, the most widely widespread and present in large numbers throughout the territory of Martinique. The history of the Dactyloidae of the eastern Caribbean that we retrace is based on the most recent data publications, in terms of research in molecular systematics, crossed with the data of the geological history of this geographical region of the Eastern Caribbean. These molecular biology works come since 2007, to inform us with certainty as for the existence of emerged lands in place of the geographic positions of banks of current islands of the Eastern Caribbean, since much older than the Miocene (24 My) , since the Eocene and more than 45 My; molecular clock attesting to the presence, for example, of the ancestors of the *Dactyloa roquet*, on a bank of islands in the Martinique proto, among species of Dactyloidae from the eastern Caribbean having diverged from their close relatives in the Orinoco Basin in South America since 37 My.

**Key-words** : Eastern Caribbean, Eocene, geology, Martinique, phylogeny, history, origin, center of dispersion, Herpetofauna, Squamates, Lizard, Anolis, Dactyloidae, *Dactyloa .roquet*.

## I. INTRODUCTION

Geological history and geosciences are key to understanding the general evolution of biodiversity. The herpetofauna of the islands of the eastern Caribbean and particularly the small amphibians and squamates were among the first occupants of land surfaces. And so the geological evolution - tectonic and volcanic - of Martinique and the Caribbean archipelago is decisive for the process of dispersions and therefore of speciations of this herpetofauna originating in the area of the current Orinoco basin. But also these processes of dispersions and speciations, must be analyzed in a logic of conjunctions of this geological evolution of the Eastern Caribbean with phenomena of great upheavals or climatic changes impacting the entire planet; periods of glaciation with the formation of ice caps at the poles leading in bathymetric terms to significant drops in sea level. With advances in genetics, research in molecular systematics makes species of this micro herpetofauna in particular indicators allowing revelation and precision of dating of geological phenomena and events. A phylogeny of a herpetofauna which is therefore revealing of a geological history of the Eastern Caribbean where Martinique stands out as exceptional and central on the scale of this Grenadian basin where it is located; playing a main role as a refuge island from - 25 My, then from center of dispersion towards - 12 My for an endemic herpetofauna older than previously thought. A proto-Martinique island refuge in this almost unique Grenadian basin (with proto-Barbados) maintained not submerged from - 25 My, which was quite naturally center of dispersion, first towards a proto-Saint Lucia in geological phase re-emergence around -12 My.

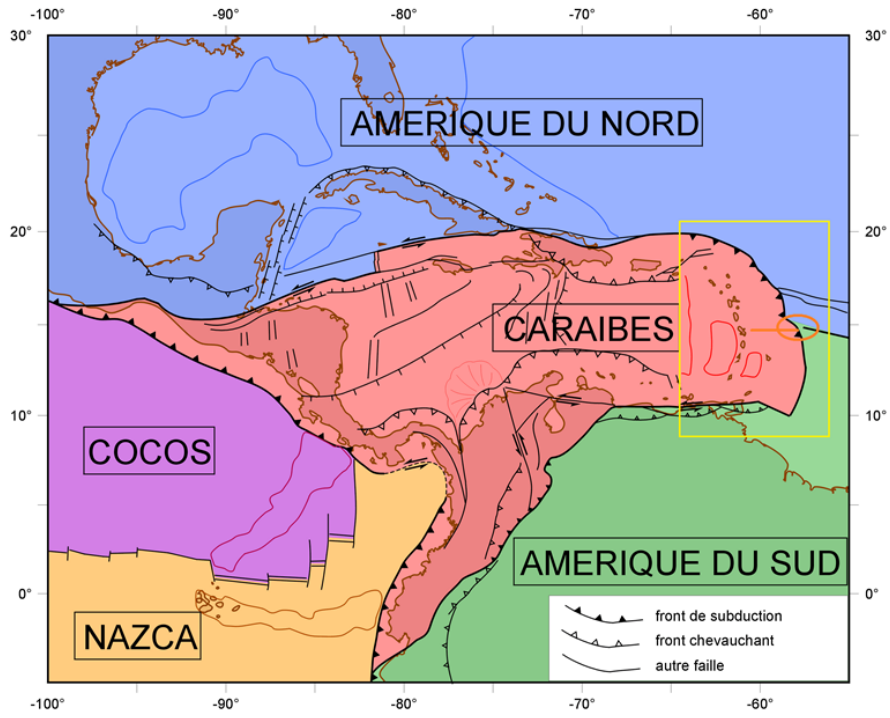
Research in herpetology and particularly the first results of work in molecular systematics (Hedges *et al.* 2007, Surget-Groba & Thorpe 2013, Hedges *et al.* 2015) relating to this Martinican herpetofauna are shaking up the geosciences and obliging a revision of the historical scenario of the basically tectonic geological formation and evolution of the Eastern Caribbean with emerged land (forming an isthmus since the Eocene, well over - 45 My), then almost all submerged around -25 My. This isthmus at the top of " a cordillera (volcanic arc), located on the southeastern edge of the so-called Caribbean plate, at the junction of the three lithospheric films (or plates), Caribbean, North America and South America, formed one of the two bridges, with that of the Aves ridge, between the Orinoco basin and the Greater Antilles. (See Fig. 2 and Fig. 3)

The history of biological endemism on the surface of land that has emerged since then does not begin there in the Miocene at "- 24 My" as it is generally accepted. It is in such a context that the Dactyloïdés of Martinique (Zanndoli, in Martinique language), are like the Spherodactyles (Ti-Mabouya), and Tétrachéilostomes (Ti-Sèpan Tè) emblematic of this evolution of biodiversity in a logic of cause and effect with the geological history of Martinique, obviously intrinsic to that of the eastern Caribbean, and in conjunction with climate change.

The base of Martinique consists of a fragment of the Aves wrinkle located east of the Caribbean tectonic film which evolved 120 My ago in the Pacific Ocean. This Aves wrinkle, with its two consecutive folds of the west to east displacement of the Caribbean lithospheric film encrusted between the two most important American lithospheric films, is part of a set called the Caribbean Mesozoic Arc . (Stephan, J.F. *et al.* 1990).

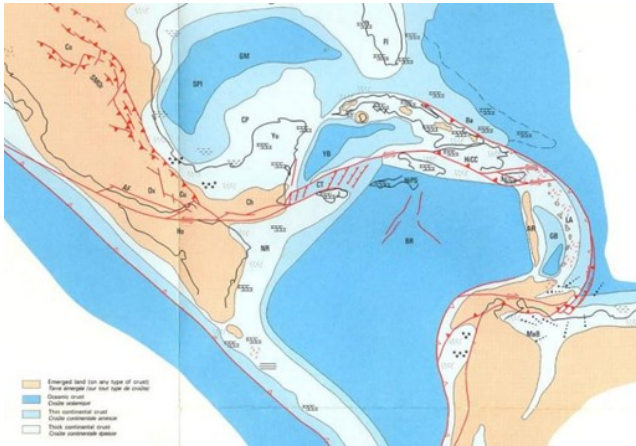
Martinique is the only island in the eastern Caribbean to present three phases of volcanic activity juxtaposed with a regular displacement of these activities from east to west since 25 My (Fig. 4 and 5, Germa, Aurélie 2008) . Located remarkably on a position in the far east of this Caribbean arc,

"where a North-South tangent passes", precisely at the latitude of the splitting of American lithospheric films. (Fig. 1: Bernard Mercier de Lépigny 2010)

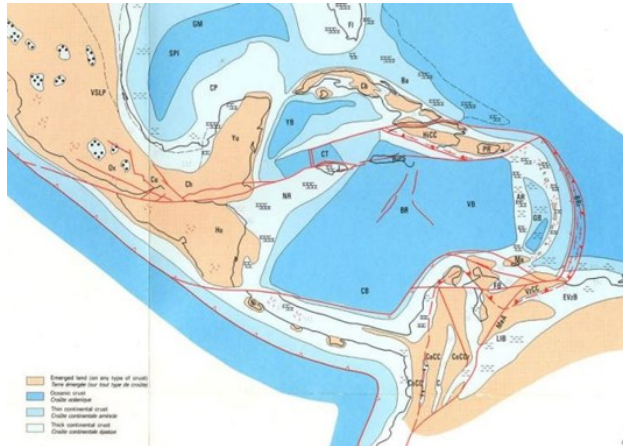


**Fig. 1 :** Bernard Mercier de Lépigny (2010)

Middle Eocene : - 49 My



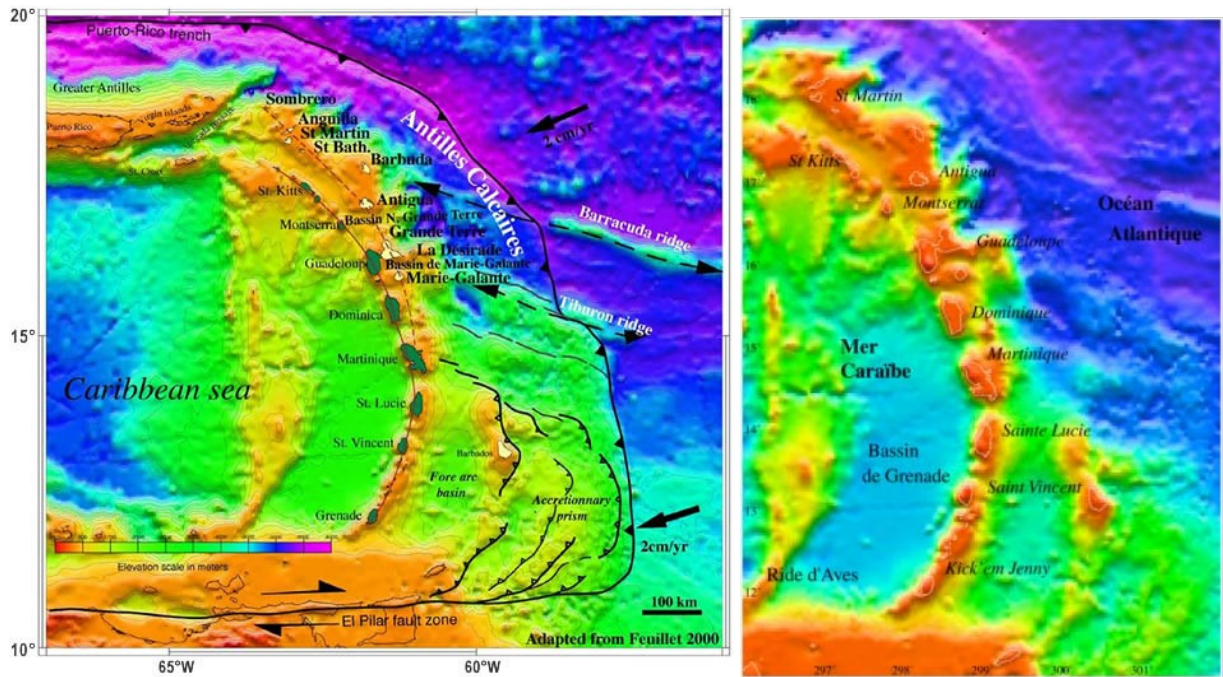
Upper Eocene : - 37 My



**Fig. 2 :** Extracts from cartographic works by Stephan, J.F. *et al.* (1990).

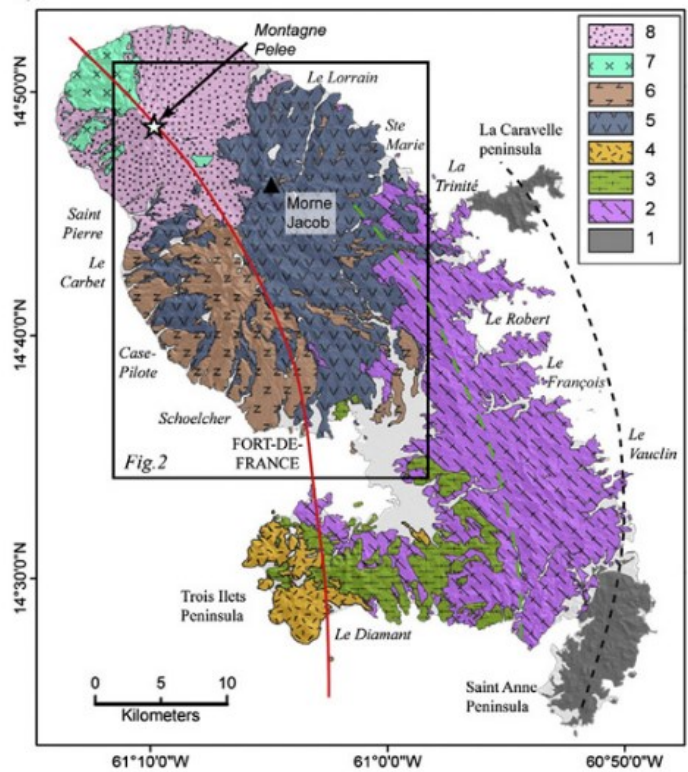
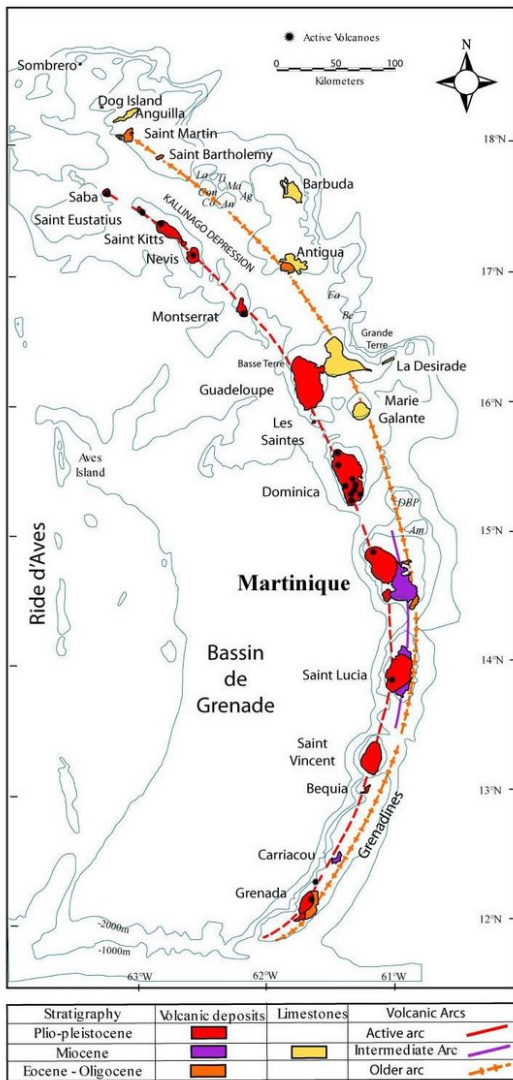
Paleogeodynamic maps of the Caribbean. Bulletin n°6





**Fig. 3 :** DIAGRAM MAP REPRESENTING THE ARCHIPELAGOS OF THE EASTERN CARIBBEAN IN THE CONTEXT OF PLATE TECTONICS

Antilles Seismological Data Center , 2004



1) In Martinique, the products of the ancient arc (gray) outcrop on the peninsulas of La Caravelle (east) and Sainte Anne (south-east). 2 - 3) Then the volcanic front moved slightly towards the west. An underwater chain was built between 17 and 8 My (Vauclin-Pitault chain, purple) then emerged to build the peninsula of Trois Ilet until 7 My (Volcanism of the Southwest, green). 4) The monogenic volcanoes of Trois-Ilets were active from 2.4 to 0.34 My (orange). 5) Le Morne Jacob (dark blue, see below) is a shield volcano which emerged around 5.5 My and was active until 1.5 My. 6) The Carbet complex began to build on the western flank of Le Morne Jacob about 1 My ago. A flank collapse affected its entire western flank and was immediately followed by the eruption of the Pitons du Carbet in the depression. 7 - 8) Mont Conil (light blue) emerged about 550 ka ago. Since then, volcanic activity has never really stopped in the northern block of the island. Around 126 ka, a flank collapse destroyed about 25 km<sup>3</sup> of the building, then the volcanic activity of Mount Pelée (pink) proper became centralized in the depression formed. Germa,Aurélie (2008).

**Fig. 4 et 5 :** Martinique and the island arches

of the eastern Caribbean (by Germa Aurélie)



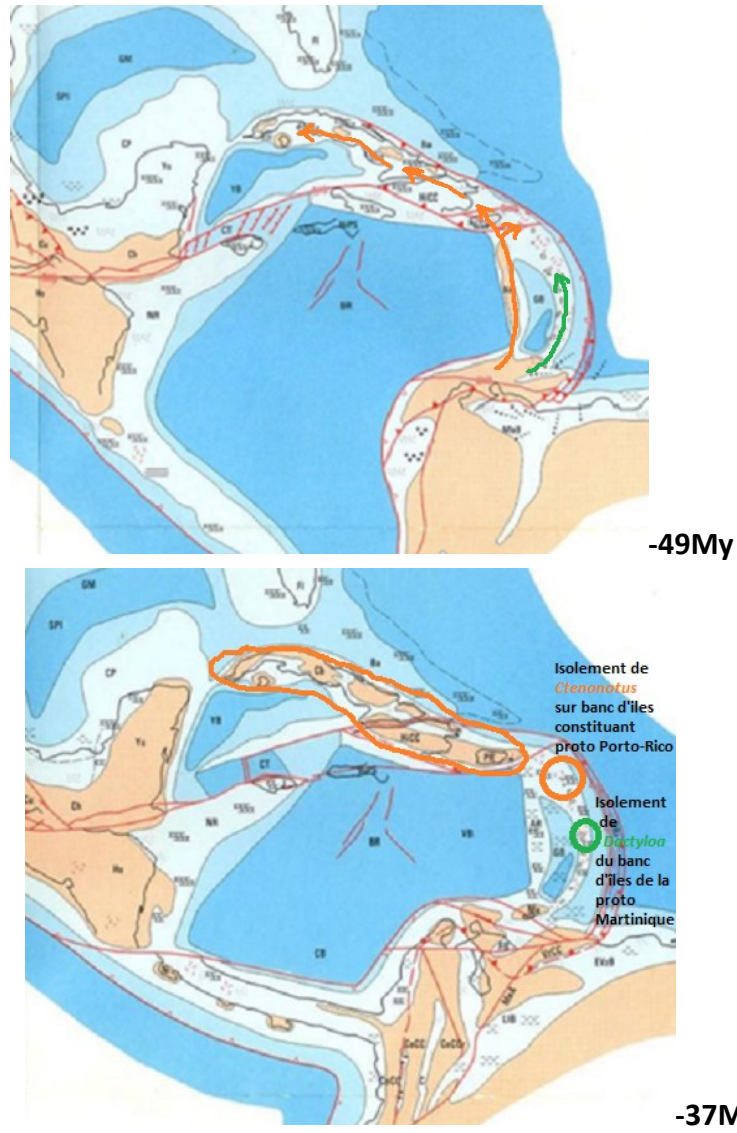


Fig.6 : Proto basin of the Orinoco and proto Eastern Caribbean bio connected since Eocene

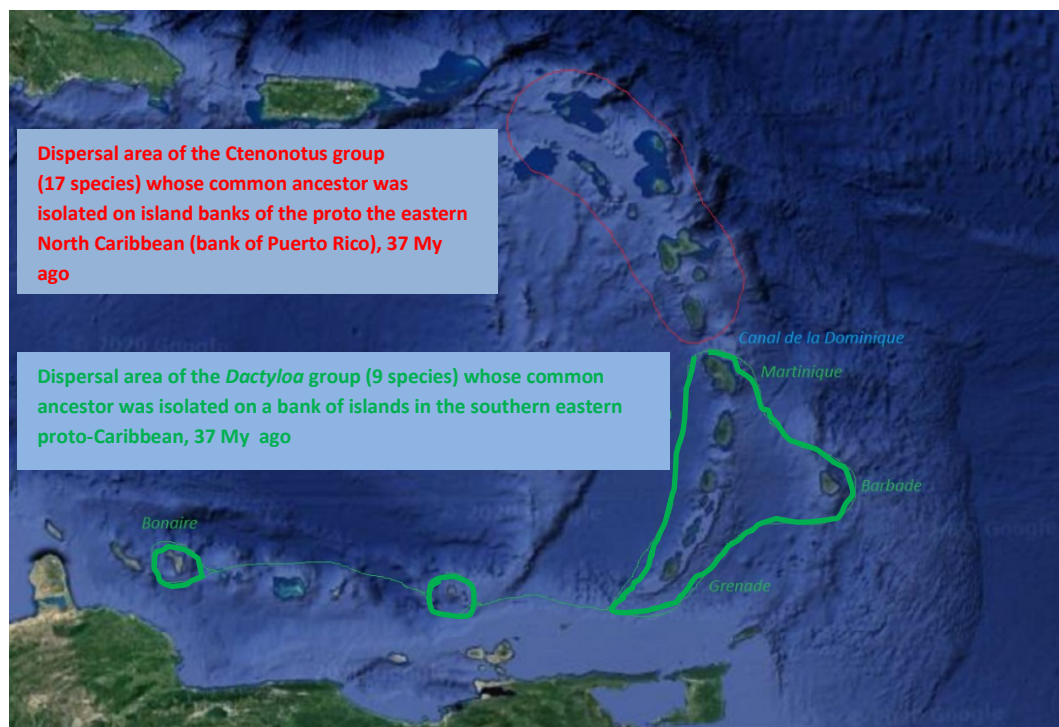


Fig. 7 : Current distribution (in green) of Dactyloid species in the south of the Eastern Caribbean

## II. MATERIAL AND METHOD

This contribution relating to the history of the Dactyloidae lizards of the Eastern Caribbean is based on field observations on the current Martinican country, and therefore concerning lines of the *Dactyloa roquet* species, by evoking origins and phylogeny of the species, and therefore by making reference to recent but also very old publications, dealing with biogeography, geology, biology and systematics : Dumeril *et al.* 1870, 1909, Barbour 1914, 1921, 1930, 1935, 1937, King 1962, Schwartz 1964, 1965, Westerkamp 1975, Lliboutry 1975, Lopez-Ramos 1975, Schwartz & Thomas 1975, Andreieff, Baubron, Gardner *et al.* 1987, Westercamp 1988, Stephan 1990, Hedges 1996, Malhotra & Thorpe 1999, Breuil 2002, 2009, 2011, 2013, Gradstein *et al.* 2005, Schulte 2005, Steinberg, Hite, Powell & Henderson 2008, Germa 2008, Hedges & Kumar 2009, Daltry 2009, Henderson & Powell 2009, Powell & Henderson 2012, Pichot 2012, Nicholson *et al.* 2012, 2018, Barat 2013, Surget-Groba & Thorpe 2013, Sepulchre *et al.* 2014, Sacco 2015, Prates *et al.* 2015, Allard Saint-Albin 2015, Hedges, Marin, Suleski, Paymer & Kumar 2015, Mauvois 2015, Powell *et al.* 2015, Poe *et al.* 2017, Saffache *et al.* 2018, Bourgade & Fong 2018, Dewynter 2018, Bourgade 2019, Dewynter, De Massary, Bochaton, Bour, Ineich, Vidal, & Lescure 2019, Bourgade 2020.



*Dactyloa roquet* Zannoli Matinik  
Lineage of the Sainte-Anne Peninsula  
south-east of Martinique

### LIST OF DACTYLOIDS FROM THE EASTERN CARIBBEAN (see Fig. 7)

**SAUROPSIDA** Huxley, 1864 ..... **SAUROPSIDES**

**SQUAMATA** Oppel, 1811 ..... **SQUAMATES**

«**SAURIA**» Brongniart, 1800 ..... **SAURIENS**

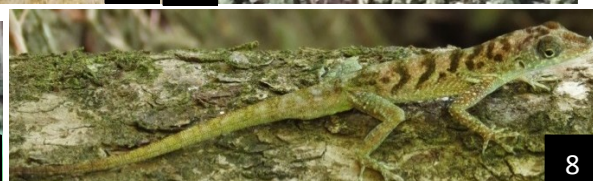
**DACTYLOIDAE** Fitzinger, 1843 ..... **DACTYLOÏDÉS**

***Dactyloa*** Wagler, 1830 ..... **Dactyloa**

- *Dactyloa roquet* (Lacepède, 1788) ..... Zannoli atè Matinik, Anolis of Martinique
  - *Dactyloa r. extrema* (Garman, 1887) ..... Zannoli atè Babad, Anolis of Barbados
- *Dactyloa luciae* (Garman, 1887) ..... Zannoli atè Sent-Lisi, Anolis of Saint-Lucia
- *Dactyloa richardii* (Duméril & Bibron, 1837) ..... Zannoli atè Grènad, Anolis of Grenada
- *Dactyloa aenea* (Gray, 1840) ..... Zannoli atè Grènad, Anolis of Grenada
- *Dactyloa grisea* (Garman, 1887) ..... Saint-Vincent
- *Dactyloa trinitatis* (Reinhardt & Lütken, 1862) ..... Saint-Vincent
- *Dactyloa blanquillana* (Hummelinck, 1940) ..... island of Blanquilla (Venezuela)
- *Dactyloa bonairensis* (Ruthven, 1923) ..... Bonaire



Diversity of traits and morphological characters of *D. roquet* in Martinique territory: diversity of general colors and patterns of the patterns, body dimensions and flaking, sizes and formations of more or less developed spiny dorsal crest,... demonstrating influences on aspects of the individuals habitat types and climatic conditions of the environments.







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Photographs of the author and data on : [inaturalist.org/observations/m-bourgade-mk](https://inaturalist.org/observations/m-bourgade-mk)

- 1 Two males of the typical *Dactyloa roquet* species by their features and patterns of their bosses of the southern line of the Sainte-Anne peninsula obviously fighting for a territory.
- 2 Two males of the *Dactyloa roquet* species observed by Christophe Auguste 2019, presenting particular phenotype within the line of northwest Martinique with a character remarkable morphological development of their spiny dorsal ridges.
- 3 Young male *Dactyloa roquet*, present on islet of Génipa bay (Morne Doré) within of the lineage in central Martinique with a pattern coloring tending towards a bluish tint.

- 4 Male specimen of the Sainte-Anne peninsula line, cradle of the *D. roquet* species.
- 5 Female specimen within the line of central Martinique (Balata) with a patternless pattern.
- 6 Male individual *D.roquet* observed on the North Atlantic coast of Martinique (Basse-Pointe, within the northwest line) with a black coloration of its head making it more visible its back crest.
- 7 Male *D. roquet* observed within the northwest line (St. Pierre), with a crest spiny spine developed. (Photo by Myriam Bouaziz)
- 8 Male individual observed on the Caravelle peninsula (lineage of central Martinique).
- 9 Male specimen from the line of southwest Martinique (Anses-d'Arlet).
- 10 Male specimen observed on Saint-Aubin islet on the North Atlantic coast of Martinique (Trinité) of the line of *Dactyloa roquet* distributed in the center of the country.
- 11 Male specimen within the lineage of central Martinique (Balata).
- 12 Female specimen within the line of southwest Martinique (Anses-d'Arlet)
- 13 Female specimen within the line of southwest Martinique (Anses-d'Arlet) showing a reddish color, like that of the bark of the tree constituting its habitat, a Red Gum (*Bursera simaruba*).
- 14 Male specimen of the Sainte-Anne peninsula line, cradle of the species.
- 15 Male specimen from the line of southwest Martinique (Vatable, Trois-Ilets).
- 16 Female specimen of the line from south-west Martinique (Vatable, Trois-Ilets).
- 17 Male specimen within the lineage of central Martinique, here on the northern flank of the Vauclin Mountain.
- 18 Female specimen within the lineage of central Martinique, here on the northern flank of the Vauclin Mountain. Females tending to present patterns with line patterns along the back.

### III. HISTORY OF A DISPERSION SINCE THE EOCENE (- 50 My), FROM THE PROTO BASIN OF THE ORINOCO TOWARDS LANDS EMERGING FROM THE PROTO CARIBBEAN, FROM THE ANOLI GENUSES: COMMON ANCESTORS TO *DACTYLOA* AND *CTENONOTUS*

The ancestors of the Anolis of the Eastern Caribbean (common ancestors of *Dactyloa* and *Ctenonotus*) are survivors, who evolved at the time on the geographical position of the proto basin of the Orinoco, north of the continental block South America, from the 5th great extinction which took place - 66 My ago. This 5th great planetary extinction of species was consequence of the impact of the asteroid which occurred 66 MY ago in Chicxulub on the tip of the Yucatan peninsula (Gulf from Mexico). (Smit *et al.* 1994, 1996)

This asteroid impact event caused major ecological changes to lower sea levels (Gradstein *et al.* 2005).

The beginning of the formation of the Aves and Caribbean bridges, allowing inter-continental terrestrial biological connection, and therefore very ancient dispersion in this Caribbean geographical position of terrestrial flora and fauna species, would result from the conjunction of both geological phenomena ( tectonics, migrations of bedding), climatic (glaciations) and the consequences of the impact of the asteroid which occurred 66 My ago at Chicxulub on the tip of the Yucatan peninsula (Lopez-Ramos 1975).

The ancestors common to *Dactyloa* and *Ctenonotus*, squamates, were then able to disperse by almost terrestrial route, respectively on the most eastern Caribbean isthmus for *Dactyloa*, and on the Aves isthmus for *Ctenonotus*, isthmus formed since 65 My (Stephan 1990).

These dispersions and separations between *Dactyloa* and *Ctenonotus* are attested by molecular biology and dated to - 50 My in the Eocene (Prates *et al.* 2015).

At -50 My (early Eocene) the temperature of oceanic water masses is close to 15 ° C (Matthew *et al.* 2009). (see Fig. 2 and Fig. 3)

The ancestors of the Dactyloïdés installed on quasi isthmus of the Eastern Caribbean since -50 My, diverged from their South American congeners of the proto basin of the Orinoco around -37 My (Prates *et al.* 2015). At -35 My (late Eocene), it is the beginning during the Tertiary era of the glaciation period still current, the temperature of oceanic water masses dropped to 11 ° C at the surface and to 9 ° C in depth ; there is then a development of mountain glaciers on Antarctica (which has been at the south pole since -100 My) and there is again significant cooling which results in a decrease of about 6 ° C in the temperature of the bottom water (Matthew *et al.* 2009).

These ancestors of the Dactyloïdés, surviving on banks of islands of the proto Martinique remained emerged following the submersion of this Caribbean isthmus which proceeded from -40 My to - 25 My, will evolve in isolation; then around -12 My, the Martinique proto will play a role as a center of dispersal of the Dactyloïdes towards banks of re-emerged islands in the south of Martinique: proto Saint Lucia, proto Grenada, proto Saint –Vincent, proto Barbados . Note the fact of a major new cooling of the planet towards -13 My with an increase in the Antarctic ice cap, and therefore a drop in sea level (Matthew *et al.* 2009). Thus there will be differentiation of *Dactyloa*, dispersed directly or indirectly, from the proto Martinique:



- to the prototype Saint Lucia, with the ancestor of *D. luciae* since around 17 My (probable age of re-emergence of island banks: Gros-Ilet and Ilets Maria)
- towards the island banks of Grenada, with the ancestor of *D. richardii* since 12 My (Hedges *et al.* 2015). Then diversification towards the Grenadines, with the ancestor of *D. aenea*.
- towards the prototype Saint-Vincent, via Saint-Lucia, with the ancestors of *D. griseus*, and *D. trinitatis*.
- to Blanquilla and Bonaire, via Ste-Lucie, with ancestors of *D. blanquillana* and *D. bonairensis*.

From proto Martinique and the old island of Sainte-Anne, the ancestors of *Dactyloa roquet* also dispersed over new areas as geological evolution and volcanic activity formed this proto Martinique (see Fig. 4 and Fig. 5), first towards banks of islets on the geographical position of the current Génipa Bay (Ducos, Lamentin), then towards the peninsula of south-west Martinique. Then as the geological evolution and the formation of volcanic massifs (Vauclin, Morne Pitault, ...), the *Dactyloa roquet* occupied the Martinican space of the center, between the peninsula of Sainte-Anne, that of the southwest and that of the Caravelle. And finally towards the north and north-west of Martinique with first the emergence of Le Morne Jacob, the Pitons du Carbet, then the island of Mont Conil (Prêcheur), and finally the Montagne Pelée.

Unlike the Eleutherodactylid amphibians and spherodactyls, the *Dactyloa* did not cross the Dominica Canal.

The phylogeny work of Thorpe *et al.* 2010 make it possible to distinguish, four (4) large lines within the *Dactyloa roquet*:

- the lineage of the Sainte-Anne peninsula;
- the southwest line;
- the center line; with a dispersion from the Atlantic coast to Barbados estimated at - 4 My.
- and the north-west line, the most recent where *Dactyloa* have experienced last volcanic episodes and therefore for some have survived. The presence observed in 2019 by Christophe Auguste, of a line presenting a particular phenotype with a remarkable morphological character of development of their spiny dorsal crests (photograph 2), remains to be studied.

*Dactyloa roquet* are also present in Saint Lucia (Daltry 2009), and are called "Zanndoli Babad" (Anolis of Barbados) by the population. Additional investigations should be carried out to confirm or deny the fact that this line observed in Saint Lucia comes from Barbados or directly from Martinique.

This historical scenario of evolution of the genus of the *Dactyloa* known as *Anolis* in the Eastern Caribbean whose ancestors knew as refuge the island banks of the Martinique proto remained emerged from - 24 My (compared to the other island banks of this Eastern Caribbean which they were submerged), presents similarities to that declined for the genus *Sphaérodactylus* of Martinique. Moreover this historical scenario would be globally valid with chronological differences, for several genera of the micro herpetofauna the most formerly dispersed from the basin of the

Orinoco towards the geographical position of the current banks of islands of the eastern Caribbean from the Eocene, for more than 45 My.

It is the particular configuration of the proto Martinique (South-East) geologically, that is to say the existence in the basement, of large limestone formations out of water, compared to that of the other islands of the Eastern Caribbean (including Barbados), to have found itself as the only possible refuge for fauna and flora, with banks of islands tectonically remained emerged between - 24 My and -12 My. It is this situation which explains this scenario of which we have scientific certainty since 2008, of a Martinique center of dispersion on the scale of the eastern Caribbean, for the *Anolis* (Johansson, Surget-Groba, & Thorpe 2008), and for the *Sphaérodactylus* (Surget-Groba, & Thorpe 2013). This global scenario is presumed to become more precise as the work in molecular biology proceeds, and to be the same for Anurans, Amphibians of the genus *Eleutherodactylus*, as well as concerning the snake reptiles of the genus *Tetracheilostoma*.

This datum of the geological history of the Caribbean, history of islands linked to the existence of volcanoes certainly, but naturally also and above all history of tectonics, sediment bedding, existence of isthmus or bridges (Aves ride) to the geographical position of the eastern Caribbean from 100 My to 35 My, makes consistent the reading of data from research results in molecular systematics and phylogeny of reptiles and amphibians, and therefore for many species of the plant kingdom. Despite the results of molecular biology, the authors underestimate this existence of tectonically emerged lands and precisely of a Martinique proto that has remained emerged since the beginning of the Eocene -50 My; and remain frozen in an approach which turns out to be deceptive of Martinique as being an "oceanic island" and only "volcanically emerged", the first parts of which have "arisen from the ocean since - 24 My".

Dewynter *et al.* 2018, 2019, interpreting the fact highlighted by the work in molecular systematics of Hedges *et al.* 2015, of a differentiation of the *Anolis* of the Grenadines (*Dactyloa richardii*) with those of Martinique (*Dactyloa roquet*) since - 12 My, implicitly suggest the thesis that the bank of islands of Dactyloïdes from the Eastern Caribbean, that therefore their geographic location of isolation of their South American congeners as of -37 My ago, would have been the proto Grenada and the Grenadines, and that the installation of the ancestor of *Dactyloa roquet* on the proto Martinique and old island de Sainte-Anne would be dated "- 8 My" (p. 66 of Bull. Soc. Herp. Fr. (2019) 169). This thesis and interpretation of molecular biology results is, in our opinion, completely wrong ; indeed, the absence on these proto islands of Grenada and the Grenadines of the genera of Spherodactyls and Tetracheilostomes pleads in favor of a total submersion of these banks of islands to count between -25 My and -12 My. As also the absence of the genera of Spherodactyls and Tetracheilostomes endemic to the proto Saint-Vincent also pleads for a total submersion of this island from - 25 My unlike the old island of Sainte-Anne. As still, the absence of the genera of Spherodactyls and *Anolis* (*Dactyloa*) endemic to the Barbados proto argues for the fact of an almost total submersion of the latter from - 24 My, and this always unlike the bench Proto Martinique island and precisely the old island of Sainte-Anne.

The existence of the eastern Caribbean isthmus, most certainly from -50 My to -35 My, essentially linked to tectonic phenomena and climate change, comes to explain data from molecular research concerning species of reptiles and amphibians from the oldest present, originally refugees on proto Martinique. The residual islands of the Proto Martinique bench, Caravelle and Sainte Anne, have become centers of dispersal of species having survived the significant extinction between -35 My

and -24 My of a biodiversity that had dispersed from the continent South American to the Caribbean isthmus since - 50 My; isthmus all the more formed during glacial periods when the sea level is estimated at 130 meters compared to the current level (Matthew *et al.* 2009). See fig. 3, allowing a visualization of the context of isthmus or double bridge, of land emerged during this geological era.

#### IV. CONCLUSION

In the current state of knowledge, and since 2015, we can state the certainty of the fact that the ancestors of the Dactyloids of the eastern Caribbean settled there -50 million years ago on the tectonically emerged lands constituting this proto Caribbean; and singularly ancestors of the *Dactyloa roquet* on banks of islands of the Martinique proto -50 My ago. These Dactyloïdes of the Eastern Caribbean found themselves genetically isolated from their parents of the proto basin of the Orinoco from -37 My. From -25 My, the benches of islands of the proto Martinique, remained emerged, constituted the almost unique and exceptional refuge for these isolated Dactyloïdes, while in the north, as in the south of this proto Martinique, the benches of islands corresponding to the geographic positions to the north, Dominica, the Guadeloupe archipelago and islands further north (Antigua, Barbuda, banks etc.); in the south, from Saint Lucia to the island of Grenada, but also probably the island of Barbados, were all almost completely submerged.

The geographical position of the current Sainte-Anne peninsula in the south-east of Martinique corresponding with certainty to the refuge area and then the center of dispersal of the Dactyloïdes which dispersed in the Eastern Caribbean to the south of Martinique only (Sainte -Lucia, Saint, Vincent, Grenada, Barbados, even along the coasts of Venezuela, on the islands of Blanquilla, and Bonaire).

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