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Quaternary biodiversity of the giant fossil endemic lizards from the island of El Hierro (Canary Islands, Spain)

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ABSTRACT

The genus *Gallotia* is an endemic lizard clade from the volcanic archipelago of the Canary Islands (Spain). This clade has five extant and extinct giant species distributed over just five islands in the archipelago: El Hierro, La Gomera, La Palma, Tenerife and Gran Canaria. On the island of El Hierro, remains of several giant species of *Gallotia* have been found. In this paper, we present a revision and description of the bones from El Hierro with similar osteological characteristics to the giant species from Tenerife, *Gallotia goliath*. The fossil remains of 24 individuals have been found in volcanic tubes of a Chibanian/upper Pleistocene-Holocene age (Quaternary). These remains confirm the presence of the species *Gallotia goliath* on the island of El Hierro and provide the first evidence of the possible coexistence of two giant fossil species of *Gallotia* on the same island. The existence of individuals of *Gallotia goliath* would imply on the one hand dietary specialization each giant species. On the other hand, it would suggest the transfer of non-flying species between islands raising the possibility that the great landslides of the Quaternary may have played an important role in inter-island migrations.

1. Introduction

The Canary Islands is an oceanic archipelago of volcanic origin located in northwest Africa (Fig. 1A and B). Its endemic herpetofauna is composed of three families of squamata reptile: Phyllodactylidae, Scincidae and Lacertidae, of which the latter is represented by the genus *Gallotia* (Boulenger, 1916). This clade is distributed throughout the archipelago with fossil and extant species of giant and small sizes (Cruzado-Caballero et al., 2019, Supplementary data 1, Fig. 1). Of the seven islands that form the Canary Archipelago, the island of El Hierro is the youngest, with an age of 1.2 million years (Troll and Carracedo, 2016). Currently, there are two species of lizards belonging to the genus *Gallotia* living on the island: *G. caesaris* (Lehrs, 1914), a small-sized endemic species (mean male adult SVL around 75–96 mm) from El Hierro and La Gomera, and *G. simonyi* (Steindachner, 1889), a large-sized species (mean male adult SVL around 143–236 mm) endemic to the island, whose only natural population is in the Fuga de Gorreta (El Hierro). The fossil record of the giant *Gallotia* shows that this genus was distributed over almost the entire island, with 19 fossils sites (volcanic tubes and an archaeological site) of a Pleistocene-Holocene age (Castillo et al., 2001).

On the basis of the fossil record, Izquierdo et al. (1989) and Rodríguez-Domínguez et al. (2000) proposed the existence of a second giant fossil species, *G. goliath* Mertens (1942) on the island of El Hierro. This idea was later rejected by Mateo et al. (1999) and Barahona et al. (2000), who identified the specimens ascribed to *G. goliath* from the Canary Islands as large individuals of *G. simonyi.* Subsequently, Maca-Meyer et al. (2003) analysed the DNA of the giant species of Canary lizard *G. stehlini* (Schenkel, 1901) in Gran Canaria (and introduced into Fuerteventura), *G. goliath* (extinct) and *G. intermedia* Hernández et al. (2000) in Tenerife, *G. bravoana*

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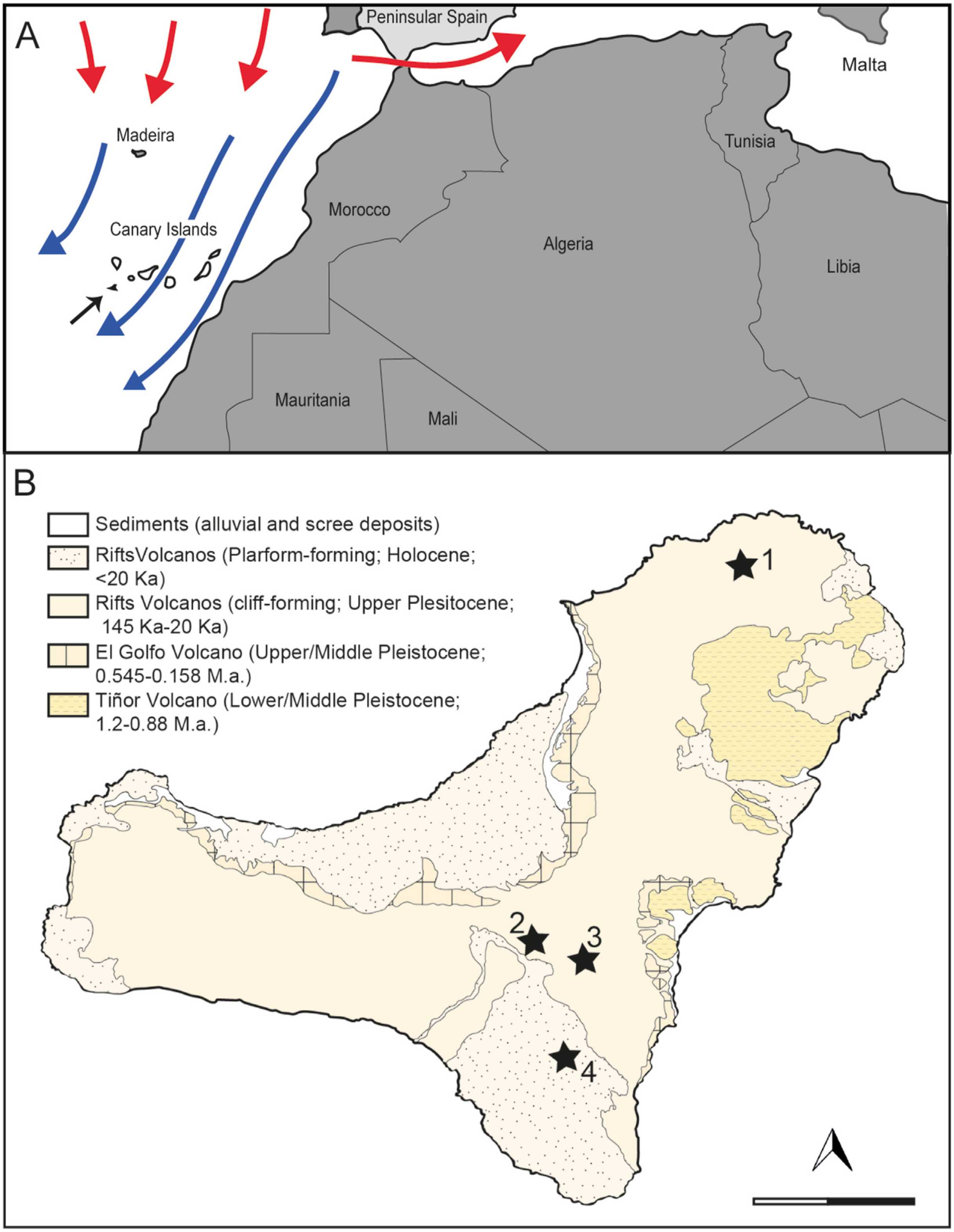

Fig. 1. Geographical and geological location of the studied palaeontological sites on the island of El Hierro. A) Map showing the location of the Canary Island and the sea currents. B) Geological map of El Hierro (after Carracedo et al., 2001) showing the situation of the deposits with fossil remains. B-1) Cueva del Curascán, B-2) Cueva del Mocán, B-3) Sima del Pico de la Mata and B-4) Cueva de El Lajial sites. The black arrow marks the island of El Hierro, the red arrows mark the North Atlantic Drift and the blue arrows mark the Canary Current. Scale bar equal 5 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Hutterer (1985) in La Gomera and *G. simonyi* in El Hierro. They ascertained that the species *G. goliath* is valid, refuting the synonymy with *G. simonyi* proposed by Barahona et al. (2000). In the present paper we follow Maca-Meyer et al. (2003) and Cruzado-Caballero et al. (2019) in accepting the validity of *G. goliath.*

Here we present a description of the morphological and ontogenetic characteristics of the fossil remains upper Pleistocene-Holocene fossil remains of several individuals of giant lizard from El Hierro, that were initial tentatively identified as *Gallotia goliath* by Palacios-García et al. (2019). We compare these remains with the fossil remains of *G. simonyi* of the same age from the island of El Hierro. In addition, we propose new characters to differentiate the species *G. goliath* and *G. simonyi* and explore the possible coexistence of these two species and a possible colonization mechanism involving landslide and wave trains.

Institutional Abbreviations: MUNA, Museum of Nature and Archaeology of Tenerife; PCCRULL, Palaeontology Collection-Carolina Castillo Ruiz, Universidad de La Laguna (Tenerife, Canary Islands, Spain); SMF, Senckenberg Museum of Frankfurt (Germany).

2. Geological settings

The island of El Hierro emerged from the ocean 1.2 million years ago, after a long history of submarine growth from the surface of the oceanic crust of the African plate. Since the island's emergence, five volcanic edifices have followed in time (Fig. 1, Carracedo et al., 2001). The oldest are two shield volcanoes, called Tiñor and El Golfo. Subsequently, the eruptions were concentrated repeatedly along large fractures or fissures in the oceanic crust and the insular edifice, which ended up, after thousands of years, forming three volcanic rifts.

The Tiñor volcano, the first to emerge in El Hierro, was formed in three stages, between 1.12 Ma and 880,000 years ago; the latter point in time marked the end of its eruptive history. This end was brought about by the great collapse of its northwestern flank. The remains of this large volcano, currently highly eroded, are only visible in the deep ravines of the northeastern sector of the island and inside the Las Playas escarpment. In these wild places, which constitute the oldest part of the island, we can see the basalt and trachybasalt flows and pyroclasts, cut by basaltic dykes, which were part of the volcanic edifice.

On the remains of the Tiñor volcano, after a break in volcanic activity of around 350,000 years, a new volcanic edifice, El Golfo, grew. This colossus came to have a diameter at its base of about 20 km and a height of approximately 2000 m. Its volcanic activity persisted between 545,000 years ago and 158,000 years ago.

After the formation of the El Golfo volcano, the volcanic activity was concentrated in three volcanic rifts oriented, respectively, in an east-west, northeast-southwest and northwest-southeast direction, which were active for about 145,000 years, until 2011, when there was a submarine eruption related to the southern rift. In these rifts, the volcanic activity was concentrated in a number of fissures, some of which were several kilometres long. The magma ascended through them, giving rise to different eruptive centres that built several aligned pyroclastic cones from which numerous lava flows started.

The instability of the El Golfo volcano and the rifts, mainly due to excessive growth and the accumulation of volcanic material, caused gravitational mega-landslides that left large deposits from these debris avalanches on the ocean floor.

The remains come from four sites distributed in the north (Cueva del Curascán; Fig. 1C—), centre (Cueva del Mocán, Figs. 1C—2, and Sima del Pico de la Mata, Figs. 1C—3) and south of El Hierro (Cueva de El Lajial, Figs. 1C-4). These sites are located in volcanic tubes dating mostly to the upper Pleistocene (Table 1, Sima del Pico de la Mata, Cueva del Mocán and Cueva del Curascán), but also to the Holocene (Table 1, Cueva de El Lajial). A general description and geological characterization of each of the palaeontological sites where the studied remains were found follow below:

2.1. *Cueva del mocán*

This simple volcanic tube, 214 m in length, has a large section with an average height of 7 m and a low slope. The mouth is a sinking or "jameo" in the roof of the upper end of the tube. Halfway along the tube there is a small crack in the roof, covered by stones. Under this crack there is an accumulation of debris (Oromí et al., 1988; Hernández et al., 1992).

The volcanic tube is found in a succession of olivine-pyroxene basaltic lava-flows covered by lapilli from nearby eruptive centres. The lava-flows come from higher eruptive centres related to the activity of the Southern Rift of El Hierro, with an age of between 145,000 years and 20,000 years (Guillou et al., 1996; Carracedo et al., 2001) or an approximate age of between 126,000 and 11,000 years (Troll and Carracedo, 2016).

2.2. *Sima del pico de La mata*

This is an inverted-funnel-shaped volcanic chasm, with a small mouth 2 m in diameter and 23.5 m in total unevenness. The base is about 50 m in diameter and in its eastern wall there is a small gallery with a short path, with numerous lava stalactite ("estafilitos"). Under the mouth there is a cone of debris (Oromí et al., 1988; Hernández et al., 1992).

The chasm is located in a succession of olivine-pyroxene basaltic lava-flows covered by lapilli from nearby eruptive centres. The lava-flows come from higher eruptive centres associated with the activity of the Southern Rift of El Hierro, between 145,000 years and 20,000 years in age (Guillou et al., 1996; Carracedo et al., 2001) or between approximately 126,000 and 11,000 years in age (Troll and Carracedo, 2016).

2.3. *Cueva de El Lajial*

This is a highly branched volcanic tube with several intersecting galleries and some spacious rooms, but always low. The total length is unknown, but exceeds 400 m. The mouth is a small opening caused by a minor landslide (Oromí et al., 1988).

The volcanic tube is located in pahoehoe olivine or olivinic-pyroxene basaltic lava-flows, somewhat vesicular in texture, originating from the eruption of the Montaña del Julán. In some areas the floor is covered with reworked lapilli from the outside, which entered the cave through fissures in the walls and roof, possibly from the pyroclastic cone of the Montaña del Julán. The eruption is related to the activity of the Southern Rift of El Hierro, with an age of less than 20,000 years (Guillou et al., 1996; Carracedo et al., 2001) or a more recent age of less than 10,000 years or 6000 years (Castillo et al., 2001; Troll and Carracedo, 2016).

2.4. *Cueva del curascán*

The Cueva del Curascán is made up of three parallel galleries at different levels. The lowest gallery, through which the cave can be accessed, presents a first section 29.8 m in length, covered with rubble in the portion closest to the mouth. This section ends in a difference of 2.5 m through which the intermediate gallery can be accessed; this is about 8 m long and free of debris, and it ends in a 5 m deep well, with a gallery at the bottom, which does not connect

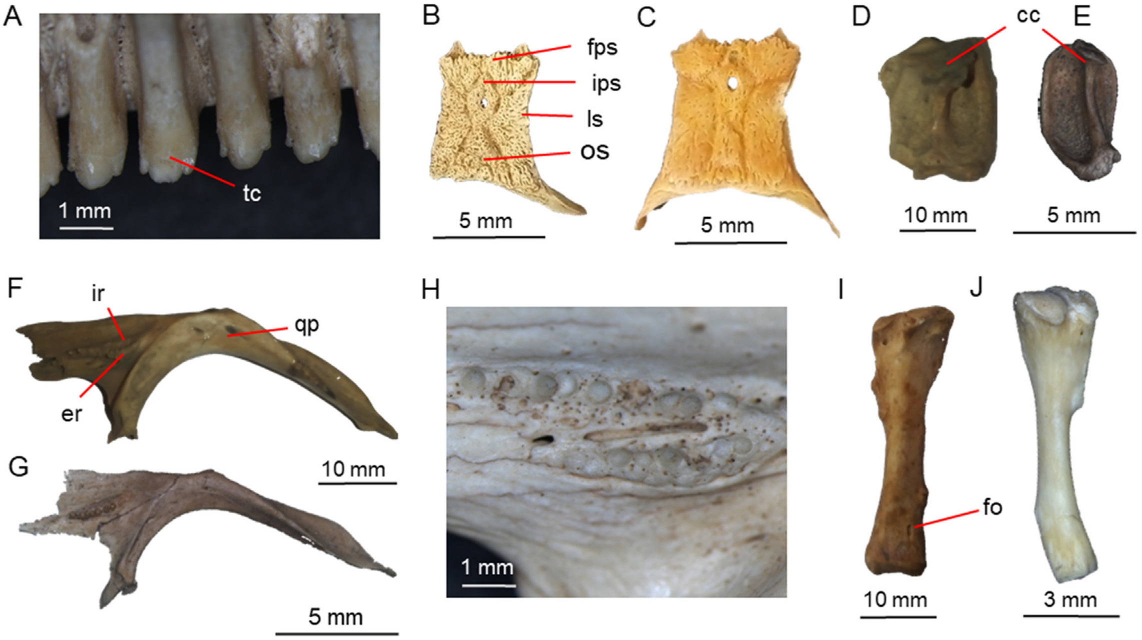

Fig. 2. Comparison between *Gallotia goliath* and *Gallotia simonyi* bones: detail of a tetracuspid maxillary tooth of *Gallotia goliath* (A), parietal in dorsal view of *Gallotia simonyi* (B) and of *Gallotia goliath* (C); quadrate in posterolateral view of *Gallotia goliath* (D) and of *Gallotia simonyi* (E); (pterygoid in ventral view of *Gallotia goliath* (F) and of *Gallotia simonyi* (G); detail of two rows of teeth in the pterygoid of *Gallotia goliath* (H); (tibia in anterior view of *Gallotia goliath* (I) and of *Gallotia simonyi* (J), Abbreviations: cc, cephalic condyle; er, external row; fo, foramen; fps: frontoparietal shield; ips, interparietal shield; ir, internal row; ls, lateral shield; os, occipital shield; qp, quadrate process; tc, tetracuspid tooth.

Table 1
Paleontological sites studied.

SITE	ALTITUDE	AGE	SPECIE	NUMBER INDIVIDUALS	POTENTIAL VEGETATION	ASSOCIATION WITH DOMESTIC FAUNA
SIMA DEL PICO LA MATA	960 m	145 ky-20 ky or 126 ky-11 ky (Chibanian/Upper Pleistocene-Meghalayan)	*G. goliath* and *G. simonyi*	PCCRULL1170-1175 (5 individuals of *G. goliath* and 1 individual of *G. simonyi*)	Pinewood endemic	Yes
CUEVA DEL MOCÁN	1090 m	145 ky-20ky or 126 ky-11 ky (Chibanian/Upper Pleistocene-Meghalayan)	*G. goliath*	PCCRULL11706-1180 (5 individuals of *G. goliath*)	Pinewood endemic	Yes
CUEVA DE EL LAJIAL	290 m	20 ky or 10 ky-6k (Holocene)	*G. goliath* and *G. simonyi*	PCCRULL1181-84 (1 individual of *G. goliath* and 3 individuals of *G. simonyi*)	"Tabaibal-Cardonal" (Spurge-dominated)	No
CUEVA DEL CURASCÁN	300 m	145 ky-20ky or 126ky-11ky (Chibanian/Upper Pleistocene-Meghalayan)	*G. goliath* and *G. simonyi*	PCCRULL1185-93 (3 individuals of *G. goliath* and 6 individuals of *G. simonyi*)	Wet "sabinar" (juniper-dominated)	No

with the first section described above. The well has two other galleries in its opposite wall: one located 3 m above the intermediate gallery, which is difficult to access and thus unexplored; and another located at the same level as the intermediate one, which forms a continuation of it. After a first section free of rubble and with a cat flap, this conduit widens considerably to give rise to a large gallery with a steep slope covered with rubble, which is over 50 m long.

The galleries are located within basaltic lava-flows from a nearby eruptive centre. The flows come from eruptive centres related to the activity of the Northeast Rift of El Hierro, with an age of between 145,000 years and 20,000 years (Guillou et al., 1996; Carracedo et al., 2001) or an approximate age of between 126,000 and 11,000 years (Troll and Carracedo, 2016).

3. Material and methods

A total of 239 cranial and postcranial bones from 24 individuals (PCCRULL1170-1193) have been studied. These fossil remains were found on the floor surface of the volcanic tubes by Castillo Ruiz and colleagues during the field trip of 1994–95. The remains were collected in accordance with the systematic methodological proposal by Castillo et al. (1996; see Table 1). The fossils formed groups occupying a surface area a few centimetres in diameter and corresponding to isolated individuals.

The primary identification of the studied remains as pertaining to *G. goliath* or *G. simonyi* was based on the photographs of the holotype (SMF36068) and paratypes (SMF36069-36075) of *G. goliath* housed in the Senckenberg Museum (Frankfurt, Germany) and photographs and bones of *G. simonyi* and *G. goliath* housed in the Museum of Nature and Archaeology (Tenerife, Spain) and the Palaeontology Area of the Animal Biology, Soil Science and Geology Department of the University of La Laguna (Tenerife, Spain). The validity of the Hutterer (1985) characters for differentiating the species *G. goliath* and *G. simonyi* was also tested. These characters are: a) the dental morphology of the maxillary teeth of *G. goliath* is columnar in form, whereas in *G. simonyi* the maxillary teeth widen towards the cusps; b) the supratemporal processes of the *G. goliath* parietal are strongly elongated, broad and rounded and have a "saddle" shape, unlike the supratemporal processes of *G. simonyi*, which are relatively short and with a rectilinear angle that gives a stool shape; c) the teeth of the pterygoid in *G. goliath* are distributed in two rows in a V-shape, unlike the single row in *G. simonyi*.

The bones were measured using a digital calliper (Supplementary data 1, Tables 2 and 3). The snout-vent length (SVL) of the studied individuals was estimated using the linear regression equations of the femur, dentary and humerus bones (Table 3). The anatomical nomenclature mainly follows Evans (2008), Rage and Augé (2010) and Klembara et al. (2010, 2014).

For the ontogenetic study of *G. goliath* 9 adult and 4 juvenile individuals were analysed, using the ontogenetic characters described by Barahona and Barbadillo (1998) and Barahona et al. (2000) for several lacertids and the extant species of *Gallotia*; these corresponded to the number of teeth and cuspids, and the ossification of the frontal, among others.

In order to evaluate the possible co-existence of several giant species on the same island, a study of the degree of taphonomic alteration of the fossil remains from the El Curascán site was undertaken. Theses specimens correspond to three adult individuals of *G. simonyi* (PCCRULL1186, 1189 and 1190) and two juvenile individuals of *G. goliath* (PCCRULL1191 and 1193; Tables 1, 3 and 4). To distinguish the juvenile and adult stages, the SVL was used, estimated according to the data recorded in Rodriguez-Domínguez et al. (1998).

This volcanic tube was specifically chosen because its entrance is artificial (it was opened as a result of the construction of a nearby road), which ensures that the remains were not manipulated by the aboriginal inhabitants of the Canary Islands. The specimens analysed were found in the same area of the volcanic tube and were subject to the same conservation conditions (for example temperature and humidity) These fossil individuals were compared with an extant individual of *G. galloti*. In order to observe the post-depositional taphonomic modification of the bones we used a binocular magnifier (Olympus SZX12, x90).

4. Results

Of the 24 individuals studied (six from Sima del Pico de la Mata: PCCRULL1170-1175; five from Cueva del Mocán: PCCRULL1176-1180; four from Cueva de El Lajial: PCCRULL1181-1184; nine from Cueva del Curascán: PCCRULL1185-1193; Fig. 1C, Table 1), 14 have been assigned to the species *G. goliath*, and 10 to *G. simonyi* (Table 1).

4.1. Morphological analysis: Gallotia goliath vs Gallotia simonyi

The 24 specimens studied show several morphological characteristics that allowed the species from the island of El Hierro to be distinguished. These related to the following: the maxillary teeth, parietal, quadrate, pterygoid and dentary teeth, and tibia.

The maxillae are triangular bones anteroposteriorly longer than dorsoventrally high; they consist of a dorsomedial facial process and a ventral alveolar portion. In lateral view, there are several nutritional foramina near the ventral side. The premaxillary process preserves the external and the internal ramus, anteriorly and medially respectively. The facial process is triangular in shape, with a convex anterior border and a concave posterior border. In medial view the supradental shelf runs almost the entire length of the maxilla, and the infraorbital foramen (or superior alveolar foramen) and the palatal process are located roughly halfway along. The number of maxillary teeth of *G. goliath* is 30 in the largest specimens, the maximum for the species *G. simonyi* being established as 24 (Rodríguez et al., 1998, 2000). The presence of tetracuspid teeth in the most posterior section of the dental battery is also observed in the large specimens of *G. goliath* (PCCRULL1174 and 1180; Fig. 2A), but not in the specimens of *G. simonyi*.

Table 2
Equations of the regression lines obtained from fossil individuals of *G. simonyi*.

INDEPENDENT VARIABLE	EQUATION OF THE REGRESSION LINE	R^2
FEMUR LENGTH	$y = 0.1171x + 1.7307$	0.99
DENTARY LENGTH	$y = 0.0779x + 5.3768$	0.84
HUMERUS LENGTH	$y = 0.1243x - 3.0733$	0.93

As regards the parietal bone, the anterior margin is interdigitated, and the anterolateral processes point anteriorly, forming parietal tabs which, as in other lacertoids, underlap the frontal. The parietal is completely covered by ornamented osteodermal shields fused to its dorsal surface, except on the processes. The ornamentation is formed by fine small foramina and grooves, more numerous in *G. simonyi* (Fig. 2B) than in *G. goliath* (Fig. 2C). In dorsal view, the shields (frontoparietal, interparietal and occipital) are delimited by grooves marking their borders on the ornamentation. The occipital shield of *G. simonyi* has a triangular shape (Fig. 2B), unlike the rectangular shape in *G. goliath* (Fig. 2C). The arrangement of the frontoparietal, interparietal and occipital shields gives an "hourglass" shape in *G. simonyi* (Fig. 2B) and a rectangular shape in *G. goliath* (Fig. 2C). The position of the parietal foramen also differs between the two species in *G. simonyi* it is located below the lines of intersection of the lateral and frontoparietal shields, whereas in *G. goliath* it is situated above or at just the same level as these lines.

In the ventral side the parietal crest is a Y-shaped crest originating from the anterolateral corners (lateral parietal crests) of the parietal that converge posteromedially (posterior parietal crest).

The quadrate is a paired bone that is roughly straights, with the posterior border slightly concave in lateral view. In medial view, its anterior outline is rounded and the medial lamina is present with an alar expansion that is well developed near the ventral end. The lateral lamina is located in the dorsal -half of the anterior surface. This is a concave rectangular platform with well-marked, rounded edges. In dorsal view, the cephalic condyle is subelliptical and posteroventrally straight. The mandibular condyle is broad and its medial portion is more ventrally expanded than the lateral portion. The general shape of this bone is rectangular in *G. goliath* (Fig. 2D) and trapezoidal in*G. simonyi* (Fig. 2E) in posterolateral view.

The pterygoid is a paired bone and it contributes to the middle and posterior zone of the palate (Fig. 2F and G). Each pterygoid is triradiate, with palatine and transverse processes anteriorly and a quadrate process posteriorly. The processes are long and slender, except for the palatine process, which is robust, and their lateral and medial borders are approximately parallel. On the dorsal side of the quadrate process is the articulation of the epipterygoid in the columenar fossa. The lateral side of the palatine process forms the medial limit of the suborbital fenestra. On its ventral surface this process presents pterygoid teeth, as in several species of lacertids (Villa and Delfino, 2019). All the specimens of *G. goliath* have two rows of pterygoid teeth on the ventral side of the palatine process (juveniles and adults; Fig. 2H), whereas in *G. simonyi* there is a single row.

The dentary is a paried bone that is triangular and is anteroposteriorly longer than dorsoventrally high. The dorsal border is slightly concave and the ventral border is convex. The lateral surface is pierced by a series of labial foramina that vary in number. In the posterior section there are two pointed processes that are wedge-shaped, the posterodorsal and the posteroventral. The medial side of the dentary is concave and presents the subdental

Table 3
Estimated measurements of the snout-vent length (SVL) of the two *Gallotia* species studied. * SVL estimated from the femur, ** SVL estimated from the humerus, *** SVL estimated from the dentary. Estimation of ontogenetic stage base on the measurements of the snout-vent length (SVL).

INDIVIDUAL	SPECIE	*SVL (CM)	**SVL (CM)	***SVL (CM)	ONTOGENETIC STAGE
PCCRULL1170	*G. goliath*	45.23			Adult
PCCRULL1171	*G. simonyi*			22.69	Adult
PCCRULL1172	*G. goliath*	X	X	X	X
PCCRULL1173	*G. goliath*	27.87			Juvenile
PCCRULL1174	*G. goliath*			48.44	Adult
PCCRULL1175	*G. goliath*	58.08			Adult
PCCRULL1176	*G. goliath*		26.57		Juvenile
PCCRULL1177	*G. goliath*	58.50			Adult
PCCRULL1178	*G. goliath*	33.98			Adult
PCCRULL1179	*G. goliath*	47.75			Adult
PCCRULL1180	*G. goliath*		45.64		Adult
PCCRULL1181	*G. goliath*		42.66		Adult
PCCRULL1182	*G. simonyi*			24.77	Adult
PCCRULL1183	*G. simonyi*	22.72			Adult
PCCRULL1184	*G. simonyi*	X	X	X	X
PCCRULL1185	*G. simonyi*			15.2	Adult
PCCRULL1186	*G. simonyi*	22.98			Adult
PCCRULL1187	*G. simonyi*	16.52			Adult
PCCRULL1188	*G. simonyi*			16.24	Adult
PCCRULL1189	*G. simonyi*	18.00			Adult
PCCRULL1190	*G. simonyi*	31.63			Adult
PCCRULL1191	*G. goliath*	22.73			Juvenile
PCCRULL1192	*G. goliath*	30.78			Adult
PCCRULL1193	*G. goliath*	16.65			Juvenile

Table 4
The bones from the Cueva del Curascán site whose taphonomic characteristics were studied.

INDIVIDUAL	CRANIAL BONES	PECTORAL AND PELVIC GIRDLE	VERTEBRAE	RIBS	LIMBS	TOTAL
PCCRULL1186 *G. SIMONYI*	10	5	12	0	6	33
PCCRULL1186 *G. SIMONYI*	11	7	28	4	21	71
PCCRULL1186 *G. SIMONYI*	14	6	9	9	11	49
PCCRULL1191 *G. GOLIATH*	36	9	37	7	31	120
PCCRULL1193 *G. GOLIATH*	18	3	2	3	5	31
TOTAL	89	30	88	23	74	304

shelf. The number of dentary teeth can vary from 18 in the shortest specimen (i.e. PCCRULL1193) to 35 in the largest specimen (i.e. PCCRULL1177) in the species *G. goliath*. The dentary teeth of *G. goliath* include between three and five cuspid teeth, whereas *G. simonyi* does not exceed four cuspid teeth, the rest being tricuspid.

The ratio of the number of teeth to the SVL of the remains studied fits an exponential curve that for *G. goliath* corresponds to $Y = 14.214e0.0122x$; $R^2 = 0.5726$ and for *G. simonyi* corresponds to $Y = 13.304e0.0218x$; $R^2 = 0.5804$ (Fig. 3A). It can be seen how the number of teeth grows as the size of the individual increases, with the curve being more pronounced in *G. simonyi* because a number of teeth similar to *G. goliath* is reached with a smaller SVL.

The ratio of the number of teeth to the length of the subdental shelf of the studied remains of *G. goliath* from Tenerife and El Hierro fits two different exponential curves. Whereas for *G. goliath* from Tenerife it corresponds to $Y = 18.085e0.0127x$; $R^2 = 0.6404$, for *G. goliath* from El Hierro it corresponds to $Y = 12.526e0.0171x$; $R^2 = 0.7434$. In addition, these curves clearly differ from that obtained for *G. simonyi*, which corresponds to $Y = 10.365e0.0347x$; $R^2 = 0.7687$ (Fig. 3B). The main difference between the populations of *G. goliath* from El Hierro and Tenerife is that the number of teeth for the same subdental shelf length is lower in the El Hierro specimens.

The tibia is an elongated and robust bone. The proximal region forms a broad contact with the femur. The distal part is flattened with a convex end. In the diaphysis there is a small foramen in the distal part in anterior view, which only appears in the species *G. goliath*. In addition, the shape of the tibia in *G. simonyi* (Fig. 2J) is more curved, whereas it is straight in *G. goliath* (Fig. 2I).

Finally, the individuals assigned to the species *G. goliath* exceed 430 mm in length, which is the maximum size of the *G. simonyi* fossils (Mateo et al., 1999). In the present work, six of the specimens analysed exceed 430 mm (PCCRULL1173, 1177–1178, 1180 and 1182–1183), with a maximum of 585 mm (PCCRULL1180, Table 2).

4.2. Ontogenetic variations in G. goliath from El Hierro

During the growth of *G. goliath* individuals, ontogenetic changes were observed between the individuals less than 28 cm in size (considered juveniles; Table 3) and those that reach larger sizes of up to 58.5 cm (considered adults; Table 3). In adult individuals the dorsal half of the lateral surface of the maxilla presents a rugose ornamentation due to the fusion of osteoderms to the surface, unlike the smooth surface in juvenile specimens (Fig. 4A and B).

The jugal is an L-shaped paired bone that consists of postorbital and suborbital processes that form the posterior and ventral borders of the orbit, respectively. The angle formed between these processes varies between approximately 120° in juvenile (PCCRULL1191) and 90° in adult specimens (PCCRULL1175). A wide

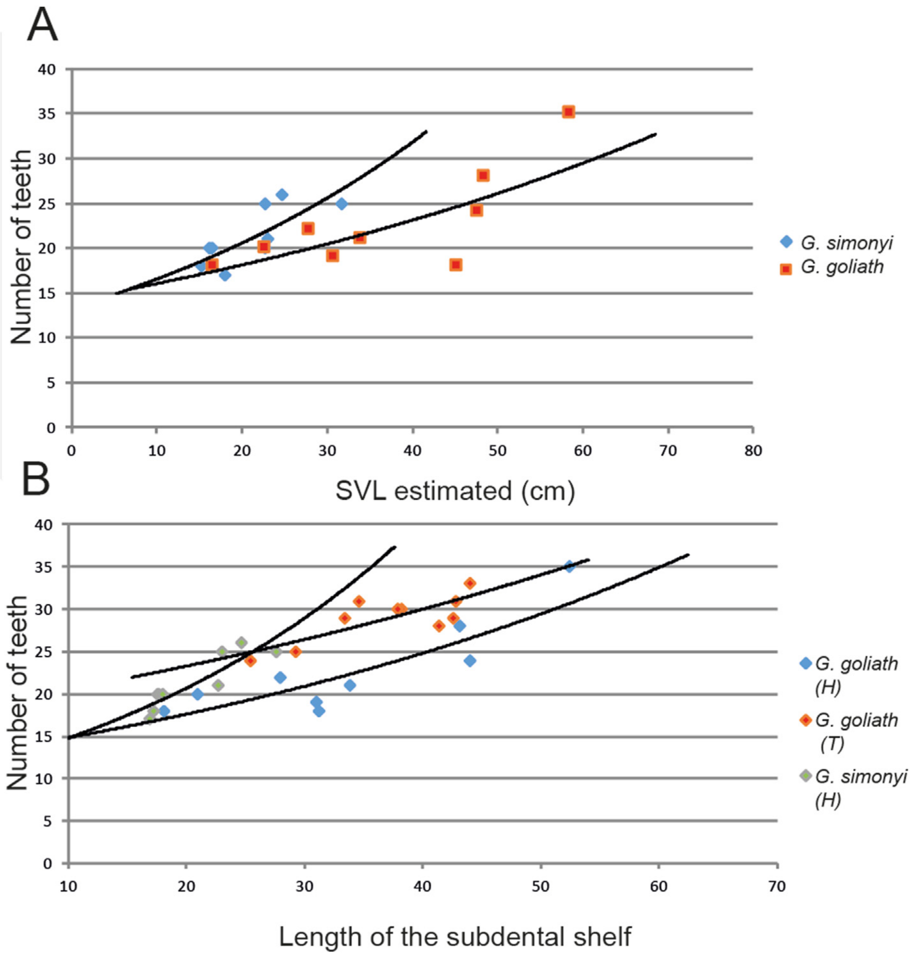

Fig. 3. A) Relationship between the number of teeth (Y axis) and the estimated snout-vent length (X axis) of the remains of *Gallotia goliath* and *Gallotia simonyi* from El Hierro. B) Relationship between the number of teeth (Y axis) and the length of the subdental shelf (X axis) of the remains of *Gallotia goliath* from El Hierro and Tenerife and *Gallotia simonyi* from El Hierro.

posteroventral process is also present. This process is triangular and more robust and strongly posteriorly directed in adults (Fig. 4K-L).

The postorbitofrontal is a paired bone with a rectangular shape; it has a concave dorsal surface that derives from the fusion of the postfrontal and postorbital. In its anterior region the anterolateral and anteromedial processes can be distinguished. The two processes define the posterior margin of the ocular orbit. The anteromedial and anterolateral processes of the postorbitofrontal are of the same size in juveniles, whereas in adults the anteromedial process is significantly longer than the anterolateral process (Fig. 4I and J).

The dorsal surface of the parietal is completely covered by ornamented osteodermal shields that are fused to it in individuals with an SVL greater than 420 mm (Fig. 4M–N). In addition, the parietal foramen is open in both young and adult individuals, differing in its arrangement. In juveniles the parietal foramen is dorsoventrally straight whereas in adults it is inclined anteroposteriorly.

In posterolateral view the quadrate shows a rectangular shape in the juvenile stages, with the length greater than its the width, becoming squarer in the adult stages, where length and width are more similar (Fig. 4C and D).

The pterygoid shows differences in the transverse process, which curves smoothly lateromedially in juveniles, whereas in adults it has an angle of almost 90° lateromedially (Fig. 4G and H). The pterygoid teeth are distributed in one row in juvenile individuals with an SVL less than 250 mm and in two rows in adult.

The posterodorsal and posteroventral processes of the dentary vary in relative length. The posterodorsal process is slightly longer than the posteroventral process in juvenile specimens, whereas in adult individuals the two processes are of a more similar length. In addition, the labial foramina decrease in number (from seven in juveniles to five in adults) and size (Fig. 4O–P).

The splenial is a long, flat and triangular bone that covers the Meckelian canal. In juvenile individuals this bone has a foramen that narrows with growth (Fig. 4Q–R).

4.3. *Taphonomic characteristics*

The individuals analysed proceed from the temporary condensation deposit (Seilacher et al., 1985) and their remains are partially articulated (number of articulate bones vs number of bones gathered for each individual; Table 5). Individual PCCRULL1190 has the greatest percentage articulated (26.53%) and a low percentage of fragmentation. An exception is individual PCCRULL191, which has a high percentage of fragmentation (28.3%) due to its large number of fragmented vertebrae, although it also has a certain degree of articulation in its jaw bones.

The results of the analysis of the preservation grade of the maxilla surface can be observed in Fig. 5. Five fossil individuals

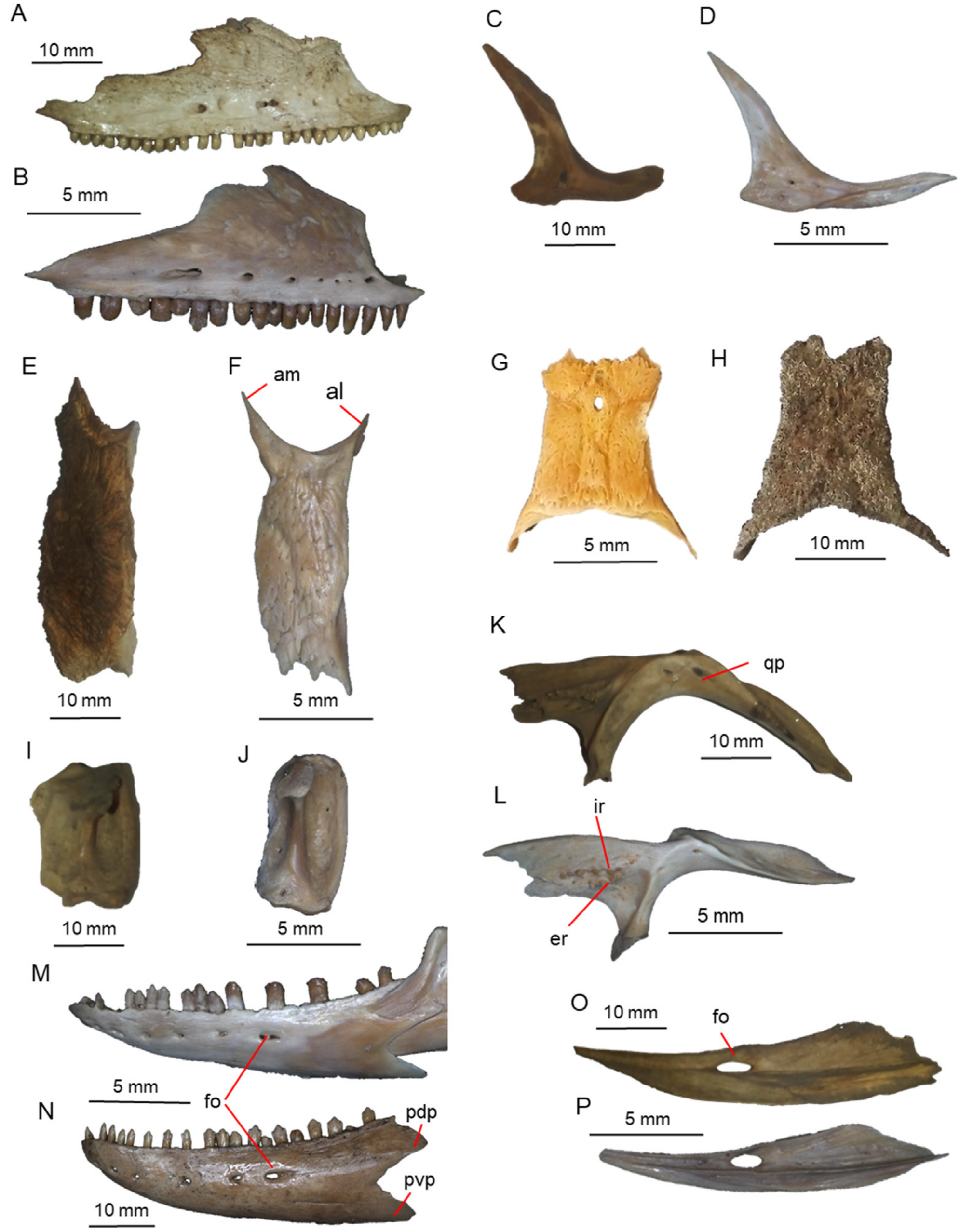

Fig. 4. Eight cranial bones with ontogenetic variation observed in *Gallotia goliath*.. right maxilla of an adult (A) and a juvenile (B) in lateral view; right jugal of an adult(C) and a juvenile (D) in medial view; left postorbitofrontal of an adult (E) and a juvenile (F) in lateral view; parietal of a juvenile (G) and an adult (H) in dorsal view; right quadrate of an adult (I) and a juvenile (J) in posterolateral view; right pterygoid of an adult (K) and a juvenile (L) in dorsal view; dentary of a juvenile (M) and an adult (N) in lateral view; splenial of an adult (O) and a juvenile (P) in lateral view. Abbreviations: am, anteromedial process; al, anterolateral process; er, external row; fo, foramen; ir, internal row; pdp, posterodorsal process; pvp, posteroventral process; qp; quadrate process.

Table 5
Percentage of fragmented and articulated bones * the high % corresponds to fragmented vertebrae.

INDIVIDUAL	PERCENTAGE OF FRAGMENTED BONES	PERCENTAGE OF ARTICULATED BONES
PCCRULL1186 *G. SIMONYI*	6.06	0
PCCRULL1189 *G. SIMONYI*	16.9	2.82
PCCRULL1190 *G. SIMONYI*	4.08	26.53
PCCRULL1191 *G. GOLIATH*	28.3*	3.33
PCCRULL1193 *G. GOLIATH*	0	0

were compared with an extant individual of *G. galloti* with white coloration of the surface of its bones and without visible sediment or striations, giving it a smooth and bright appearance (Fig. 5A and G). PCCRULL1186 and 1189 of *G. simonyi* (Fig. 5C and E) are reddish

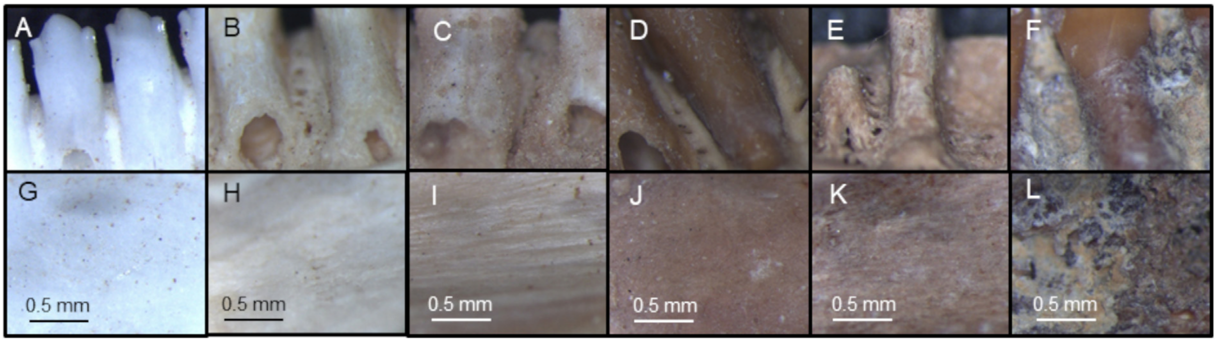

Fig. 5. Different degrees of preservation of the maxillary teeth and posterior process of the maxilla of different individuals from the Cueva del Curascán site. From left to right the sequence of images runs from less to more deposition time. extant *Gallotia galloti* for comparison (A and G); *Gallotia goliath* (PCCRULL1193) (B and H); *Gallotia simonyi* (PCCRULL1189) (C and I); *Gallotia goliath* (PCCRULL1191) (D and J); *Gallotia simonyi* (PCCRULL1186) (E and K); *Gallotia simonyi* (PCCRULL1190) (F and L).

in colour, with striations on the posterior process of the maxilla and an accumulation of very scarce sandy sediments that barely cover the cavities of the teeth. PCCRULL1191 of *G. goliath* (Fig. 5D) presents the same reddish colours, but without showing striations on its surface; its teeth are orange ochre instead. PCCRULL1193 of *G. goliath* (Fig. 5B) has a lighter bone colour, with a smooth surface and without adherent sediments (the cavities of the teeth can be seen to be without filling). Finally, PCCRULL1190 of *G. simonyi* (Fig. 5F) presents a large layer of hardened sediment all over its surface, which gives it brown, yellow and black colorations, with orange ochre teeth.

5. Discussion

In accordance with Arnold (1973) the remains studied can be ascribed to *Gallotia* genus due to a robust skull; undepressed skull with a thick osteodermal layer; the ossification of the temporal scales presents in *G. atlantica* and *G. simonyi*, which is much reduced or absent in *G. galloti* and *G. stehlini*; postorbital and postfrontal bones that are fused throughout life; and the presence of pterygoid teeth. Other characters observed in the *Gallotia* genus are that both processes of the jugal are long, narrow and sharp, as in most species of lacertids in lateral view (Villa and Delfino, 2019) and that the palatine process of the pterygoid presents teeth its ventral surface, as in several species of lacertids (Villa and Delfino, 2019). With respect to Hutterer (1985) and the comparison with holotype and paratype remains of *G. goliath* and *G. simonyi* (see Material and Methods), 14 individuals out of the 24 *Gallotia* specimens showed characteristics of *G. goliath* and ten of *G. simonyi* (Table 1). As a result of our osteological analysis of *G. simonyi* remains from El Hierro, we found that the diagnostic character of Hutterer (1985) relating to the distribution of the pterygoid teeth in only one row is only valid when the SVL is no greater than 210 mm; otherwise, some teeth are incorporated in a second V-shaped row, as in *G. goliath* (Mateo et al., 1999). In addition, we observed new differences between the *G. goliath* and *G. simonyi* remains from El Hierro, which could further support the specific distinction. These new possible diagnostic characters are: a) that the arrangement of the parietal shields is rectangular in *G. goliath* unlike the “hourglass” shape in *G. simonyi* (Fig. 2B and C); b) the morphology of the quadrate is rectangular in *G. goliath*, unlike the trapezoidal shape in *G. simonyi* (Fig. 2 D-E; and c) the tibia foramen is present in *G. goliath*, whereas it is absent in *G. simonyi* (Fig. 2I and J). Moreover, according to Mateo et al. (1999), the SVL of the specimens is another character that differentiates *G. goliath* from *G. simonyi* as the former reach estimated sizes greater than 430 mm.

In addition to the characters described by Barahona and Barbadillo (1998) and Barahona et al. (2000) we have identified other ontogenetic changes: the angle between the jugal processes (measured between the postorbital and suborbital processes), the development of the anterolateral and anteromedial processes of the postorbitofrontal, the ornamentation of the dorsal surface of the parietal, the shape of the quadrate, the curvature of the transverse process of the pterygoid, the development of the posterodorsal and posteroventral processes of the dentary, and the presence of a narrow foramen in the splenial. Some of the osteological characters of *G. goliath* that vary with ontogeny, are similar to those observed by Barahona and Barbadillo (1998) in *G. galloti*, as is the case with the smooth lateral surface of the maxilla in juveniles of *G. goliath*. Others relate to the processes of the jugal being long, narrow and sharp in lateral view; or to the area of the parietal fossa in ventral view, the lateral and the posterior parietal crest being more developed in adult specimens, as is the case in most species of lacertids (Villa and Delfino, 2019).

During the accumulation of fossil remains in a volcanic tube (condensation deposit) their entry into the tube theoretically starts with the formation of the volcanic tube and continues until its collapse or until the present day if still standing, bearing the geological cycles (Howarth, 1973). Our assessment of the taphonomic state of the remains takes into account that in concentrations of vertebrates in cavities or caves, mineralization produces a change in colour (depending on the predominant minerals) and a greater amount of sediment adheres to the remains when the deposition time is longer (Behrensmeyer, 1978).

The taphonomic analysis showed PCCRULL1193 of *G. goliath* to be in the best state of preservation, and so it can be ascribed a more recent age (Fig. 5B). PCCRULL1186 and PCCRULL1189 of *G. simonyi* and PCCRULL1191 of *G. goliath* have a very similar coloration and surface of the bone that suggesting a longer period of deposition in the Cueva del Curascán. PCCRULL1190 of *G. simonyi* is in the worst state of preservation, indicating the longest time in the site.

These results confirm the presence of *G. goliath* on El Hierro and may indicate that the two species coexisted there in the past, confirming the proposal made by Izquierdo et al. (1989) and Rodriguez-Domínguez et al. (2000). On the other hand, researchers have studied the important role of lizard – plant mutualisms on oceanic islands. In such context, small lizards would be nectar consumers and pollinators whereas big lizards would act as seed dispersers (Valido, 1999; Olsen and Valido, 2003; Valido and Olsen, 2019). These are more common than in continental environments.

In the case of El Hierro during the upper Pleistocene-Holocene, the seed dispersal role would have been played by the lizards *G. goliath* and *G. simonyi*. The bones studied here indicate that these species were distributed according to altitude. *G. simonyi* was thus located in the low and midland areas, where the potential vegetation was "tabaibal-cardonal" (spurge-dominated; Cueva de El Lajial) or "sabinar" (juniper-dominated; Cueva del Curascan), whereas *G. goliath* was found in midland and high areas, where the potential vegetation was pinewood endemic to the island (del Arco Aguilar et al., 2017). This may indicate dietary specialization based on the predominant elements in each plant formation and therefore differentiation in the dispersive role.

6. Palaeobiogeography

El Hierro is the most recently formed island in the Canary Archipelago, with 1.12 million years of geological history (Troll and Carracedo, 2016, Fig. 6). The colonization of this island by a population of *G. goliath* from one of the older surrounding islands (La Palma, La Gomera or Tenerife) must have been very recent in geological time. There are two different hypotheses for what occurred: a) *G. goliath* arrived first at La Gomera and later colonized the island of El Hierro (Cox et al., 2010); or b) *G. goliath* arrived directly from Tenerife at El Hierro, without first passing through La Gomera. As regards the first hypothesis, remains of *G. goliath* have not yet been found in La Gomera, but this absence does not rule out the possibility that they may be discovered in the future (Fig. 6). The second hypothesis involves a direct route from Tenerife, where there are recorded fossil remains of *G. goliath* (from the early Pleistocene; see Cruzado-Caballero et al., 2019) that are older than the fossil record from El Hierro (Chibanian/upper Pleistocene-Meghalayan). In both cases, the most probable manner of colonization is transport by floating rafts (Brown et al., 2006; García-Olivares et al., 2017). These rafts would have been transported from one island to another by the waves generated after a mega-landslides from Tenerife (Fig. 6). Following the mega-landslide, the entry of slipped island blocks into the ocean surrounding the island would have caused a tsunami and a subsequent wave train. The propagation of these waves could have been influenced by the cold current of the Canary Islands, which is estimated to have remained relatively unchanged over the last 22 Ma (Løvholt et al., 2008; Giachetti et al., 2011). This current descends from the north and revolves around the archipelago. The mega-landslide(s) that gave rise to colonization must have happened less than a million

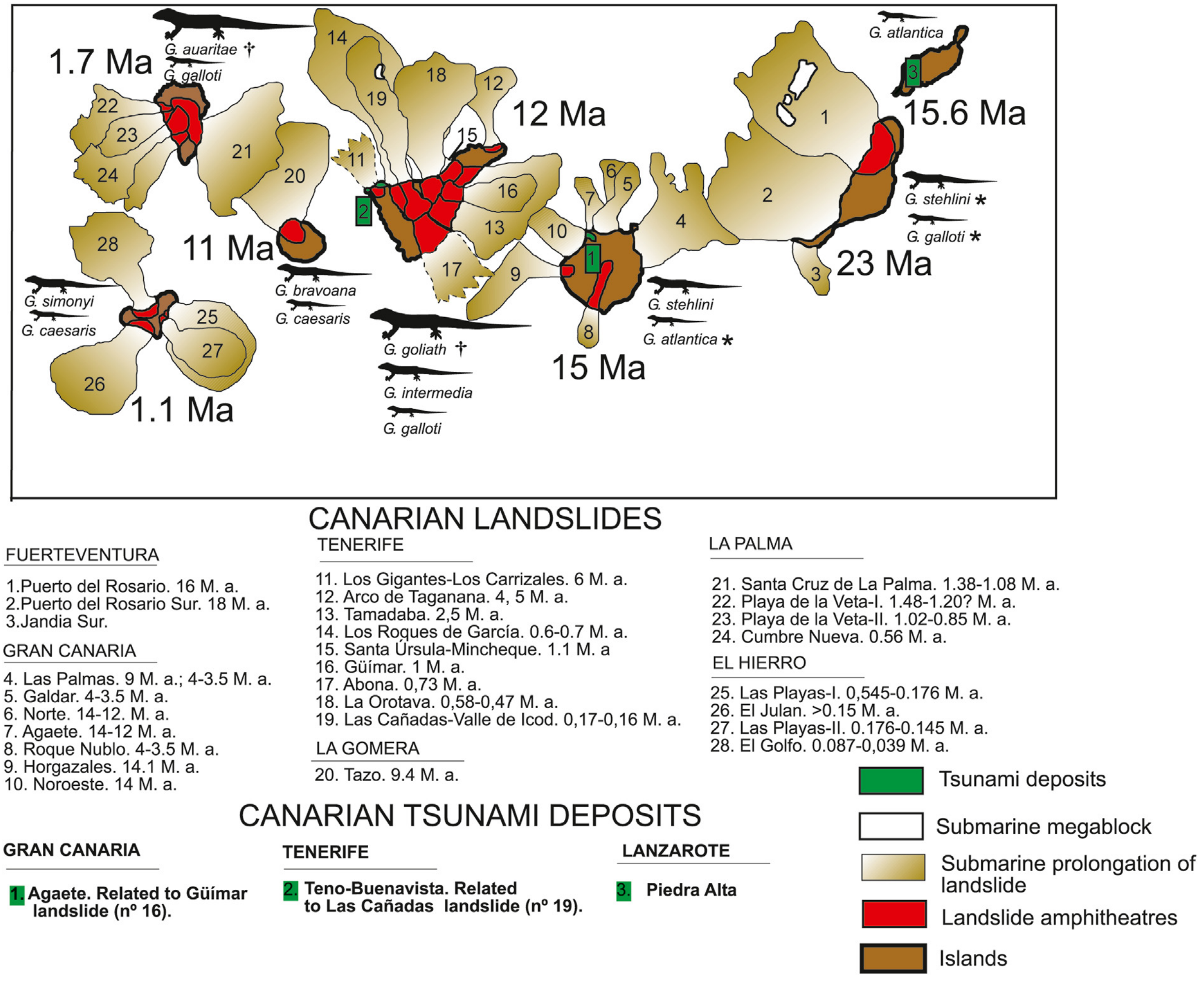

Fig. 6. Distribution and age of the Canary Island landslides during the Neogene and Quaternary thought likely to have been part of the colonization events of the different islands. The landslides numbered 14 to the 19 are those thought most likely to have been the source of the migration event that led *G. goliath* to colonize El Hierro. Asterisk, introduced species. Cross, extinct species. The position of the amphitheatres formed by the mega-landslides, according to island data, come from the following reference sources: El Hierro (Carracedo et al., 1999), La Palma (Ancochea et al., 1994; Carracedo et al., 1999b; Colmenero et al., 2012), La Gomera (Casillas et al., 2010), Tenerife (Watts and Masson, 1995; Cantagrel et al., 1999; Walter and Schmincke, 2002; Seisdedos et al., 2012; Coello et al., 2020), Gran Canaria (García Cacho et al., 1994; Mehl and Schmincke, 1999) and Fuerteventura (Ancochea et al., 1993, 1996; Stillman, 1999; Acosta et al., 2003; Casillas et al., 2012). Most deposits generated by these lateral movements are found accumulated in the adjacent seabed (Acosta et al., 2003; Canales et al., 2000; Masson et al., 2002; Urgeles et al., 1998, 1999). The layout of the tsunami deposits associated with some of the landslides is also shown (Pérez Torrado et al., 2002; Pérez Torrado et al., 2006; Meco et al., 2008; Giachetti et al., 2011; Madeira et al., 2011; Ferrer et al., 2011).

years ago (since the emersion of the island of El Hierro; Troll and Carracedo, 2016). These landslides in question, which could have transported a large amount of material along with the lizards, could be those of Roques de García (occurring between 0.6 and 0.7 Ma), Santa Úrsula-Micheque (about 1.1 Ma), Güimar (1 Ma), Abona (about 0.73 Ma), La Orotava (between 0.58 and 0.47 Ma) or Las Cañadas-Valle de Icod (between 0.16 and 0.17 Ma), all of which transported a volume over 100 km^3 of materials and occurred after the formation of El Hierro (Fig. 6).

7. Conclusion

From a morphological point of view, the studied fossil remains from El Hierro confirm the presence of *G. goliath* in addition to *G. simonyi* throughout the north and southeast sector of the island. As well as new diagnostic characters that differentiate to *G. goliath* from *G. simonyi*, new ontogenetic characters of *G. goliath* have also been established. These data broadens our understanding of these species and of the ontogenetic development of the giant lizard *G. goliath* and will help prevent errors of identification of juvenile *G. goliath*. Moreover, it has been observed that the maximum SVL of the studied individuals of *G. goliath* surpasses the size of the specimens from Tenerife (585 mm compared to 546.4 mm). The same occurs with the fossil individuals of *G. simonyi*, which exceed the size of extant specimens (316.3 mm compared to 236 mm), confirming a decrease in size probably due to a decrease in survival rate.

The presence of *G. goliath* on El Hierro in the last 145,000–126,000 years confirms the existence of two giant lizards on the same island during the Pleistocene-Holocene. The taphonomic signal suggests the possibility that the two giant species coexisted both in time and space.

From a palaeobiogeographical point of view, the presence of *G. goliath* on the island of El Hierro highlights the role that older Neogene islands played in the colonization of more recent islands that emerged during the Quaternary. It also suggests that geological events such as mega-slides influenced in island colonization events involving both invertebrates and vertebrates.

The different ecological roles of *G. goliath* and *G. simonyi* as megaherbivores are associated with their different sizes and morphological characters. It is very important to analyse the palaeo-biological changes in extinct and extant species to help in the conservation of the giant lizard species of the Canary Islands (*G. intermedia, G. bravoana* and *G. simonyi* being critically endangered according to the IUCN; *G. stehlini* being of least concern), particularly in the light of their potential role in maintaining the seed dispersal ecosystem service.

Author contribution

Sergio Palacios-García (S.P.-G.) designed the research plan. S.P.-G., Carolina Castillo Ruiz (C.C.R.), Penélope Cruzado-Caballero (P.C–C) and Ramón Casillas (R.C.) wrote the paper. S.P.-G. performed the comparative and prepared figures and tables. All authors performed the analytical work and prepared figures and discussed and commented on the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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