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New subfossil bones of a Réunion Giant Tortoise, *Cylindraspis indica* (Schneider, 1783), from a lava tunnel under a mid-elevation windward rainforest on Réunion Island

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Abstract. We report the discovery of subfossil remains of a juvenile Réunion Giant Tortoise, *Cylindraspis indica*, in a lava tunnel beneath remnant mid-elevation native tropical rainforest on Réunion Island. Located at an elevation of 726 m in the Plaine des Grègues managed forest, this find is the highest fossil record of the species on the island. For the first time, these remains provide paleontological confirmation of historical accounts from the 17th–18th century reporting tortoises in upland areas. These specimens also highlight the potential of submontane and montane lava tubes as paleontological archives. Radiocarbon dating yielded an age of 665 ± 30 BP with 95.4% probability, corresponding to AD 1296–1399 and indicating that the specimen predates permanent human settlement (ca. 1665) by approximately three centuries. Although palynological analyses were unsuccessful, flora inventories revealed a diverse assemblage of native fleshy-fruited trees, suggesting that *C. indica* may have played a crucial role as megafaunal seed disperser. Beyond its paleontological significance, this discovery thus lends legitimacy to rewilding experiments involving functional analogues of extinct tortoises.

Keywords. Réunion Island, *Cylindraspis indica*, subfossil, palaeontology, extinct tortoise, ecological restoration.

Introduction

The extinct giant tortoises of the Mascarene Islands, genus *Cylindraspis*, are an ancient lineage estimated to have diverged at the end of the Eocene and is phylogenetically distant from other southwestern Indian Ocean tortoises, such as *Aldabrachelys*, *Astrochelys*, and *Pyxis* (Kehlmaier et al., 2023). Little is known about the biology or ecology of the five *Cylindraspis* species, and the last surviving populations possibly went extinct in the 19th century on Round Island, an islet off Mauritius, and in a montane refuge at Cilaos on Réunion Island during the 1840s (Bour, 1981; Cheke and Hume, 2008; Cheke and Bour, 2014). In this context, paleontology can provide key insights into their past distribution and behavior, as recently revealed on Rodrigues Island with the discovery of the first *Cylindraspis* nesting site in the Mascarenes (Hume et al., 2021).

Compared with Mauritius and Rodrigues, paleofauna study sites on Réunion remain limited (Hume, 2013), primarily due to the island's geomorphology, which offers few depositional environments suitable for fossil preservation (Hume, 2005). Until recently, all sites containing *Cylindraspis* subfossil bones were concentrated in a small area in the driest part of the west slope of the island (Fig. 1). The first subfossil discovery was made by Louis Maillard at Cap Lahoussaye in 1854 (Maillard, 1862). It was more than a century before Émile Hugot found additional bones in sediments at

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Étang de Saint-Paul, but this find went unnoticed. Interest was rekindled in the 1970s with the discoveries in Grotte Vergoz (La Saline les Hauts) and Grotte des Premiers Français (Saint-Paul), followed in the 1980s by systematic excavations at these sites led by Harry Gruchet, curator of the Muséum d'Histoire Naturelle de La Réunion (MHNRE). The discovery of well-preserved remains in the Marais de l'Hermitage in 1989 (Fig. 1) prompted extensive excavations in the 1990s led by Sonia Ribes, Cécile Mourer-Chauviré, Roger Bour, and others, culminating in the recovery of thousands of bones of tortoises and other extinct fauna (Mourer-Chauviré and Moutou, 1987; Mourer-Chauviré et al., 1994, 1995a, b, 1999, 2006), which made this Réunion Island site equivalent to the Mare aux Songes on Mauritius (Bour et al., 2014). More recently, remains were found by chance in Petite-Île's coastal cliffs (Sanchez and Bour, 2014) and during a 2023 preventive archaeological dig in Saint-Pierre at sea level (Hélène Silhouette, pers. comm., 2023; Fig. 1).

Despite these discoveries, a gap remains between the paleontological record and historical observations. All fossil sites are located at elevations < 300 m, yet numerous historical accounts and local place names suggest the presence of tortoises at higher altitudes. François Martin (1634–1706), initially a clerk of the French Indies Company and later the first governor of Pondicherry, reported in the 1660s (cited in Lougnon, 2006) that

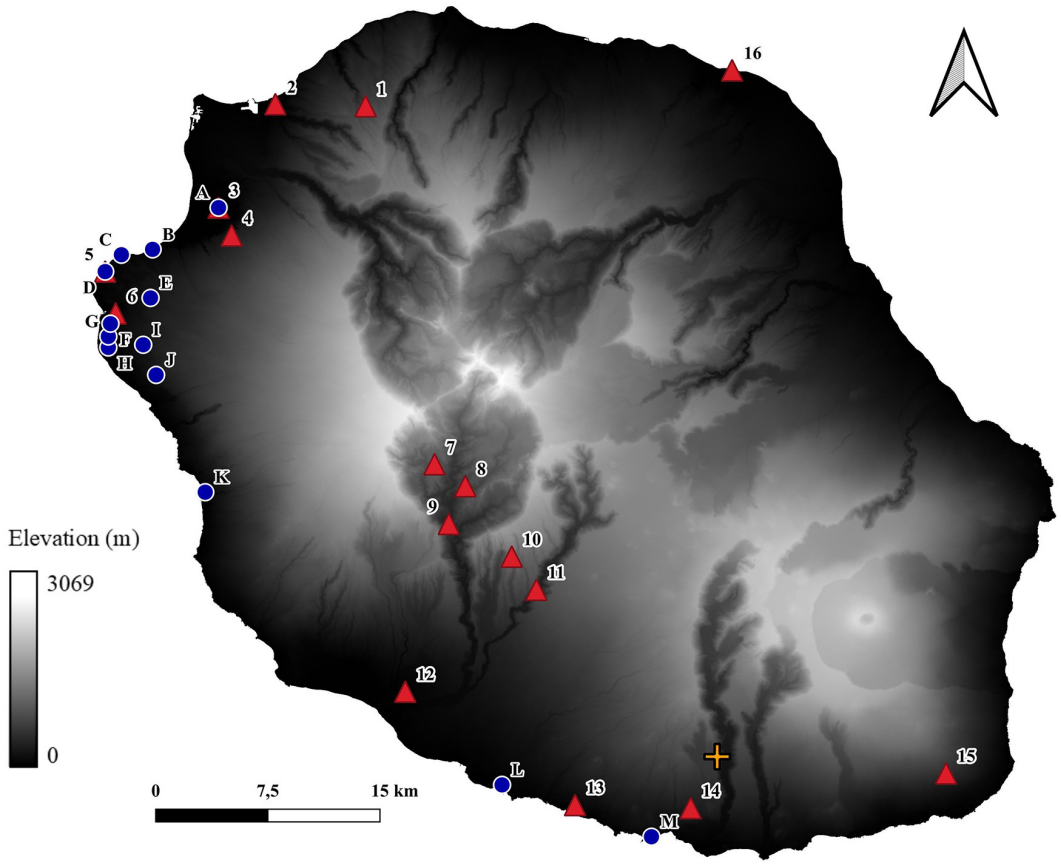

Figure 1. Localization of paleontological sites for *Cylindraspis indica* (blue dots with letters), and historical accounts or place names referring to *C. indica* (red triangles with numbers) on Réunion Island. The yellow cross marks the location of the newly discovered deposit at Plaine des Grègues. Sites are identified by the following numbers and letters: La Montagne massif (1); La Possession (2); Étang de Saint-Paul (3); Mountain above Saint-Paul (4); Anse du Canot (5); Carosse (6); Ilet à Cordes (7); Cilaos (8); Parc à Tortues (9); Dimitile (10); Bras de la Plaine (11); Saint-Louis (12); Pointe des Grand-Bois (13); Ravine Carosse (14); Mare d'Arzule (15); East coast (16); Étang de Saint-Paul (A); Grotte des Premiers Français (B); Cap La Houssaye (C); Boucan Canot (D); Céline Cave (E); Sable Cave (F); L'Autel Cave (G); Marais de l'Hermitage (H); Caverne de la Tortue (I); Vergoz Cave (J); La Surprise Cave (K); Saint-Pierre city centre (L); Cliffs of Petite-Ile (M). Full details, including dates and references, are listed in Appendix 1.

"There are many tortoises, and what is surprising, is that one can find these tortoises on mountains where men can only get to with much effort and great risk." Similarly, the French explorer George Luillier de la Gaudière (1674–1734) was cited by Lougnon (2006) as stating in 1703 that "These tortoises are found at the top of a mountain, which is almost entirely covered by them," and in another quote in Lougnon (2006), "Sieur Durot" (personal data unknown) mentioned hunting tortoises "which are abundant in the mountains." The last surviving tortoises on Réunion were from Cilaos and occurred at an elevation of up to 1214 m (Bour, 1981; Cheke and Bour, 2014). These observations indicate that *Cylindraspis* likely used habitats that were never previously represented in the fossil record. In this regard, it is noteworthy that on Mauritius, tortoise bones have also been found at an elevation of 480 m (Florens, 2002), suggesting that the use of montane habitats may have been more widespread across the Mascarenes than currently reflected by the fossil record.

Here, we report for the first time in the Mascarenes the recent discovery of subfossil bones of *Cylindraspis* in a submontane context (elevation 726 m), in the Plaine des Grègues Protected Area (PDG) in the south of Réunion (Fig. 1). We primarily present excavation details, a description of the subfossil bones attributed to *C. indica*, and radiocarbon dating results. We also present the current environmental conditions and forest composition, which allows us to discuss the taphonomic and ecological implications of this discovery.

Materials and Methods

Study area. In 2022, Arnaud Rhumeur, Kalyan Leclerc, and Étienne Prolhac explored three cavities in PDG, a 6-ha protected area owned by the Réunion Island Department since the early 2000s (Fig. 2). Exploration showed these cavities to be collapsed ceiling sections of lava tubes. In one of the tubes, subfossil bones were found partially exposed at the foot of a pile of collapsed boulders, prompting the initiation of systematic excavations.

The area where excavations were conducted comprises several fragments of native tropical rainforest embedded within an agricultural matrix, including small patches of secondary vegetation and agroforestry plots. It is bordered to the east by the Rivière des Remparts canyon, which supports drier, more open vegetation types and creates a sharp environmental gradient. Mean annual rainfall at PDG is estimated at 2000–2200 mm, based on data from the Les Lianes Meteorological Station (elevation 570 m).

In this heterogeneous landscape, the lava tunnel containing the tortoise bones is in the northernmost forest block at an elevation of 726 m, near the edge of the Rivière des Remparts canyon. The tunnel was formed from basaltic flows originating at Morne Langevin, a volcanic peak derived from the Piton de la Fournaise shield volcano and dated to 65–150 ka (Merle et al., 2010; Smietana, 2011). The lava tube measures 22.5 m in length, 2.1–9.3 m in width, and 1–4 m in height and covers an area of 95.5 m². It is filled with shallow, waterlogged sediment.

Excavation details. In 2024, an excavation was undertaken by a team from the Institut National de Recherches Archéologiques Préventives (INRAP) in collaboration with the Initiative pour la Restauration Écologique en Milieu Insulaire (IRI) and the MHNRE. The lava tunnel was mapped (scale 1:100) using a Leica Viva TS11 surveyor device. Large basalt blocks were cleared, but due to wet sediment from recent rains excavation was limited. Samples were extracted and moved off-site for processing. Subfossil bones were carefully collected with a trowel and brush, and their positions were recorded using a digital tablet camera (Fig. 3). The subfossils and sediments were stored in five labelled sample bags (P1–P5) and sent to MHNRE. The sediment was sieved with a 5-mm mesh, and all bones were cleaned, labelled, and photographed.

Bone analysis. A preliminary inspection conducted by INRAP assessed the archaeological potential of the site. Photographs of the bones were sent to Julian P. Hume for identification and palaeontological analysis. For radiocarbon dating, bone analyses were carried out using accelerator mass spectrometry. Bone samples were sent to the RadioCarbon Dating Centre at the University of Lyon 1 (Lyon, France) for preparation, then sent in gas form to the Centre for Isotope Research at the University of Groningen (GrM; Groningen, The Netherlands), where they were transformed into graphite and measured. A second bone sample was also sent to the Museum für Tierkunde (Dresden, Germany) for ancient DNA extraction and sequencing as part of an ongoing research project (specimens MHNRé-2024.E.3.13, MHNRé-2024.E.3.20).

Present and past forest composition. Floristic inventories conducted by IRI documented the current vegetation above the lava tube. To explore the past composition of the forest, a sediment sample beneath the subfossil remains was sent to the Institut des Sciences de l'Évolution de Montpellier (ISEM) for pollen extraction.

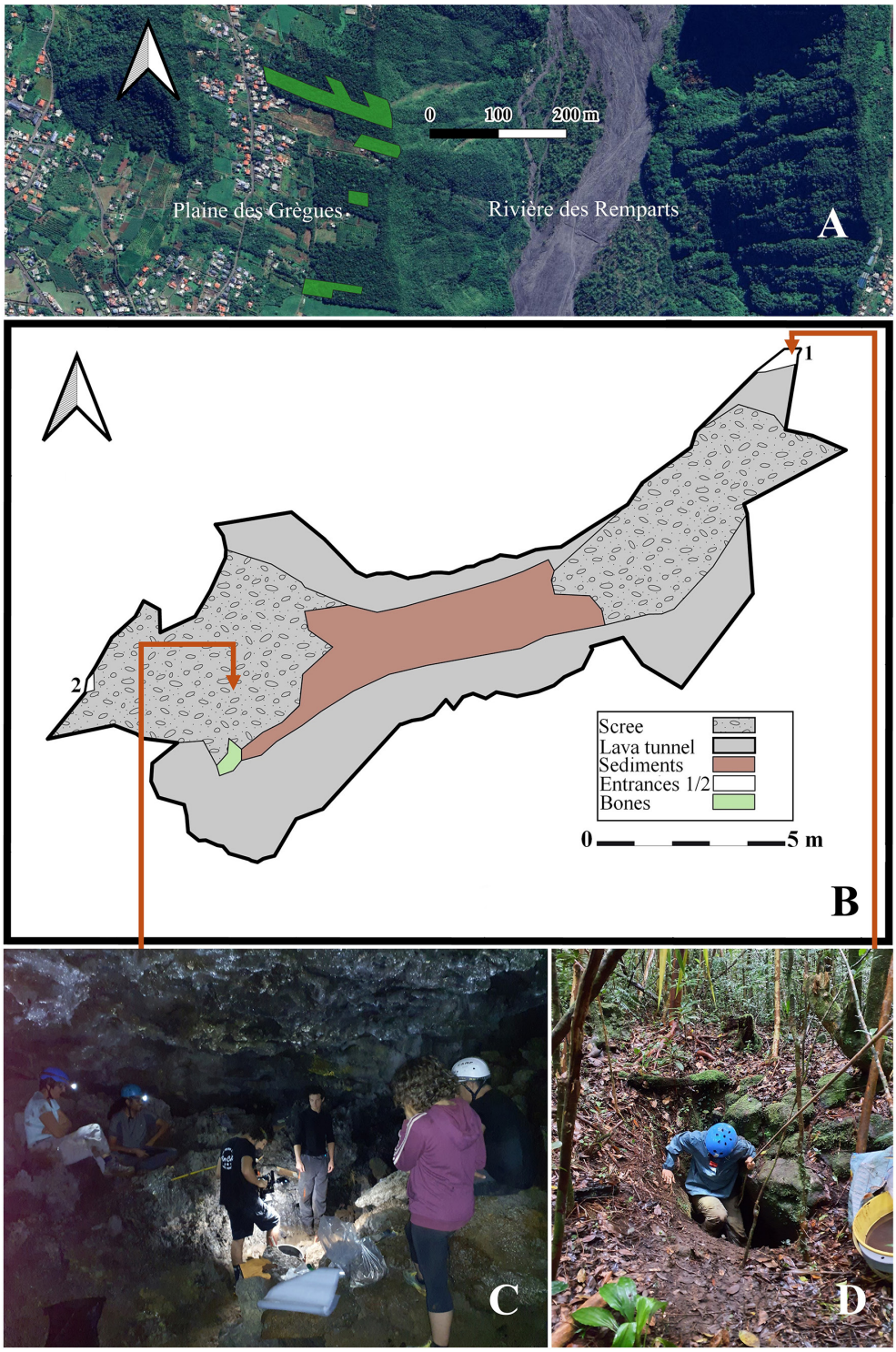

Figure 2. Study area and lava tunnel. (A) Map of the Plaine des Grègues plateau in Saint-Joseph Municipality. The green polygons correspond to the boundaries of the protected areas. (B) Map of the lava tunnel (scale 1:100). (C) Interior view of the lava tunnel. The image was taken at the position indicated by the red arrow in (B). (D) One of the lava tunnel entrances. Map surveyed by N. Parizeau-Philion on 14 December 2024.

Figure 3. Discovery and excavation of the *Cylindraspis indica* bone deposit in the Plaine des Grègues lava tunnel. (A) Bone deposit at the time of discovery. Note the scapulocoracoid (arrow), which is also depicted in Fig. 4A. (B) Further excavation revealed the proximal humerus (arrow), as seen in Fig. 4A. (C) Exposure of the plastron with associated femur (arrow), fibula and tibia, reproduced in Fig. 4C. (D) Remains of the plastron with pelvic fragments (arrow), reproduced in Fig. 4B.

Results

Sediment and associated remains. The bone-bearing layer was composed of light brown silty clay mixed with collapsed wall fragments, with root penetration, signs of invertebrate and rodent activity, and recent seed input. Subfossil shells belonging to the endemic land snail *Plegma caelatura* and the introduced Spike Awlsnail (*Allopeas clavulinum*) were found atop the sediment layer with recent seeds of two endemic trees, the evergreen *Labourdonnaisia calophylloides* and the hardwood *Mimusops balata* (Aubl.) C.F. Gaertn., 1807.

Bone analysis. A preliminary inspection conducted by INRAP in the lava tube found no archaeological artefacts. The excavation revealed several clustered bone layers in an area measuring 33 × 20 cm, within a layer approximately 3 cm thick. All subfossil bones appeared associated and belonged to a single juvenile *C. indica* (Fig. 4). The first bones found on top of the sedimentary layer consisted of a scapulocoracoid, part of the anterior plastron, part of the pelvis, a possible femur, and carapace fragments. The excavation revealed anatomical associations among certain bones (femur, tibia, fibula, and phalanges). Apart from a few fragments, the remaining carapace was not found, and only the lower limbs, pelvis, and part of the plastron were sufficiently well preserved to be collected. Only a single femur (length 13 cm) was complete. The apparent absence of human influence on the skeleton, both before and after death, precluded its being of archaeological origin. Radiocarbon analysis of bone collagen yielded an age of 665 ± 30 years (specimen Lyon-21323 [GrM]), with a measured ^{14}C activity of 92.08 ± 0.17 percent modern carbon. Calibration produced a date range of 1296–1399 with 95.4% probability. These results confirm that this turtle lived several centuries prior to the human settlement of Réunion (ca. 1665), thereby supporting

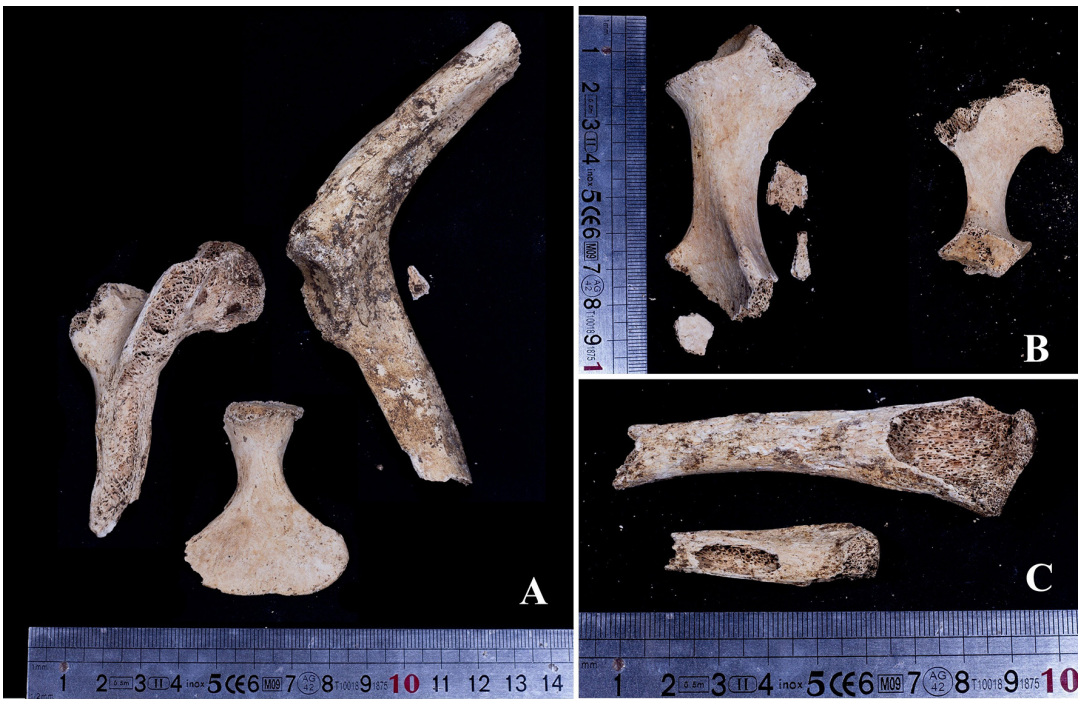

Figure 4. Selected subfossil bones of the Réunion Giant Tortoise *Cylindraspis indica* from Plaine des Grègues. Images show the best-preserved specimens. (A) Two sections of the scapulocoracoid (top), and associated proximal humerus (below), MHNRé-2024.E.3.5 and MHNRé-2024.E.3.7.5. (B) Pelvic fragments, MHNRé-2024.E.3.7 (left) and MHNRé-2024.E.3.10 (right). (C) Tibia (top) with partial fibula (bottom), MHNRé-2024.E.3.14. Photos by G. Salvan.

the palaeontological nature of the deposit. This means that the tortoise entered the cave on its own or its body fell into the tunnel accidentally. No genetic results are reported here, as these analyses are being conducted independently and are not part of the present study.

Present and past forest composition. Palynological analysis did not yield sufficient well-preserved pollen to reconstruct past vegetation. However, current vegetation is classified as mid-elevation tropical rainforest, a biome of which only around 14% of its original area remains on Réunion (Strasberg et al., 2005). The canopy includes native trees reaching heights of 25–30 m. The PDG site lies at the intersection of environmental gradients, enabling coexistence of lowland and montane flora from both wet and dry zones. Species richness reached 50 woody species per 1000 m^2, with 88% of these producing fleshy fruits, including many with large fruits (> 1.2 cm) from diverse families such as Apocynaceae (dogbanes), Calophyllaceae (NCN), Ebenaceae (ebony), Myrtaceae (myrtles), Moraceae (mulberries and figs), Oleaceae (olives), Putranjivaceae (NCN), Salicaceae (willows), and Sapotaceae (sapodillas).

Discussion

The 726 m elevation is unprecedented for *Cylindraspis* remains on Réunion, since all other known deposits are located at elevations < 300 m. This discovery provides, for the first time, consistent palaeontological evidence supporting the historical accounts by Martin, Luillier, and Durot that mention the presence of tortoises in upland areas between 1665 and 1705 (see quotes above; Lougnon, 2006) and one by Jean-Jacques de Melet, who in 1671 suggested possible seasonal migrations (cited by Sauvaget, 1998). Similarly, some *Cylindraspis* bones have also been discovered at an elevation of 480 m in Mauritius (Florens, 2002), although most deposits are found at elevations < 50 m.

Historical accounts mention tortoise presence in the south of Réunion, including in the vicinity of Saint-Philippe, as reported by Samuel Castleton of the English East India Company, captain of *The Pearl* (cited in by Lougnon, 2006) and by Bory de Saint-Vincent (1804). Tortoises have also left their mark on the local toponyms of a neighbourhood near the PDG

called Carosse, referring to the tortoise's morphology (Turpin and Probst, 1998). Indeed, some individuals had saddleback shells resembling a carriage (*carrosse* in French), while others had domed shells; but, unlike on Mauritius and Rodrigues, the two forms on Réunion did not represent distinct species (Bour et al., 2014).

The taphonomic conditions observed in the PDG lava tunnel correspond to those described for other caves in the Mascarene Islands, where extremely humid environments, alkaline basaltic sediments, and episodic hydrological activity rapidly degrade bone material (Hume, 2005). In such contexts, chemical alteration and intense bioerosion can destroy skeletal elements within relatively short timescales, as evidenced by the poor preservation of even very recent remains in the lava tunnels of Réunion. The partial nature of the recovered skeleton, as well as the absence of bones from other small vertebrates, likely reflect these destructive processes. In this light, the survival of a 665-years-old juvenile *Cylindraspis* skeleton is remarkable, given that juvenile bones are especially vulnerable to degradation in such humid volcanic environments. Nevertheless, the preservation of identifiable material in this unusually wet context suggests that other submontane or montane lava tunnels on Réunion may still contain overlooked deposits, offering promising prospects for future discoveries.

The presence of a remnant of native forest on the site reinforces the significance of our findings. Indeed, all traces of original vegetation have now disappeared from most other excavation sites on the west coast of Réunion (Bour, 1981; Bour et al., 2014). Despite the lack of palynological data, the diversity of forest structure and the presence of large native trees suggest long-term persistence at the study site, consistent with accounts by pioneers who noted the presence of forests throughout the island (Cheke and Hume, 2008). Furthermore, in the absence of volcanic activity at PDG over the last 700 years (Merle et al., 2010), vegetation has probably changed little, aside from possible anthropogenic fires.

Giant tortoises were the dominant endemic herbivores on small western Indian Ocean islands (Hansen and Galetti, 2009). While the last surviving giant tortoise species in the Indian Ocean, *Aldabrachelys gigantea* (Schweigger, 1812) from Aldabra Atoll, is mostly a grazer in open environments (Gerlach, 2014), *Cylindraspis* occupied a broader range of habitats, including montane regions as well as the numerous offshore islets, and had a more diverse diet (Burleigh and Arnold, 1986; Cheke and Hume, 2008; Van Der Sluis et al., 2014). The tortoises predominantly fed on C_3 plants, which would have included abundant deciduous and evergreen trees and shrubs. In addition, the osteological material recovered from the present site offers promising opportunities for future stable isotope analyses that could further refine our understanding of the diet and habitat use of *C. indica* in upland environments. Recent studies have also shown the impact of the loss of frugivores on the recruitment of native fleshy-fruited plants, emphasizing the presumed past ecological role for *Cylindraspis* in seed dispersal on Réunion (Albert et al., 2020) and also on Mauritius (Albert et al., 2021). Tortoises may therefore have played a crucial role in the past in the PDG forest, which still retains a high proportion of tree species with large fleshy fruits.

Although extinction is irreversible, ecological replacements may help restore lost interactions of tortoises and perhaps contribute to the preservation of the remaining indigenous flora (Hansen et al., 2010; Griffiths, 2014). Part of the PDG protected area could serve as a pilot site on Réunion for such rewilding experiments with introduced tortoises, which could serve as potential ecological substitutes and offer educational value to local communities.

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Appendix 1. Paleontological sites and historical records of *Cylindraspis indica* on Réunion Island. In the Year column, we list the year of discovery or, if it was reported in a secondary source, the year with the discoverer. The tortoise remains found in 2023 were recovered during a preventive excavation led by Hélène Silhouette (INRAP; report in preparation).

ID	Location	Year	Source	Comments
A	Étang de Saint-Paul	1960	Bour et al., 2014	Paleontological site
B	Grotte des Premiers Français	1974	Bour et al., 2014	Paleontological site
C	Cap La Houssaye	1854	Bour et al., 2014	Paleontological site
D	Boucan Canot	1990	Bour et al., 2014	Paleontological site
E	Céline Cave	1994	Bour et al., 2014	Paleontological site
F	Sable Cave	1980	Bour et al., 2014	Paleontological site
G	L'Autel Cave	1980	Bour et al., 2014	Paleontological site
H	Ermitage Marsh	1991	Bour et al., 2014	Paleontological site
I	Caverne de la Tortue	1994	Bour et al., 2014	Paleontological site
J	Vergoz Cave	1974	Bour et al., 2014	Paleontological site
K	La Surprise Cave	1980	Bour et al., 2014	Paleontological site
L	Saint-Pierre city centre	2023	Hélène Silhouette, 2023	Paleontological site
M	Cliffs of Petite-Île	2014	Sanchez and Bour, 2014	Paleontological site
1	La Montagne massif	Vinson, 1868	Lougnon, 2006	Historical account
2	La Possession	Houssaye, 1689	Bour, 1981	Historical account
3	Étang de Saint-Paul	Carpeau du Saussay, 1666	Bour, 1981	Historical account
4	Mountain above Saint-Paul	Luillier, 1703	Lougnon, 2006	Historical account
5	Anse du Canot	Houssaye, 1689	Bour, 1981	Historical account
6	Carosse	—	—	Place name
7	Îlet à Cordes	Rochefeuille, c. 1840	Cheke and Bour, 2014	Historical account
8	Cilaos	Vinson, 1868	Bour, 1981	Historical account
9	Parc à Tortues	—	—	Place name
10	Dimitile	Anonymous, 1743	Cheke and Bour, 2014	Historical account
11	Bras de la Plaine	de Villers, 1709	Bour, 1981	Historical account
12	Saint-Louis	Provincial Council, 1728	Bour, 1981	Historical account
13	Pointe des Grands-Bois	Athalanthe, 1722	Bour, 1981	Historical account
14	Ravine Carosse	—	—	Place name
15	Mare d'Arzule	Kerautrai, 1777	Cheke and Bour, 2014	Historical account
16	Rivière Saint-Jean, mouth	Castleton, 1613	Bour, 1981	Historical account