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The case of *Rebuffoichnus* in Lanzarote: ichnological and neoichnological approaches to the study of insect trace fossils from the Pleistocene

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Thesis Content

ABSTRACT

AIM OF THE STUDY

The purpose of this work is to clarify the origin of the insect trace fossils found in the Quaternary deposits of Lanzarote, providing new data and refining our knowledge of this ichnospecies (*Rebuffoichnus* ispp.). The research focuses on four aspects. Firstly, new localities from Lanzarote bearing specimens of *Rebuffoichnus* ispp. are here described along with the stratigraphy of the deposits; secondly, neoichnological studies have been conducted through micromorphology and tomography to compare Noctuidae (Lepidoptera) pupation chambers and Canarian *Rebuffoichnus.* A third goal was to study the larval behavior of modern species of Noctuidae in order to decipher the behavioral and paleoenvironmental significance of the Canarian *Rebuffoichnus* ispp.*;* the fourth point regarded preliminary studies on Canarian Sphingidae (Lepidoptera). In the future it will be necessary to conduct further investigations to validate their role as paleoclimatic proxies, contributing to our knowledge of Lanzarote's past climatic conditions.

Within the framework of this research, particular attention must be given to Argentina, which was selected as the site for conducting neoichnological studies and for advancing the understanding of insect trace fossils, in collaboration with the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires.

INTRODUCTION

CHAPTER 1: Ichnoentomology

1.1: Introduction

Ichnoentomology is a branch of ichnology focused on the study of insect traces and trace fossils, which are nowadays buried and preserved in sedimentary rocks. Unlike ichnology, which deals with trace fossils left by all organisms including animals, plants, and microorganisms, ichnoentomology is much more specifically focused on insects and is probably one of the most specialized disciplines within paleontology. Moreover, ichnoentomology studies complex fossil traces that can often be attributed to specific producers, which is much more difficult, for example, in the ichnology of marine traces (Genise, 2017).

Through the analysis of insect trace fossils, it is possible to understand the evolution of their producers, as well as their ecological and behavioral aspects throughout different geological time scales.

These traces include those as simple as holes, tunnels, pellets, nests, footprints and other patterns made by insects from the past.

The book "Ichnoentomology: insect traces in soils and paleosols" by Genise (2017) has made it easier to classify insect trace fossils today, but it remains a topic that is not simple to deal with. The classification of insect trace fossils, in fact, is a complex system which uses different criteria such as behavior, morphology, substrate type, biological parameters, and preservation of the traces.

In order for a fossil structure to be considered a trace, however, one thing is essential: there must be a wall, which also gives information about the producer and the conditions that preserved the trace (Sarzetti et al., 2024). An initial classification based on ethology was first proposed by Seilacher (1953) and has been subjected to several changes and updates over time (Bown & Ratcliffe, 1988;

Ekdale, 1985; J. F. Genise et al., 2007). All ichnotaxonomic classifications of trace fossils follow the same parameters and rules as the taxonomic classification of organisms according to the International Code of Zoological Nomenclature (ICZN).

The ethological classification according to Sarzetti (2024) includes the following types of traces:

- movement traces (*Repichnia*: prints left by insects during locomotion)
- feeding traces (*Fodinichnia*: tracks of digging such tunnels to search for food; *Pascichnia*: meal leftovers)
- resting traces (*Cubichnia*: small hollows in which the insects used to rest or sleep)
- - traces of habitation (*Domichnia*: tunnels and cells created for protection but also for reproduction)
- traces of nesting (*Calichnia*) and pupation (*Pupichnia*)
- construction of structures (*Aedifichnia*: structures such as termite tumulus or wasp nests)
- escape traces (*Fugichnia*: traces that are escape attempts from rapid sedimentation events such as turbid currents)
- death traces (*Mortichnia*: the path the insect takes before dying, which is often irregular and chaotic)

Certainly, *in situ* traces yield valuable palaeoecological insights due to insects' capacity not only to construct nests but to colonize in all such habitats: volcanic ash deposits, costal dunes, and other habitats where they alter sediments and incorporate organic materials (Retallack & Boucot, 1990). Insects are actively involved in soil formation processes. Majority of the fossils that are associated with insects include nests, or parts of the nests, as well as structures that are dug and excavated into the soil or built by the adult insects in order to create habitations for larval development. These traces are more frequent and more developed as paleosols get older and by the larvae to protect their next stage as pupae (pupation chambers) (Genise, 1999). Most of the palaeoecological information derived from insect trace fossils pertains to humidity and the availability of water, which are critical in this respect. High soil moisture is disadvantageous for those insects that construct cells for larvae using organic materials such as excrement or pollen since these would deteriorate. On the other hand, extreme dryness or insufficient moisture can cause desiccation and therefore death of some larvae which unlike the adults do not possess a hard cuticle. Besides humidity, vegetation, soil type and direct solar radiation are some of the other important conditions that are crucial.

Therefore, environmental conditions play a key role in site selection for nesting, while deposits offer considerable data regarding the environmental conditions of the site during the nest formation period.

Indeed, the unique attribute that makes ichnoentomology quite outstanding is that it shows indications of acting as an indicator of alterations of climate and environments in ancient times. In fact, some insect traces are sensitive climate indicators, and their occurrence and frequency in the fossil record are directly associated with fluctuations in temperature and humidity and other factors.

In order to approach the field of ichnoentomology, a branch that is relatively little known and poorly explored compared to other academic fields, multidisciplinary techniques including paleoenvironmental, morphological, and stratigraphic analyses must be employed.

1.2 Lanzarote case: geographical and geological setting

Lanzarote (29°03′N 13°37′W) is part of the Canary Islands archipelago and is the closest island to the African coast: the distance is approximately 125 km. It is also one of the oldest islands in the archipelago. Its volcanic history began around 15.5 million years ago, during the Miocene. Volcanic eruptions profoundly reshaped the island and continued until 1824 (Becerril et al., 2017; Tomasi et al., 2023). Lanzarote can therefore be considered as a mature volcanic island. Its volcanic activity is linked to a deep mantle plume, which originated in the Canary Islands Seamounts Province (Tomasi et al., 2023). Its landscape is composed of deeply eroded volcanic massifs, tall cliffs and valleys which are mostly filled by gravity flow and fall deposits (Carracedo & Troll, 2016).

The climate of Lanzarote is arid, with a medium rainfall of 109 mm per year (Arrecife Airport Meteorological Station; http://www.aemet.es). Dating back, past climatic fluctuations have modeled the environment of Lanzarote, influencing sediment deposition and ecosystem dynamics over time. The impact of strong winds and aeolian processes have led to the development of dunes and sandy formations, shaping the landscape.

A simplified geology of Lanzarote is shown in Figure 1. In the northern eastern part of the island lie the oldest deposits, dating back to Miocene and Pliocene (in blue and grey in Fig.1), forming the Macizo de Famara area. Nowadays these deposits are strongly eroded and represent the remains of the ancient volcanic edifice. In the central part of the island are the Pleistocene volcanic deposits (marked in various shades of green) with large lava fields and cones.

A special mention deserves the evolution of the island during the Holocene. The 1730-1736 eruption (shown in red in Fig. 1), covers the central-western part of the island (Timanfaya) and is the result of fissure eruptions that produced vast fields of basaltic lava and hundreds of pyroclastic cones. The eruption of 1824 is indicated in pink (Fig. 1) and is characterized by more limited deposits (Tinajo area). Moving to the coast, these areas include sand dunes and flood deposits and are formed by recent and still active sedimentary processes.

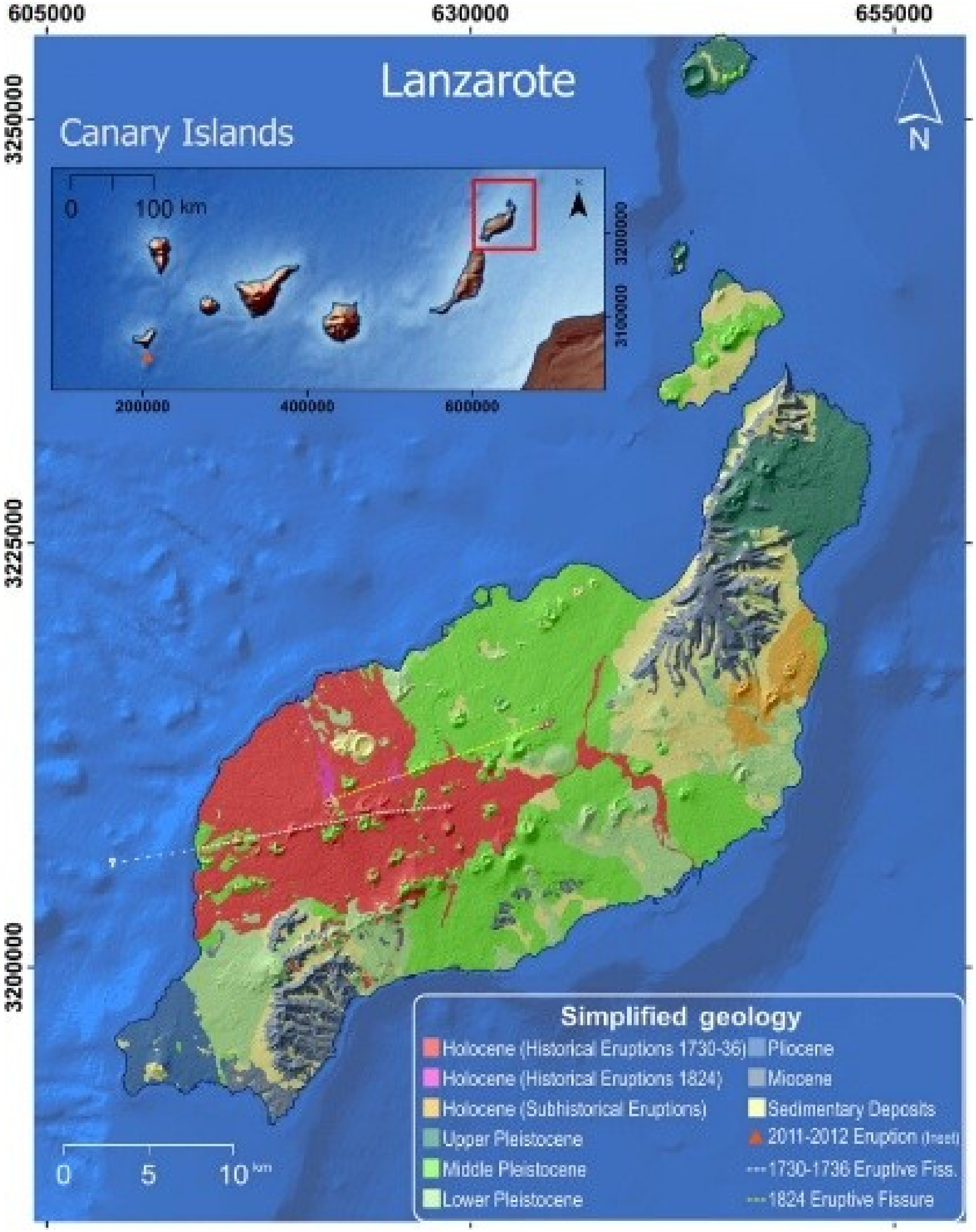

Figure 1: geological map of Lanzarote. Take from Becerril *et al.* (2017)

1.3: Study area

The central part of the island is occupied by a plain, known as El Jable, which means “sand” in Arab language. It is a huge sandy plain which extends about 21 km in length and 10 km in width in the northeastern part of Lanzarote. This area is bordered to the east by the Famara escarpments, to the south by the Monte Mina volcanic complex, to the west by the Tao volcanic complex, and to the north by a coastal rocky platform. The exception is the eastern end, where the wide Famara beach opens up. It is a key geological site, and its evolution is closely linked to the island’s volcanic activity (Fig.1). The basement is made up of lava flows and pyroclastic deposits coming from eruptions that have occurred from the Middle Pleistocene to the present (Becerril, Marti, et al., 2017).

El Jable is mostly filled with aeolian dunes formed by organogenic rich coastal marine and windblown sand; these last largely coming from the Sahara (Cabrera et al., 2006; Heinrich et al., 2021; Meco et al., 2011; Muhs et al., 2010). Alluvial fans, fed by ephemeral streams, are found at the edge of the plain, although they are more developed along the slope of the Famara escarpments (Cabrera et al., 2006).

Recently, the area has been heavily altered by human activities: agriculture, goat grazing and the extraction of construction materials have erased much of the original sedimentary structures (Cabrera et al., 2006) (Fig. 2).

Figure 2: El Jable plain. The sedimentary features have been almost deleted due to man-related activities such as sand pits, farming and grazing. Taken from Faedda *et al.* (2025) (*in preparation*).

Since the climatic fluctuations of the late Pleistocene influenced the sedimentary processes on Lanzarote, El Jable has been chosen as the study area, offering a clear insight into past environmental conditions.

STUDY AREA

Two are the area selected for this study: the Muñique sand pit and the Famara cliff.

Muñique sand pit

The sand pit is located in the south-eastern part of the basin, close to the village of Muñique (29°03’51”N; 13°37’5”W). In the pit walls a well exposed, 10 m thick section of the late Quaternary sedimentary fill of the southeastern part of the El Jable plain occurs (Fig. 3).

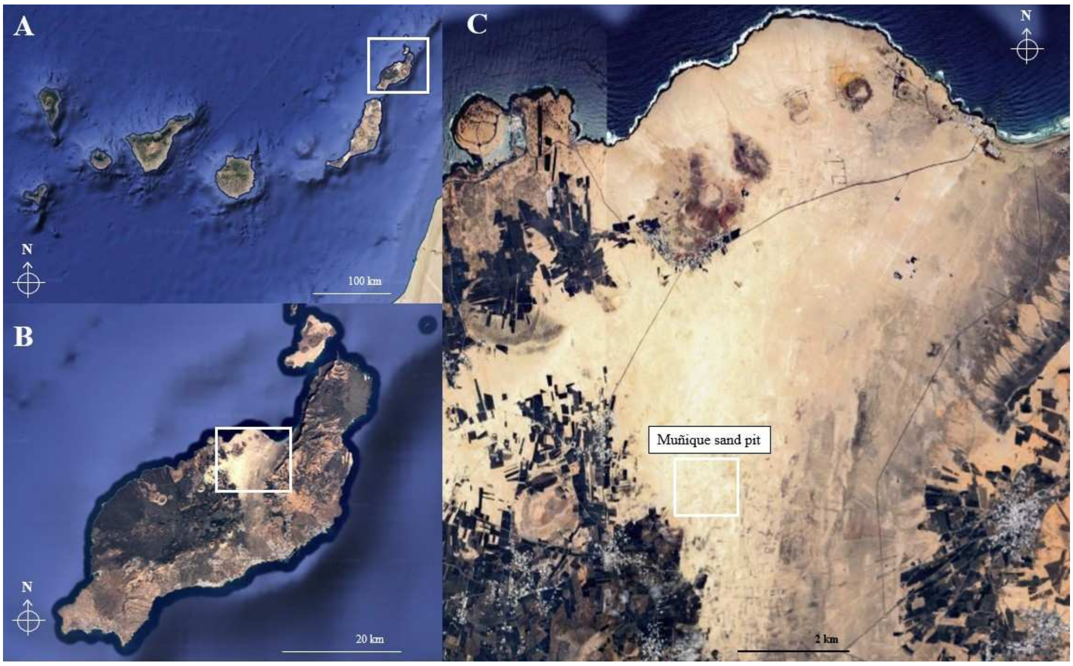

Figure 3: satellite image of the Canary Islands and location of El Jable plain and Muñique sand pit. A) the Canary archipelago showing Lanzarote in the northeast. B) Close-up of Lanzarote, the square indicates the El Jable plain. C) close-up of El Jable plain with location of the Muñique sand pit. *The images were obtained using Google Earth, with data sourced from Airbus, SIO, NOAA, U.S. Navy, NGA, and GEBCO. (Google Earth, 2023).* Taken from Faedda *et al.* (2025) (*in preparation*).

The pit succession has been previously studied and dated by Henrich *et al.* (2021) (Fig. 4). They subdivided the outcropping succession in three depositional sandy sequences composed of Type 1-3 deposits separated by hard Facies Associations (Facies Associations A-C) (Fig. 4).

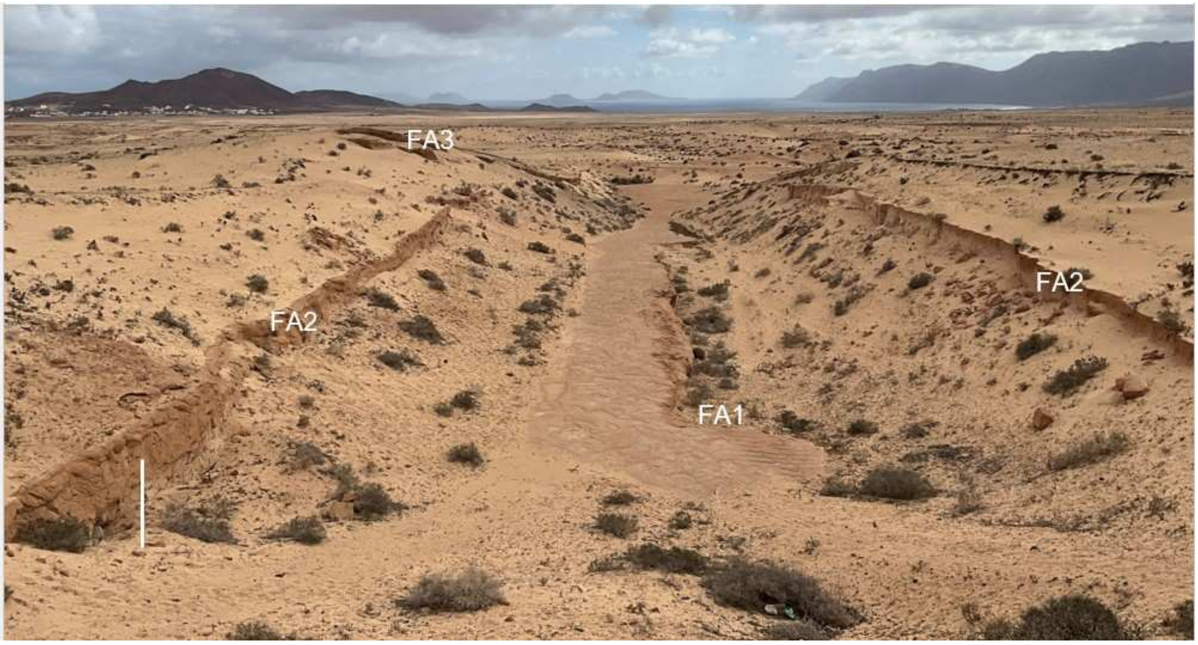

Figure 4: The Muñique sand pit succession, made of three depositional sandy sequences composed of Type 1-3 deposits separated by hard Facies Associations (Facies Associations A-C). Taken from Faedda *et al.* (2005).

According to Heinrich's study, the sand pit exhibits a repetitive succession of interstadial and stadial climatic conditions, which led to the formation of multiple sequences of eolian deposits, each generally comprising three depositional types. Insect trace fossils belonging to *Rebuffoichnus* ichnogenus have been found in every depositional system of the sand pit.
The sand pit levels were dated using IRSL luminescence methodology by Heinrich et al. (2021)~~.~~

Famara Cliff

The Famara Cliff occurs in the north-eastern part of Lanzarote (29.104101, -13.558474) (Fig. 5).

Figure 5: Green square: the localization of Famara escaroments within Lanzarote island; yellow square: Famara alluvial conoids system. Taken from Ostera (2025).

The cliff has an altitude of 671 m and extends for about 20 km from Punta Fariones in the north, to Teguise in the south, with a gradual descent towards the south. It was probably larger originally, but erosion and recent volcanic activity have reduced its size. At the Strait of El Río, there is a Pleistocene-Holocene marine platform that bears witness to a collapse of the western flank, followed by intense erosion.

The western part of Famara Caldera is characterised by alluvial fans dating back to the Pleistocene. Fans are cut by gullies (barrancos in Spanish) allowing the exposition of the sedimentary succession. Four of these gullies (named LZ403, Horca, Las Piletas and Falls) have been chosen to search for *Rebuffoichnus* ispp. (Figs. 6-7).

Figure 6: close of fans where the incisions that cut the structures are visible. LZ40, Horca, Las Piletas and Falls have been chosen to be explored searching for insect trace fossils. Taken from Ostera (2025).

Figure 7: the Famara Caldera view from El Jable plain.

1.4: Ichnotaxonomical debate

Although there are mentions referred to Lepidoptera as producers of the Canary Island traces (Genise, 2000and Genise & Edwards, 2003a), these pupa chambers have always been attributed to other orders such as Hymenoptera or Coleoptera. No detailed studies have been conducted on Lepidoptera, although families such as Noctuidae and Saturnidae have species in the Canary Islands and include moths that pupate underground in chambers that strongly resemble those attributed to *Rebuffoichnus* species.

The next sections examine the main insect orders that have been suggested in literature as producers of *Rebuffoichnus* in Lanzarote. Therefore, a review of the literature on Hymenoptera, Orthoptera, and Coleoptera has been conducted to better understand the following hypotheses.

1.4.1 Hymenoptera

An early theory linked the construction of cells in Lanzarote to certain hymenopteran species, such as wasps or bees, and more especially to Anthophora (Coello et al., 1992; Coudé-Gaussen & Rognon, 1988; Damnati, 1997; Damnati et al., 1996; Petit-Maire et al., 1987; Petit-Maire & Page, 1992; Rothe & Schmincke, 1968).

The order Hymenoptera represents a high number of diversities within the Canary Islands and, as such as 967 identified species are documented up to date.

The endemic species of the Canary are 23.5%: this important evidence underscores the importance of the archipelago as a center of biological diversity. Also, the presence of numerous nesting sites contributes to this richness. For example, the Gran Canaria sites stand as the oldest, dated back approximately 400,000 years. In contrast, the most recently identified site on Lanzarote dates back 3,500 years.

An interesting finding is that Hymenoptera seem to have a preference especially for colonizing coastal areas. This high population density suggests that past environmental conditions have favored the proliferation of these insects in the Canary Islands.

While invasions of hymenopterans have occurred in the past, their frequency is by no means comparable with those associated with locusts and grasshoppers but also is less well-documented.

In history, there are cases of bee invasions which are rare when colonies of some stingless bees, especially in the tropics, act aggressively in response to threats. These invasions are characterized by large numbers of bees defending their colonies with some colonies expanding and moving into new territories including urban spaces such as towns and cities.

Some examples include cases where disturbed stingless bee colonies have increased their territories into human living areas, presenting a problem because of their aggressive nature. However, such bee invasions are different from the large-scale invasions that are typical of locusts and grasshoppers and cause significant harm to agriculture.

Notable species include *Vespa mandarina* in Japan, which is considered quite aggressive and has been known to attack bees colonies with a serious potential to cause significant harm to the population of bees and thereby to the local ecosystem; *Vespula vulgaris* and *Vespula germanica* are the two invasive species in New Zealand that have caused ecological damage by outcompeting native species; *Vespa crabro* in North America is another notable species.

Even if the invasions by wasps are bothersome and result in localized disturbances and can have adverse impacts on regional wildlife and ecosystems, they do not cause damage to agriculture, which is a hallmark of a locust invasion.

Another attractive issue is solitary wasps and bees. Among these, the solitary wasps can make either single-celled or multi-celled nests with mud, wood, and pieces of plants. These can be used either for laying eggs or for protection while the larvae develop.

The Anthophora genus includes solitary bees that are classified as members of the Apidae family, quite commonly known as "ground bees", and play a crucial role in plant reproduction. They exhibit such a specific kind of nesting behavior, by tunneling or burrowing in the ground or other surfaces like soil or wood walls. Anthophora bees develop distinct sections (cells) inside these tunnels where they place their eggs and store both pollen and nectar to feed their larvae.

There are colonies of Anthophora bees in Europe, North America and Africa, besides other parts of the world. Meadows, grasslands, and natural ecosystems represent the open spaces that they frequently belong to. Nowadays, the Anthophora include solitary bees that mostly nest in simple cavities dug in the ground: the female, after fertilisation, builds a nest with multiple chambers where she deposits an egg in each cell. It is known that the distribution of the genus Anthophora is cosmopolitan but mainly centred in the northern hemisphere. Since Bravo's work (Bravo, 1954), there have been numerous publications on this topic (Coello et al., 1992; Coudé-Gaussen & Rognon, 1988; Damnati, 1997; Damnati et al., 1996; Petit-Maire et al., 1987; Petit-Maire & Page, 1992; Rothe & Schmincke, 1968).

Whether the insect trace fossils found in the Canary Islands have been constructed by Anthophora specimens is a theory supported by the following points. First, the material with which the traces were built is usually the same as the deposit one, it was not carried from elsewhere. This can be assumed by looking at the structure of the wall, which was not built piecemeal; moreover, the texture of the material suggests that, even if moistened, it would not have been easily transportable (Ellis & Ellis-Adam, 1993). Another supporting point of the Anthophora hypothesis is the fact that the walls of the cells are very compact, well-defined, and relatively hard (Fig. 8).

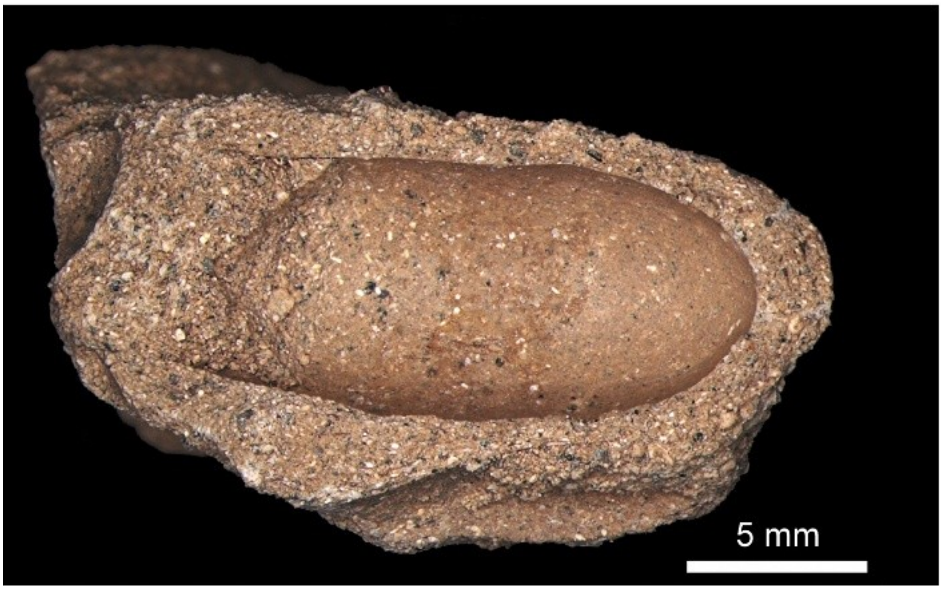

Figure 8: Longitudinal section of *Palmiraichnus castellan*osi. Taken from La Roche et al. (2014).

In fact, these insects fill their nest cells with a protein secretion, in some cases with a nectar and pollen mixture (as a source of growth for the larvae): the consequence is that the cell walls are harder and longer lasting than those of other insects (Ellis & Ellis-Adam, 1993; Torchio & Trostle, 1986). Ecologically speaking, this may partially have favoured protection from predators and thus the spread of this genus in this area.

According to some authors (Edwards & Meco, 2000; Von Suchodoletz et al., 2009), the presence of fossilized nests of Anthophora bees suggest an interesting clue to the precipitation rate and it is known that the moisture regime rate was higher than todays in Lanzarote. In fact, these bees spawn in areas with a minimum annual precipitation rate of 200 millimetres, while the actual Lanzarote rainfall rate is of 100 to 200 millimetres.

The first authors who contested the theory attributing fossil cells to Anthophora bees were Genise and Edwards (Genise & Edwards, 2003b): they based their argument on the lack of a spiral closure (Fig. 9) in all specimens that had previously been analysed by other authors (La Roche *et al.*, 2014).

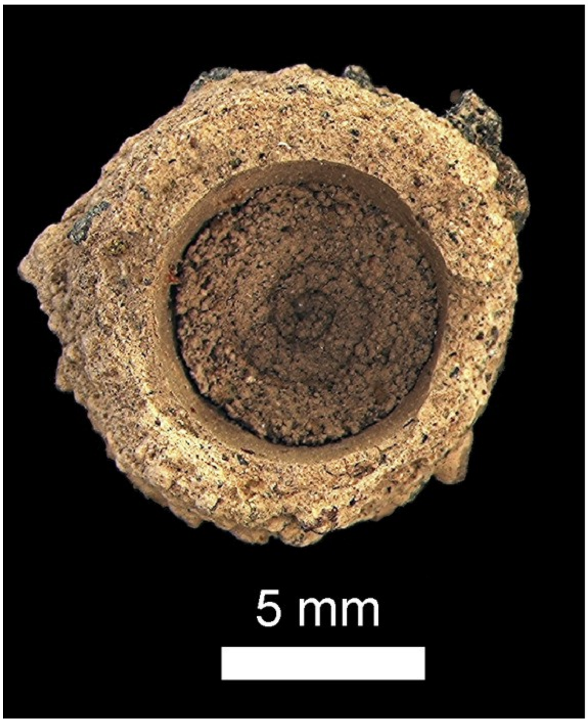

Figure 9: View of spiral closure of the cell of *P. castellanosi*. Taken from La Roche *et al.* (2014).

This type of spiral structure is an identifying character found in fossils bee nests. Therefore, from that moment on, theories were put forward to consider other insects, such as Coleoptera (Genise & Edwards, 2003b), Ichneumoidae (Alonso-Zarza & Silva, 2002), or locusts, as suggested by (Meco et al., 2010, 2011), such as *Dociostaurus maroccanus*. Other points that go against this theory include, firstly, unlike locust invasions, there is no historical record of bee invasions in the Canary Archipelago; secondly, ground-nesting bees typically collect materials for constructing cells from distant sources. In contrast, the insect trace fossils found in Lanzarote Island were constructed using the same sediments as the deposit's soil.

1.4.2: Orthoptera

Based on numerous records, such as historical documents, archaeological findings and scientific research, it can be stated that throughout history there have been invasions by locusts and grasshoppers worldwide. However, the accuracy of records has some biases depending on historical periods, geographical areas and religious and cultural movements perceived by humankind over time.

One of the most famous examples is certainly that of Pliny the Elder, who wrote in his encyclopedia *Historia Naturalis* that there were locust invasions from Africa in Italy at the time, which were so infesting that they left entire areas without vegetation.

According to the author, the magnitude of locusts is that they are "dimming both sky and land, never leaving day nor light”, with such high numbers that they almost obscured the sun and cast a shadow over the land (Historia Naturalis, book 11, chapter. 29 “Of the Insects Which Have No Wings or Few”). Finally, he adds that the great loss of crops by locusts is likely to be associated with famine and impinge seriously on the social well-being of the area inhabiting societies.

However, one of the most famous accounts is the plague of locusts from the Book of Exodus in the Old Testament. To date, though, conclusive archaeological evidence to support this is still wanting.

An example of fossil locust’s nest is reported in Figure 10.

Figure 10: fossil evidence of a grasshopper egg pod found in Oregon, USA. Taken from Lee et al. (2024).

There is a correlation between locust invasions and climate changes or extreme weather events. This connection is often piloted by two key factors: climatic oscillations (e.g. temperature fluctuations, rainfall irregularities and wind alterations) and heavy rainfall. Firstly, a period of heavy rainfall followed by a drought can create an ideal environment for locusts to prosper; secondly, after a strong rainfall the following growth of vegetation offers source of nutrition to the locusts. Meco's (2010, 2011) theory concerning *Dociostaurus maroccanus* specimens as the producers of Lanzarote *Rebuffoichnus* ispp. is supported by the fact that Hymenoptera or Coleoptera invasions have never been reported in the Canary Islands, as opposed past locust invasions from North Africa, such as *Schistocerca gregaria* (Forskål, 1775) (Cyrtacanthacridinae) or *Locusta migratoria* (L., 1758) (Oedipodinae).

Actually, Meco did not consider these two last species as they construct a type of oothecae with a different shape and without embedded sediment particles, as *D. maroccanus* does. Female Saharan locusts (especially *D. maroccanus*) bury their eggs in soft, clayey, and humid soils using their ovipositors. Under optimal temperature and humidity conditions, there is a surge in reproductive activity, leading to the hatching of numerous eggs and a rapid increase in parasite numbers. Saharan locusts enhance the protection of their eggs by thickening the oothecal wall with adhered soil particles, forming a robust shell. These eggs can even be encircled by concentric layers of hardened material, considerably augmenting the size of the structure.

It is possible that the temperate climate of the Canary Islands, combined with the presence of moist soils (plausible with the climatic shifts of the Quaternary period), may have favoured the abundance of this species.

But, as Genise (Genise, Alonso-Zarza, et al., 2013) points out, this theory is poorly supported, firstly because mention of plagues of organisms is not an adequate argument in order to attribute the oothecae to any locust species; secondly, because the smooth inner wall and the concave shape of both ends are a clear sign of a chamber that has been built and smoothed out entirely from the inside, as is common in beetle pupation chambers, and a locust with its abdomen can not smooth out the inner wall of a chamber from the outside.

1.4.3: Coleoptera

Other recent theories regard Coleoptera (Genise & Edwards, 2003b) or both Hymenoptera and Coleoptera (Ortiz et al., 2006).

The hypothesis that beetles (coleopterans) could be responsible for the fossilized traces observed in the Canary Islands seems to be supported by several features. These encompass the ellipsoidal configuration of the cells, utilization of surrounding material, polished inner surface of the walls of the chambers, and a horizontal orientation within the soil (Fig. 11).

Figure 11: Pupation chamber of weevil from Australia. Scale in mm. (Specimen from the S. W. Veatch collection. Photo by S. W. Veatch)

The discovery of an adult weevil inside a larger but comparable *Rebuffoichnus casamiquelai* specimen from Quaternary limestones in Australia supported this theory; the position of the exit hole is coherent with weevil pupation chambers (Ellis & Ellis-Adam, 1993; Genise et al., 2013; Lea, 1925). This might also imply a certain geographic uniformity in the adoption of this behaviour. However, it should be noted that in order to understand the ichnological traces an evaluation of all the available data is required and comparing them to modern or known behaviours of insects. The lack of a spiral closure, a feature that is characteristic of bee cells, supported the Coleoptera hypothesis even further.

While outbreaks or beetle invasions instances in history are not frequent, one of the most well-known examples is given by the outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) in North America: emerging in the early nineties, this beetle destroyed millions of hectares of coniferous forests in the USA and Canada. Climate changes have contributed to the outbreak by providing conducive environment.

According to Genise (2013), the interpretation of *Rebuffoichnus* as pupation chambers of the Curculionidae and Scarabaeidae families (Coleoptera) has been widely debated. Johnston (2011) discussed it under the name *Fictovichnus*, while Genise et al. (2002) compared it with modern coleopteran pupation chambers. However, Ellis & Ellis-Adam (1993) found out weevils as the producers of these trace fossils in the Canary Islands due to the subapical position of the emergence hole.

1.4.4: Lepidoptera

The order Lepidoptera (from ancient greek: λεπις (lepis): scale and πτερόν (pteron): wing) does not have a wide record of trace fossils, in contrast to the orders mentioned above. That very few Lepidoptera fossils have been studied probably depends on their very fragile body structure, and therefore the difficulty of preserving themselves during the fossilization process (Sohn et al., 2015). The most well-known examples, as well as the most numerous fossils, are those belonging to the Cenozoic era, especially the Eocene (56-33.9 million years ago), while they are rare in the Pleistocene (2.8 million years ago-11,700 years ago) (Meyer & Smith, 2008). These are mainly fossils from primitive species of moths, such as *Prodryas persephone*, one of the best preserved of the Eocene (Meyer & Smith, 2008). Some other fossils consist mostly of fragments of wing scales, such as those studied by Van Eldijk (2018) dated to the Triassic-Jurassic transition (Fiorelli et al., 2025). According to Val Eldijk, the finding of lepidopteran fossils from more recent time periods means that they were poorly affected by the mass extinction that characterized the late Triassic, but on the contrary, they displayed remarkable diversification during the subsequent period of ecological turnover.

Probably climatic fluctuations typical of the Pleistocene did, however, influence the distribution and adaptation of lepidopterans, although there is no reliable evidence or fossils attributed with certainty to this period. It should be kept in mind that, in addition to their fragile structure that makes their preservation in a fossilization process challenging, current climate changes and exogenous agents indirectly impact on the preservation of Pleistocene fossils.

Despite the rarity of Lepidoptera fossils, and consequently also of the trace fossils left by them, previous mentions to Lepidoptera as *Rebuffoichnus* producers (Genise, 2000and Genise & Edwards, 2003a) have been pointed out but remained unsupported until now. The similarities between

Rebuffoichnus trace fossils and modern Noctuid pupation chambers are remarkable in several ways and will be explained below.

Since it is difficult to find fossils from the Pleistocene, it is important to examine the behavior of Lepidoptera in relation to climate change through the study of paleoecology. Marine Isotope Stages (MIS) are alternating cycles of glaciation and warmer periods with variations in ice volume and in ocean and land temperatures during the Pleistocene (Lisiecki & Raymo, 2005). These events have influenced terrestrial habitats and ecosystems, along with high frequency Dansgaard-Oeschger (DO) events that punctuated the cold MIS 3. These events measured in Greenland ice archives and marine sediments (Hodell et al., 2023), are characterized by sudden warming and cooling during a general glacial stage.

Lepidoptera, which are host-plant dependent during their larval stage, must have found more abundant and stable habitats during the rainy and humid phases of the Pleistocene, which favoured greater expansion of vegetation cover (Hill et al., 2021). Climate fluctuations have therefore regulated the expansion and regression of forest and grassland habitats, with direct effects on food availability and thus on the diversity and abundance of Lepidoptera populations (Bale et al., 2002). Factors linked to climate fluctuations, such as temperature, have also influenced voltinism (the number of annual generations of a species): higher temperatures facilitate an increase in the number of generations per year, accelerating life cycles and thereby potentially increasing the reproductive capacity and spread of species (Forrest, 2016). Probably Lepidoptera adapted their phenology and behaviour due to the rapid temperature oscillation during Pleistocene, to better match the availability of plant supplies.

While studies on other insects and animal groups confirm the importance of MIS and DO events as key factors in structuring biodiversity and terrestrial ecosystems (Davis et al., 2003), there are no evidence that link Lepidoptera to MIS or DO events. However, Lepidoptera usually act as part of terrestrial ecosystems, responding dynamically to these climatic oscillations in terms of distribution, phenology and diversity, as part of terrestrial ecosystems.

CHAPTER 2: Neoichnology

2.1: Introduction

Ichnology distinguishes paleoichnology and neoichnology. Neoichnology is the study of tracks and traces left by living organisms. Compared to paleoichnology, it provides immediate insights into how certain organismal adaptations are connected to the surrounding environment, as well as into their ecology, social interactions, and biology. The study of modern traces allows for the development of techniques and models that can also be applied to fossil traces. Examining the tracks left by contemporary insects, for example, can help clarify various ichnoentomological uncertainties.

Shape and size of the traces are indispensable features when insect species formations must be identified. In fact, when studying insect trace fossils preserved in environments exposed to exogenous agents, such as the deposits in Lanzarote, it must be considered that organic matter can not be preserved.

Neoichnology is a field of study that has been crucial during this PhD, making it possible to compare modern and fossil traces. The goal was to improve the knowledge of morphology, formation environment and the behavioral patterns of the insects involved. Furthermore, studying both extant insects and their fossilized traces can yield valuable information on their phylogenetic history and evolutionary processes.

2.2: Noctuidae

This study proposes Noctuidae as the most plausible candidates among the insect groups previously suggested in the literature as producers of the *Rebuffoichnus* ispp. from Lanzarote.

The Noctuidae are one of the largest families belonging to the order Lepidoptera. They are nocturnal insects, as their name suggests (from the Latin word Noctua, meaning night).

They have a global distribution and have a crucial role in ecology of bats and birds, serving as food source. On the other hand, they can be harmful to crops. Some of the most notorious Noctuidae pests include *Agrotis ipsilon* and *Spodoptera* spp. Moreover, Noctuidae larvae, such as *Spodoptera exigua*, are polyphagous and therefore attack a variety of different plants (Simon et al., 2021).

While adults primarily feed on nectar, larvae are phytophagous (Keegan et al., 2021).

When in larval instars, Noctuidae individuals consume several plant parts such as leaves, stems, roots, and sometimes even fruits and flowers. Since they cause significant damage in agriculture, they are called "cutworms" because they cut plants near the base.

Due to the damage that Noctuidae species do in the agriculture and economy of countries, they are one of the most studied family insects.

Noctuidae larvae seem to have preference for some plant families such as Mimosaceae, Malvaceae, Euphorbiaceae, Gramineae, Anacardiaceae, Leguminosae, Myrtaceae, Apocynaceae, Verbenaceae, Coniferae and Moraceae, with Gramineae and Mimosaceae being the most damaged (Singh Kriti et al., 2014).

Although the larvae are generally considered to be more harmful, the adults can also cause trouble: with their well-developed proboscis they can perforate the skin of fruits such as apples and figs, to suck out the nectar, causing damage that results in the premature fall of the fruits.

The economic damage is huge: for example, *Helicoverpa armigera* has such a major impact on crops in Asia, Europe, Africa and Oceania that the loss exceeds USD 2 billion per year (Tay et al., 2013).

2.2.1: Morphology and development

Structural characteristics, shape, color, size and morphological traits are key features that facilitate the identification of Noctuidae individuals. Holometabolous insects such as Noctuidae family have a life cycle composed of four stages: egg, larva, pupa, and adult. Regarding their morphology, adults (Fig. 12) have filiform antennae, often ciliated and sometimes pectinate, a well-developed proboscis and moderately long palps, which can occasionally be exceedingly elongated.

Figure 12: Adult specimens of *Agrotis gentiliana* (Noctuidae) photographed at the entomological collection of the Bernardino Rivadavia Museum of Natural Sciences in Buenos Aires. Morphological features such as the threadlike antennae, the mouthparts and the different coloration between forewings and hindwings are visible.

Ocelli are nearly always present. Regarding forewings and hindwings, they differ in patterns and color. The hindwings are usually simpler in patterns and are broader, featuring three medio-cubital veins extending to the distal margin and an unbranched subcostal (Sc) vein originating near the wing base (Coto., 1988); additionally, tympanal organs are located at the base of the hindwings (*General Entomology, NC State University*, 2015).

While the adult morphology is crucial to define taxonomic information, the larval traits are equally significant for species identifications, especially since these species are economically important pests in agricultural contexts. Typical traits of Noctuidae larvae include a cylindrical body structure which is composed of head, three thoracic segments and eleven abdominal segments (Fig. 13). Head size usually reflect the developmental instar, has a sclerotized cephalic capsule, antennae and a complex chewing mouth. Each one of the three thoracic segments has appendages and other typical features such as the prothoracic shield and spiracles.

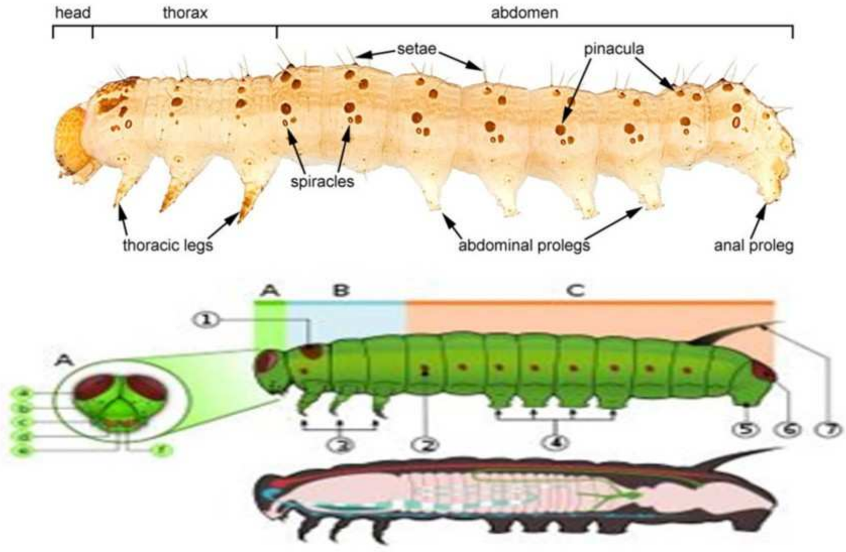

Figure 13: Larval Morphology Overview (A. Head, B. Thorax, C. Abdomen, 1. Prothoracic shield, 2. Spiracle, 3. True legs, 4. Midabdominal prolegs, 5. Anal proleg, 6. Anal plate, 7. Tentacle, a. Frontal triangle, b. Stemmata (ocelli), c. Antenna, d. Mandible, e. Labrum). Taken from Khan et al. (2023).

The abdomen and its segments play a key role in respiration, due to the presence of spiracles. Prolegs for locomotion are often present. The last two abdomen segments are fused to form the anal segment. Few specific setae (hairs) on the body are useful for taxonomic identification. (Coto Daniel A., 1988).

During the larval stage, individuals pass through six or seven instars before pupating (Montezano et al., 2013). This larval phase can last from 30 to 50 days: key factors such as diet or environmental conditions (humidity, temperature etc.) deeply influence the duration of larval instars. It also depends on the species, for example the larval stage of *Agrotis* sp. can last up to 61 days, while in *Spodoptera* sp. it lasts only 13 days of (Montezano et al., 2019; Specht et al., 2013).

Among the primary causes of larval mortality, predation by birds, insects, and other arthropods- is the most significant. Additionally, heavy rainfall can lead to larval displacement, drowning, or the development of pathogenic fungi (Gielen et al., 2023; Varella et al., 2015).

In contrast to other Lepidoptera larvae, Noctuidae individuals do not have urticating setae, however they have developed other strategies for escaping predators, such as mimicry. In fact, when disturbed, Noctuidae larvae curl up on themselves and adopt a coiled posture (Fig. 14) that is similar to a land snails shell, which usually are abundant in the area where they live and are avoided by predators (Rowland et al., 2020).

Due to mimicry strategy, their coloration is often cryptic, with shades of green, brown, and grey that help them to hide into the substrate or recall plant structures.

Figure 14: An example of a mimicry strategy. left, a Noctuidae larva adopting the typical defensive posture resembling terrestrial gastropods; right, the shell of a terrestrial gastropod. Both larva and shell have been found in San Patricio locality, Mar del Plata (Argentina).

Some species, such as *Agrotis* spp., *Spodoptera* spp., *Euxoa* spp., and many others—especially those living in harsh climates or areas with high predation pressure—have developed an adaptation that allows their larvae to pupate directly in the soil or sand, where they build a pupation chamber (ØGård, 1986; Zheng et al., 2011b). Some examples of modern chambers of Noctuidae are shown in Figure 15.

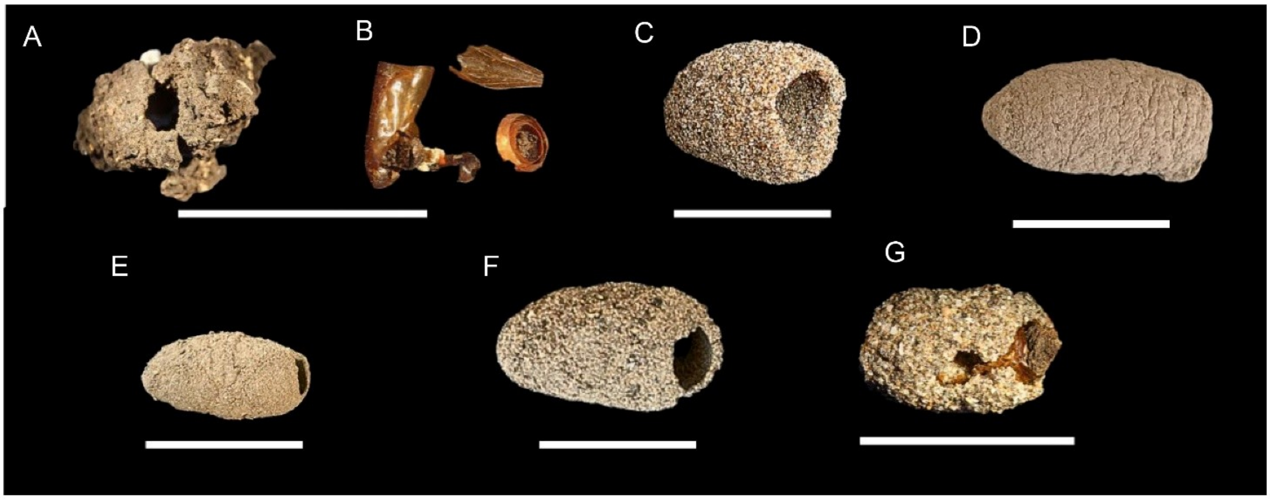

Figure 15: Six studied and measured extant pupation chambers of Noctuidae. A-B) the first pupation chamber as fragmented specimen (A) with its remnants of the exoskeleton of a Noctuidae pupa (B); C) the second measured pupation chamber from Mar del Sur, Argentina; D) the third measured pupation chamber from Santa Fe, Argentina; E) the fourth measured pupation chamber from Santa Fe, Argentina; F) The fifth measured pupation chamber from Chubut, Argentina; G) the sixth measured pupation chamber from San Eduardo del Mar, Argentina. Scale bars = 20 mm. Taken from Faedda *et al*. (2025), in prep.

Only larvae that are at the last instar can begin the construction of a pupation chamber, searching for a place to pupate. The process of building the pupation chamber can vary from species to species, but it follows a general pattern. Firstly, the larvae select a suitable substrate depending on factors such as moisture levels and grain size of the sediment.

After choosing a protected site from predators and weather agents, larvae use their mandibles to dig into the soil, helping themselves with peristaltic movements.

Depending on larvae species and environmental conditions, the depth that they reach could range from a few centimeters to ten. In some cases, larvae can secrete glandular, anal or salivary fluids to move into the substrate and solidify it while constructing the chamber (Vegliante & Hasenfuss, 2012).

After completing the pupation chamber, depending on the species, larvae can cover the entrance with sediment or plant fragments. Inside the chamber larva will go through the metamorphosis process and will enter in the pupation phase. It can last from a few weeks to a couple of months, depending on several factors. These factors include temperature, humidity, substrate type and "diapause", a strategy that allows the pupa to survive severe conditions like winter (Caio, 2024.). During the pupation stage, transformations happen to the individuals, including the development of wings, final coloration, and the maturation of reproductive organs. At the end of this stage, the adult emerges by breaking through the pupation chamber.

After a short period spent expanding and drying its wings, the adult is ready to fly (Arthur et al., 2016; Calatayud et al., 2007).

Once it emerges, the adult will enter another complex life stage, such as the search for a partner, mating, and oviposition. Every stage of life has a complex biology behind, for example, in order to attract a partner, adult females of Noctuidae release sex pheromones that are picked up by males through their antennae even at distances of more than 100 meters (Stepien et al., 2020). Pheromones often facilitate reproductive isolation from species to species: this is the case for species belonging to the same genus such as *Spodoptera littoralis* and *S. litura*, which due to differences in pheromone components cannot mate with each other (Saveer et al., 2014).

In addition, acoustic communication is helpful in mating process, although it is employed in rarer cases. The male can produce sound signals (ultrasounds) during courtship through organs called tymbals (Nakano et al., 2010).

Being nocturnal insects, the mating process usually happens after sunsets. The mating consists of males transferring the spermatophora, a package that contains both sperm and nutrients, into the female's reproductive system. Then, the sperm is stored in the female's spermatheca, and the eggs will be fertilized as they are released. After mating, the females will lay eggs on host plants on which larvae will later feed.

2.2.2: Distribution and migration

Noctuoidea is the most diverse superfamily of Lepidoptera, and it is known to be one of the most globally spread moths' families, even if the number of Noctuidae belonging to the Lepidoptera order is unsure. Keegan, for example, reported that there are more than 12.000 species of moths belonging to this family (Keegan et al., 2021), while Falck and Karsholt thought that there are more of 40.000 species worldwide (Vives Moreno, 2014). The number of species who inhabits the Canary Archipelago is unsure, since the lepidoptera fauna of those islands has never been described in detail (Falck & Karsholt, 2022). According to Vives Moreno there were 133 species of Noctuidae present in Canary Archipelago (Vives Moreno, 2014) but a more recent work has reported 149 species, with only 63 are endemic ones (*Banco de Datos de Biodiversidad de Canarias*, n.d.; *INaturalist*, 2024).

The literature unfortunately has no specific results showing that the distribution of the family Noctuidae may vary according to altitude, although climatic and vegetation differences occurring at different altitudes may actually be a factor influencing their distribution.

In theory at low altitudes plenty of vegetation (and thus host plant) along with more favorable climatic conditions, may facilitate the presence of more species of Noctuidae. This is the reason behind the fact that species found in coastal or hilly areas tend to be more common and widespread. On the other hand, regarding high altitudes, some species of rarer and specialized Noctuidae have adapted to live in mountainous environments, where climatic conditions are more rigid, and vegetation is different (Parenzan et al., 2005). In the Canary Islands, Noctuidae are widespread in very different ecological environments: high mountains (2000 meters above sea level), pine forests

(2000-1200m asl), fayal-brezal (1500-1000m asl, laurisilva (1200-500m asl), the thermophilus woodland (700-200m asl), cardinal-taibal (600-0m asl), and azonally distinct areas (*Banco de Datos de Biodiversidad de Canarias*, n.d.).

Their ability to colonize almost every environment is strictly connected to migratory strategies, which led to a global distribution of Noctuidae family. Migration is a key strategy used to survive in adverse conditions such as winter (Tauber et al., 1986). Due to their low flight speed (around 5 m/s) and because of their size, they may appear to be unsuitable insects for large-scale migrations. Yet, they manage to cover very long distances, for instance by taking advantage of favorable winds and high airflows (Chapman et al., 2008).

Among diurnal and nocturnal butterflies, migration occurs mainly in several species of the following families: Pieridae, Nymphalidae, Sphingidae, Arctiidae, Noctuidae, Pyralidae (Andaloro et al., 2009). Although some species are thought to be involved in this complex ecological phenomenon (among the Noctuidae for example *Autographa gamma*, *Agrotis ipsilon* and *Noctua fimbriata*), the migration of nocturnal moths has still not been well documented (Zheng et al., 2011a).

Some moths, such as *Chorizagrotis auxiliaris* (known as army cutworm), maintain a constant direction, regardless of wind direction, although flight altitude is influenced by wind speed and direction (Pruess & Pruess, 1971). Others, such as *Spodoptera frugiperda*, on the other hand, show a remarkable flight capacity (Accademia Nazionale Italiana Di Entomologia, 2011).

Their direction is kept correct due to their ability to orient themselves mainly with the Earth's magnetic field, as in the case of *Noctua pronuba* and *Catocala nupta* (Dreyer et al., 2018) but also with light references, e.g. by maintaining a constant angle to nocturnal light sources (moon, stars, Milky Way). This is not news that insects are sensitive to polarized light, a feature that allows them to orient themselves even in poor visibility conditions (Heinloth et al., 2018). In more complex environments, such as forests, they rely instead on terrestrial landmarks, relying on the arrangement of vegetation to follow predictable paths (Wiegmann et al., 2016).

Noctuid' migratory behavior may change depending on geographical areas and environmental conditions. In some regions, such as southern Europe, these movements are often irregular and less well defined compared to the classical migratory routes of other insects, thus taking the form of “vagractions”, which are movements that are not always precisely repeated (Alerstam et al., 2011; Eizaguirre & Fantinou, 2012; Kravchenko et al., 2015).

However, apart from their predictability, the migrations of these moths play an essential role in the ecology of the ecosystems they cross. Indeed, migration contributes to the gene flow between moths’ populations, influences the dynamics of insect communities and provides a source of food for numerous predators, ensuring the balance of trophic networks.

Migratory journeys can be influenced and disrupted by climate change, whose conditions can extend migration times or drastically affect food resources along the route (Outhwaite et al., 2022); human activities, such as the construction of road infrastructure or the degradation and impoverishment of habitats, can also constitute physical obstacles that block migration. Since several insects use the moon as a reference point, light pollution can also cause dispersion along their path (Andaloro et al., 2009).

2.3: PhD field research campaign in Argentina and larval rearing

The PhD research stay abroad took place in Buenos Aires, Argentina, at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”.

The purpose was to work for three months at the museum's Ichnology Division under the direction of Dr. María Viktoria Sánchez. The choice of this institution was intentional: since the PhD project focused on the application of ichnoentomology in the field of palaeoclimatology, and since a large number of *Rebuffoichnus* ispp. specimens have been found in sedimentary deposits in Argentina, this location has been selected.

The PhD objectives included both field and laboratory activities, with the goal of comparing fossil specimens from two distinct geographical areas (Lanzarote and Argentina) and present-day Noctuidae specimens. Moreover, collaborating with the museum’s team of world-famous experts in the field of ichnoentomology, provided an opportunity to learn new techniques and methodologies.

2.4: Palaeoecological significance of *Rebuffoichnus*

Two point six million years ago started a period with significant climatic oscillations, the Quaternary. During the Quaternary glacial periods alternated with interglacial. The proof of these climatic fluctuations has been found in geological deposits, oxygen isotopic studies in marine sediments and in fossil remains (Damnati et al., 1996; Mecol et al., 2008).

In Lanzarote these climate shifts have shaped not only the island's soils but had an impact on vegetation and fauna communities. Periods of greater aridity succeeded wetter phases, influenced by both Atlantic circulation and Saharan winds (Muhs et al., 2021; von Suchodoletz et al., 2009a). Studies have shown that during wet phases, often linked to interglacial periods, soils developed, and vegetation expanded, while during glacial periods the landscape was dominated by dust deposits and desert conditions. The alternation between Saharan dust deposition and phases of alluvial fans development or palaeosols formation provides clear examples of these changes (Muhs et al., 2021; Von Suchodoletz et al., 2008; von Suchodoletz et al., 2009a).

Among these deposits, insect trace fossils such as *Rebuffoichnus* isp. could act as informative proxies: in fact, structures such as burrows or pupation chambers can reflect some properties of the deposits, such as moisture availability or the type of vegetation present at the time. Thus, their variety and abundance can help to predict the degree of soil development: for example, abundant and diversified *Rebuffoichnus* ispp. are often associated with mature soils that provided suitable conditions for the life cycle of insects, thus associated with wet phases. On the other hand, dry phases often leave fewer or simpler traces (Von Suchodoletz et al., 2009b).

Ichnoentomological data support other proxies and records such as pollen and isotopes and together provide a solid reconstruction of Quaternary climates in Lanzarote.

Rebuffoichnus isp. is widely distributed in Quaternary and Pleistocene deposits in Europe, Australia and South America.

For example, in Italy some specimens comparable to the ichnogenus Rebuffoichnus Roselli 1987 have been found within a paleosol interbedded with pyroclastic deposits attributed to the Pleistocene (Sacchi & Petti, 2008).

In Lanzarote, its presence within specific alluvial fan layers is particularly significant, as it marks episodes of soil stability and biological activity.

MATERIALS AND METHODS

CHAPTER 3:

The areas of Muñique and Famara have been investigated using a physical stratigraphy approach. *Rebuffoichnus* ispp. have been examined *in situ* in both study areas and in the laboratory, with statistical and micromorphological analyses focused mainly on Muñique specimens.

3.1: Stratigraphy

Stratigraphy of Muñique sand pit

The sand pit site is located in the southwestern part of the basin, near the village of Muñique (29°03’51”N; 13°37’5”W). Here, a well-exposed, 10-m thick succession of late Quaternary deposits crops out. The stratigraphy of the Muñique sand pit has already been investigated and dated by Heinrich’ et al. (2021) and Stelletti (2024) using post IRSL luminescence technique (Fig. 16). Their study identified three depositional types (DepoType 1-3), based on sediment colour, carbonate content and grain size distribution. In this research the sand pit deposits have been described in terms of sedimentary lithofacies, including cross-bedded sandstones (Sa), bioturbated sandstones (Sb), well-cemented, laminated, normal-graded sandstones (Wlg) and channelised, normal-graded sandstones (Wcg) (Fig. 16). These lithofacies partly correspond to DepoTypes 1–3 as defined by Heinrich *et al*. (2021) and according to Faedda *et al*. (2005) have been grouped into three facies associations (FA A-B-C) (Fig. 16). These facies associations are of particular importance because they host the *Rebuffoichnus* traces described in this study. Each association represents a dune–alluvial fan system, interpreted as the product of alternating arid and humid phases (Stelletti, 2024). Since the insect trace fossils themselves cannot be directly dated, land snail shells (*Hemicycla sp.*) recovered from the same levels were analysed and AMS 14 C radiocarbon dated (Fig. 16).

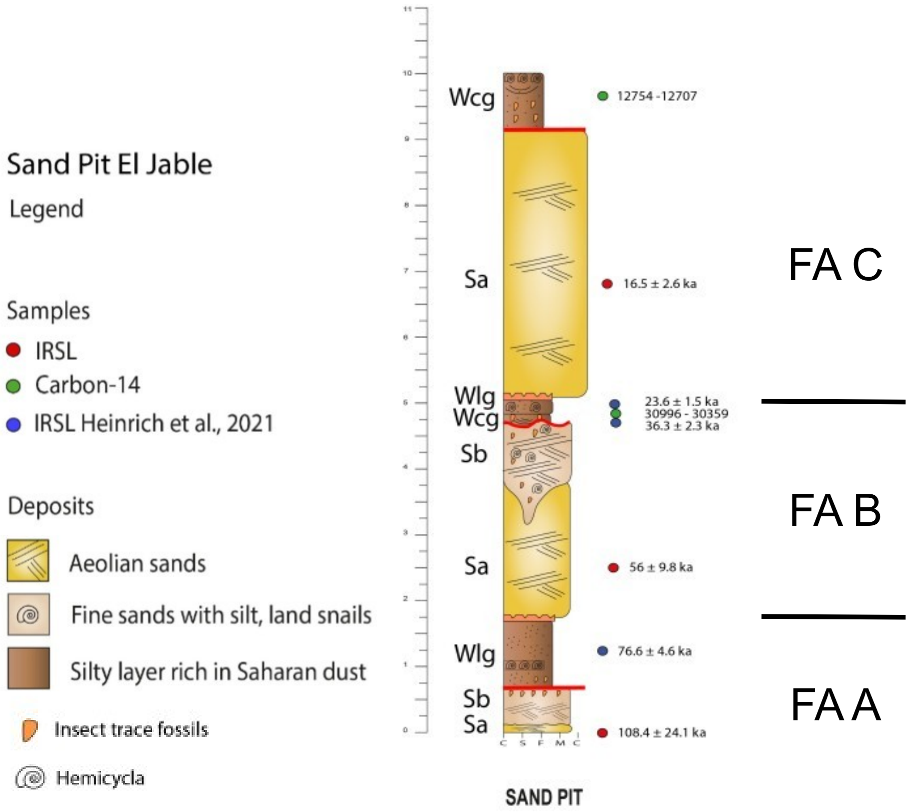

Figure 16: Stratigraphic column of the sand pit of Muñique. Modified after Heinrich *et al*., 2021 and Stelletti, 2024

Stratigraphy of Famara Cliff

The stratigraphy of Famara Cliff has previously been studied and analysed in two bachelor's and doctoral theses (Ostera et al., 2025; Stelletti, 2024). The considerations made from this point onwards are based on the results reported in these works. Sections representative of the area and the barrancos were examined. In addition to facies analysis, six *Hemicycla sp.* shells were sampled and ^{14}C radiocarbon dated. Additional ages are derived by the work of Stelletti (2024) who dated the alluvial fan deposit of the Famara Cliff using luminescence methods (Fig. 17).

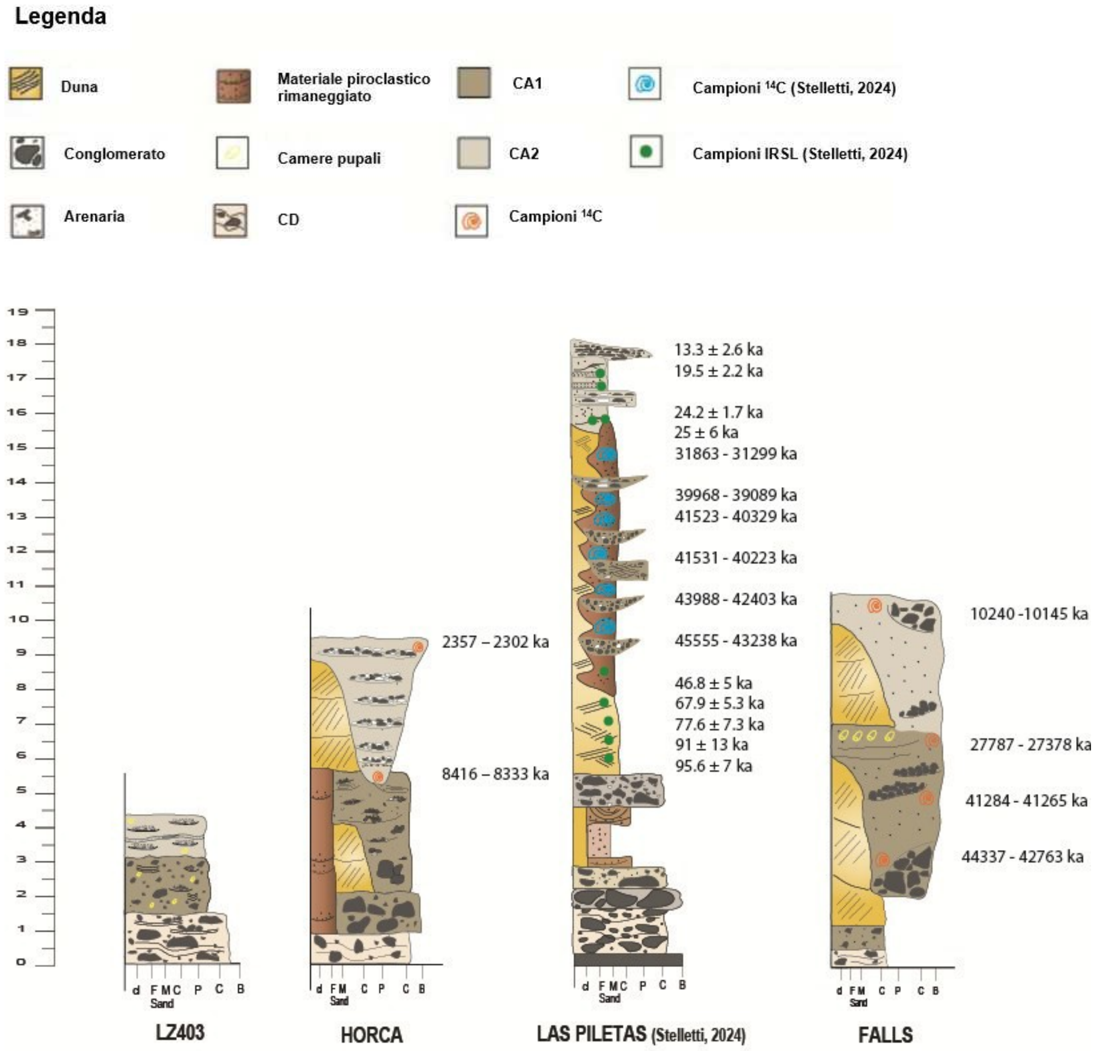

Figure 17: Correlation between the stratigraphic logs carried out in the four study areas (LZ403, Horca, Las Piletas and Falls). The radiocarbon dates obtained from six *Hemicycla* sp. shells are indicated by the orange snail symbol in the stratigraphic columns. Taken from Ostera (2025) and Stelletti (2024).

3.2: Ichnology sampling and statistical analysis

Insect trace fossils were found in study areas where there were particularly bioturbated deposits. Thus, after a general evaluation of the sedimentological deposits and the geological characteristics of the area, sampling was conducted (Fig. 18).

To extract the specimens from the deposits, tools such as metal spoons and tweezers were used in a very delicate way to avoid any risk of damaging the structures and to keep them intact. Before each specimen was placed in plastic jars, the external morphological details were observed, and the exact coordinates were taken.

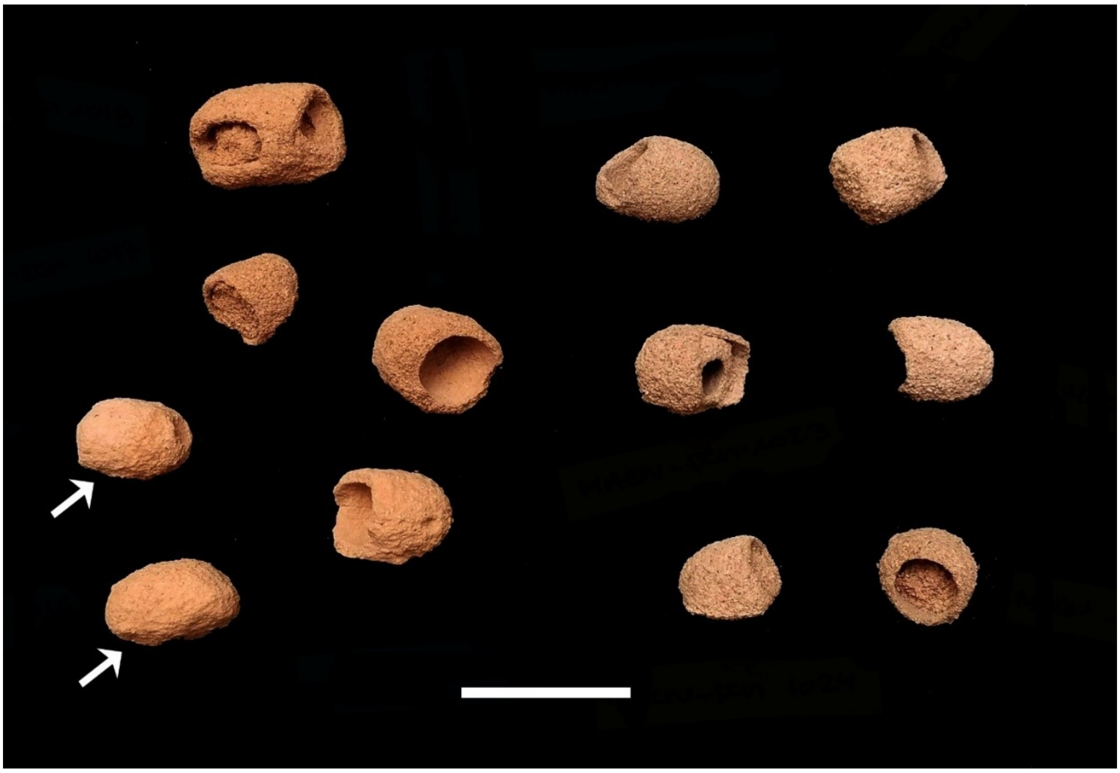

Figure 18: Some specimens of *Rebuffoichnus* ispp. collected in Muñique sand pit, El Jable plain (Facies Wcg). The six specimens of the left (MACN-Icn 1015-1020) come from the lower outcrops of the level and the other six (MACN-Icn 1022-1027), the other six specimens on the right of the image, come from the upper outcrops. Specimens indicated by a white arrow, MACN-Icn 1015 and 1016, are closed. Scale bar: 3cm. Taken from Faedda et al. (2025), in prep.

Coordinates of the geographical points were taken to ensure that the specimens could be traced and to simplify any further studies. Each jar containing the specimens was tagged with information such as the name of the deposit, the date and the sampling site.

Once all the specimens had been collected and brought to the laboratory at the Università degli Studi di Sassari, it was necessary to perform a statistical analysis (ANOVA) to determine if there was any real difference between the fossil and actual specimens, as well as between one study area and another.

3.3: Micromorphology

For micromorphological studies, four specimens of *Rebuffoichnu*s ispp. collected in facies Sa (ELJ10, ELJ12) and Wcg (ELJ3, ELJ8) have been considered to make thin sections.
Specimens were cut along both its long and short axes to observe its internal features. Thin sections were prepared by impregnating specimens with blue-stained polyester resin (Van Meer, 1986) and examined under a Nikon HFX-DX Optiphot-pol petrographic microscope.

Transmitted plain light was used to observe micromorphological features, while the anisotropism, isotropism and birefringence of fine material were examined using polarized light. The terminology used in the micromorphological descriptions follows the soil micromorphology nomenclature proposed by (Bullock, 1985) and published in similar studies (Sánchez & Genise, 2015; Faedda et al., 2025), in prep.

3.4: Tomography

The internal structure of the trace fossils has been previously examined by computerized tomography (CT) (Genise & Cladera, 1995). Three specimens—two fossilized traces attributed to *Rebuffoichnus* isp. from facies Sa (MACN-Icn 1015) and Wcg (MACN-Icn 1016) in Lanzarote and one modern specimen attributed to Noctuidae (MACN-Icn A84) from Santa Fé province (Argentina)—were analyzed to obtain CT images. These images were obtained beforehand to ensure that all internal characters were present without any modification.
Specimens were scanned through a Nikon XT H 225 ST 2X micro-CT system with a static

reflection X-ray source. The system was configured with an acceleration voltage of 80 kV and a current of 125 µA, a tungsten target, and no filter other than the 2-mm-thick beryllium window. A 360° scan was performed with 2200 projections. The resulting voxel size was a symmetrical cube with a 13-µm side. The entire specimens were scanned in each case.

3.5: ImageJ analysis

In order to investigate if there were any significant differences among the insect trace fossils found in Muñique sand pit, an image analysis study through ImageJ software was applied. Each depositional system of the sand pit, named A, B, and C, has been divided into 3 sections (Fig. 19). Image analysis was performed for each section. The sampling method chosen was systematic, through 60 cm^2 squares placed randomly to the right, left and center of each Facies Association of the sand pit.

The shells of a land snail, *Hemycicla sp.,* were also considered as their presence could probably be correlated with periods of humidity. For every square, only embedded *Hemicycla* sp. shell fragments and embedded insect trace fossils were examined considering in the counts.

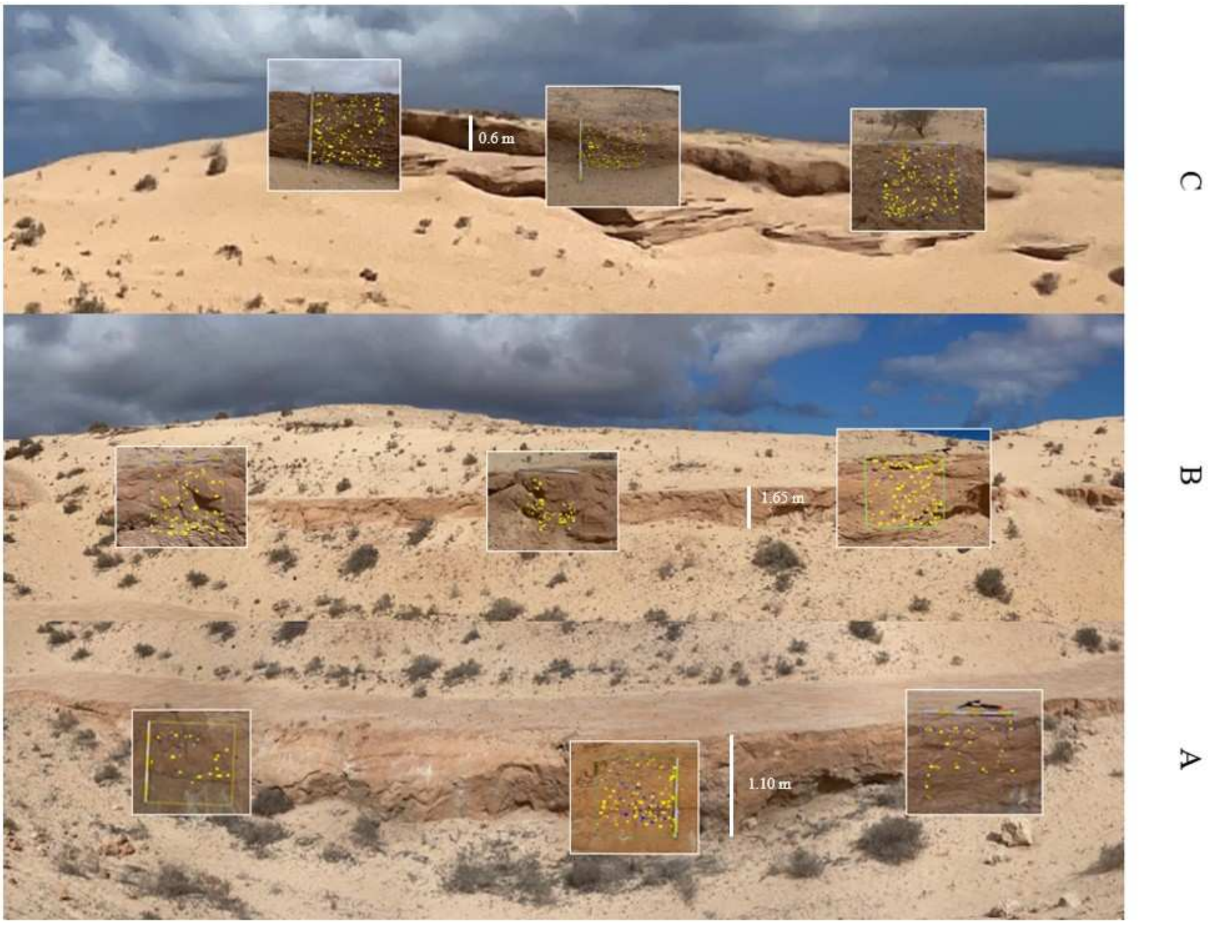

Figure 19: location of the 60x60 squares section specimens in the Muñique sand pit for ImageJ analysis. Taken from Faedda *et al.* (2025), in prep.

After image analysis was performed, Levine’s test was conducted to check the homogeneity of variances between groups (number of insect trace fossils, number of *Hemicycla* sp. fragments, size of insect trace fossils, size of *Hemicycla* sp. fragments). Later, a one-way ANOVA has been applied through R studio software.

3.6: Dating the specimens and sedimentary deposit

Dating of the deposit

After the sampling (Fig. 20), the shells of *Hemicycla sp*. were dated at the Beta Analytic laboratory through the radiocarbon dating analysis using the Accelerator Mass Spectrometry (AMS) standard delivery method.

Figure 20: Sampling in Facies Association C of Muñique sand pit for radiocarbon dating of *Hemycicla sp.* shells found in the same levels as insect trace fossils

3.7: Larval identification and taxonomic classification

A pupation chamber was accidentally broken after the collection when carried to the laboratory, revealing a well-preserved *Noctuidae* (order: Lepidoptera) larva inside (Fig. 21). The identification of the larva was based on a deep review of entomological literature and consultation with taxonomic specialists. Morphological features were compared with descriptions available in scientific studies, with particular attention to traits characteristic of the family Noctuidae. Expert opinions were also considerate to verify the classification and ensure consistency with established taxonomic criteria. This combined approach allowed for a detailed identification of the specimen. The larva was examined under a Leica DM4500 P LED petrographic microscope with an integrated camera.

Figure 21: Larva found inside a broken specimen of *Rebuffoichnus* isp. in level C of Muñique sand pit. A) ventral portion; B) dorsal portion with the distinct darker lines; C) sclerotized cephalic capsule.

The specimen, 1.4 cm long and 0.5 cm wide, has a cylindrical morphology with thirteen distinct segments: cephalic capsule, three thoracic and nine abdominal segments. Pseudo-paws are visible in abdominal segments 3, 4, 5, 6 and 10. Its body has a uniform brownish-yellow ochre coloration with two darker dorsal bands. Despite some signs of deterioration, such as lesions in the posterior portion, the sclerotized cephalic capsule is well identifiable and ventrally oriented.

3.8: Dating the larva

The larva was dated at Beta Analytic laboratories, with the same protocol of *Hemicycla sp*. shells (Beta Analytic, 2025).

3.9: PhD field research campaign in Argentina

Patagonia

The first field trip took place in the province of Río Negro, Patagonia (Fig. 22), from 11th to 18th November. This area of Argentina has been chosen due to its climate, which is very arid and represent a perfect environment for the preservation of trace fossils.

In fact, the focus of the field trip was to find specimens of *Rebuffoichnus* ispp. and to improve knowledge of ichnoentomology through the direct study of trace fossils left by the insects.

The itinerary followed during this field trip was inspired by the travels of Joaquín Frenguelli (1883–1958), one of the pioneers of geology, palaeontology and ichnology in Argentina. He made numerous trips and studies in Patagonia starting in 1924, and his research contributed significantly to the knowledge of the stratigraphy, palaeontology and geomorphology of the region, with a focus on trace fossils (ichnofossils), opening the way for the development of South American ichnology (Mayer et al., 2017).

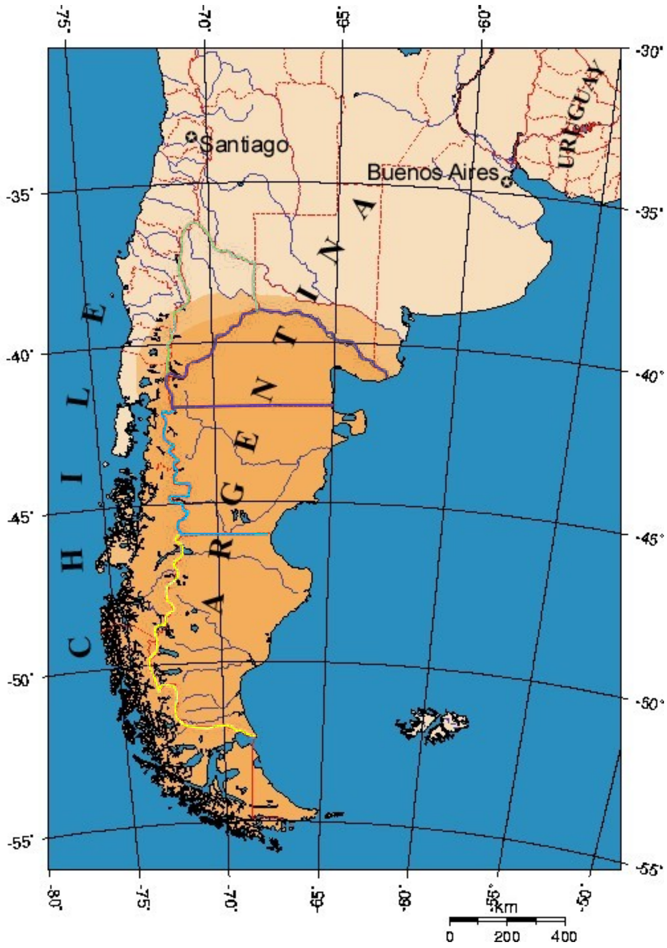

Figure 22: The Patagonia region is composed of the following provinces (from north to south): La Pampa, Neuquén, Rio Negro, Chubut, Santa Cruz, Tierra del Fuego, Antártida e Islas del Atlántico Sur. Modified after Wiesner & Bandinelli (2014).

The town of Comallo was chosen as the base for the field trip, due to its strategic location (Fig. 23).

Figure 23: View of part of Patagonia. The focus is on Comallo, a village in Río Negro Province in Argentina. *The images were obtained using Google Earth, with data sourced from Airbus, SIO, NOAA, U.S. Navy, NGA, and GEBCO. (Google Earth, 2023).*

From a geological point of view, this is a region that offers a range of different environments, from basaltic plateaus to arid steppes, from river deposits to paleosols rich in carbonate concretions to lake basins cut by glaciers over geological eras. Río Negro geological map is shown in Figure 24.

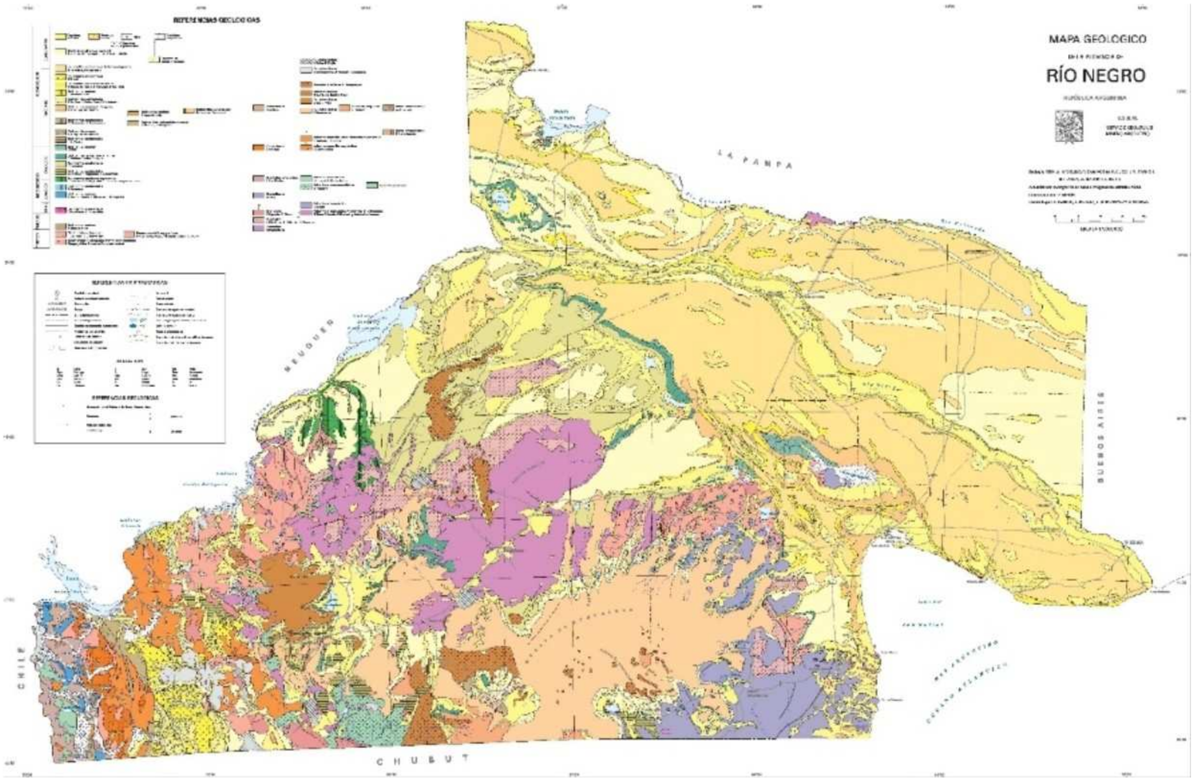

Figure 24: the geological map of Río Negro Province (see Fig. 22 for location of the region), Argentina. Taken from SEGEMAR (Servicio Geológico Minero Argentino).

These sediments have favored the preservation of fossil traces left by burrowing organisms, including numerous arthropods. As mentioned above, it has been decided to follow the route of the naturalist Joaquín Frenguelli reported in his 1939 manuscript “Viaje a las zonas central y andina de Patagonia septentrional por Joaquin Frenguelli”. Therefore, two areas of the province have been explored. The first one is the Andean zone, and the second is the southern zone of this province. They have distinct geological features and climatic characteristics.

Clearly, from a geological point of view, the processes who led to the formation of the Andes Cordillera strongly influence the former area, and several processes such as volcanism, tectonic uplift and seismicity related to subduction are still active. The morphology of this area shows glacial mountains and valleys.

The latter, the southern zone of the province, corresponds to the northern Patagonian massif called

"Somuncurá", a stable structure of Paleozoic age with basaltic plateaus dated from the Cenozoic. Whereas in the Andean zone the predominant rocks are metamorphic rocks (schists, gneisses) from the pre-Cenozoic and plutons from the Jurassic-Cretaceous, in the southern zone there are basaltic plateau from the Plio-Pleistocene and sedimentary rocks such as sandstones and limestones from the Upper Paleozoic(Serra Varela, 2019). The landscapes are composed of semi-desert plateaus and depressions (Fig. 25).

Figure 25: Semi-desert landscape of the southern zone of the Río Negro Province, Argentina.

Mar del Plata

Mar del Plata is a coastal city of the Buenos Aires province and it was chosen to observe the behavioral and features of both larvae and pupation chambers of Noctuidae. The field trip took place during December 2024. The study area is shown in Figure 26. It was selected because of its similarity to the arid and coastal areas of Lanzarote (known as the Cordonal-Taibal zone), where the ecosystem adapted to dry conditions and xerophilous and succulent plants' vegetation predominates.

Figure 26: Mar del Plata localization. *The images were obtained using Google Earth, with data sourced from Airbus, SIO, NOAA, U.S. Navy, NGA, and GEBCO. (Google Earth, 2023).*

Since during the day Noctuidae larvae usually bury themselves into the soil (Faedda et al., 2025, in prep.), under the plants from which they feed on, the work mostly involved digging in the sand to search for larvae. Eight Noctuidae larvae were found in two different locations near Mar del Plata (Fig. 27) and were later reared and studied to investigate their behavior and obtain pupation chambers.

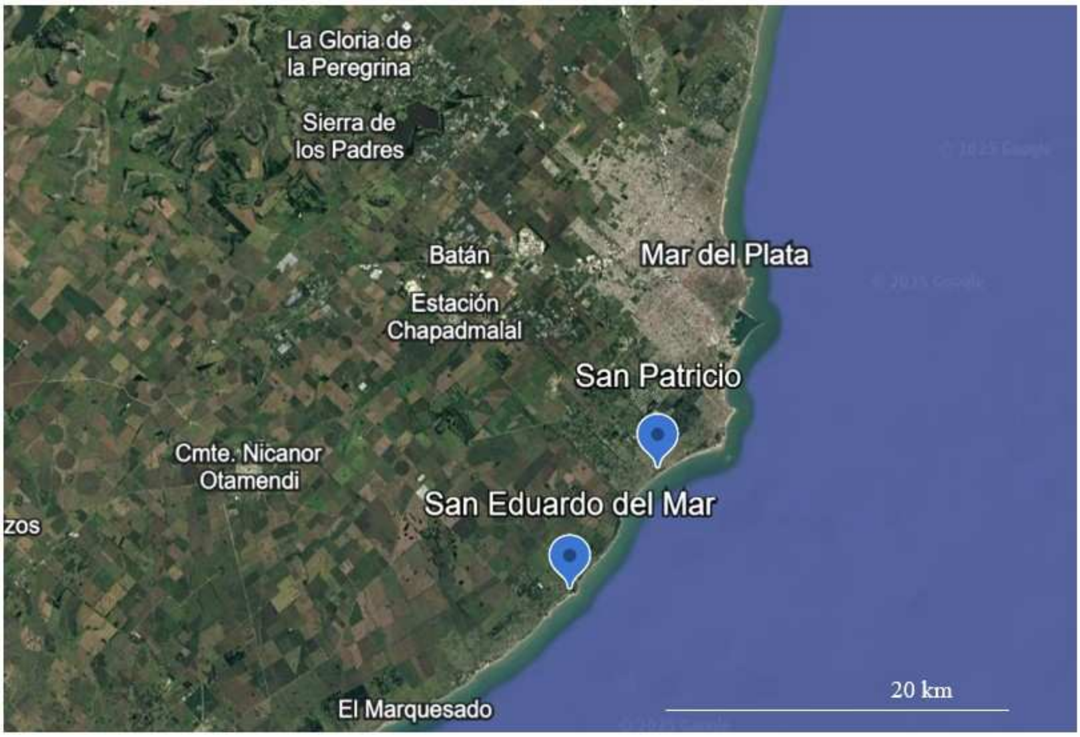

Figure 27: two sites near Mar Del Plata city have been selected: San Patricio and San Eduardo del Mar. *The images were obtained using Google Earth, with data sourced from Airbus, SIO, NOAA, U.S. Navy, NGA, and GEBCO. (Google Earth, 2023).*

San Patricio (13th December 2024)

San Patricio (38° 06' 45.2" S; 57° 35' 01.3" W) is in a region called Pampa Ondulada, in Buenos Aires Province, approximately 25 km northwest of the city of Mar del Plata. One of the particularities of this region is its soil composition (mainly clay and silt), which makes it particularly prolific and fertile, from a botanical point of view. Although flora mainly consists of halophytic plants and grasses such as *Stipa spp*. and *Poa spp*., intensive agriculture has replaced much of the native vegetation with crops such as corn, soybeans, and sunflowers. For this reason, the area has been chosen for the study of Noctuidae, as this family includes numerous agricultural pest species (Faedda *et al*., 2025, in prep.).

The research in San Patricio consisted of carefully searching for specimens of Noctuidae at the base of the mentioned plants, and finally four were collected. The larvae found were in their early instars, as shown in Figure 28.

Figure 28: four Noctuidae larvae (on the right) have been found by moving leaves and searching close to the base of several plants.

Moreover, two adults individuals have been collected, but their immediate identification was not possible. The adults have been frozen for preservation and subsequently delivered to researcher Sebastián Daniel Lupo at the Museo Municipal de Ciencias Naturales Lorenzo Scaglia for further analysis.

San Eduardo del Mar (14th December 2024)

The second sampling site lies near San Eduardo del Mar (coordinates: 38° 10' 30" S, 57° 38' 15" W), approximately 35 km southwest of central Mar del Plata and 8 km northeast of Miramar. This area of the Atlantic coast is mainly characterized by Cenozoic sedimentary cliffs. Processes, such as marine erosion, or those produced by exogenous agents, strongly affect these cliffs and have led to the formation of medium-grained sandy beaches at their base. As San Patricio site, the vegetation is composed of halophytic species adapted to marine aerosol exposure and sandy soils (Fig. 29). Additionally, some invasive species, such as *Carpobrotus spp.*, are present, competing with native plants (Novoa et al., 2023; Novoa & González, 2014).

Figure 29: The search for Noctuidae larvae and pupation chambers took place by digging in sandy substrates near halophilous plants typical of the area. Invasive alien species *Carpobrotus spp.* is visible.

In this area, a pupation chamber was found approximately 4–5 cm below the surface beneath a plant (*Melilotus albus,* Medikus 1787) belonging to the *Fabaceae* family.

Near the plant, four additional Noctuidae larvae were collected. They were collected using a sieve, in which a large quantity of sand was poured (Fig. 30). The sieve was then gently shaken to isolate the larvae.

Figure 30: sampling of Noctuidae larvae: firstly, a large amount of soil or sand is placed on top of the sieve and lightly shaken to isolate the larvae (right); secondly the larvae were temporarily kept inside a plastic jar (left) for measuring.

The larvae were found curled up, a fascinating example of cryptic mimicry used for survival, as previously mentioned in the description of Noctuidae (Fig. 14). Notably, their appearance closely resembles the empty shells of terrestrial gastropods, likely serving as a defense mechanism to make them unappealing to birds, their primary predators (Fig. 31).

Figure 31: another example of larval mimicry. A) the curved position that the larvae assume when disturbed; B) gastropod shells found in the same area as the larvae; C) typical dune landscape with numerous gastropod shells that make the larvae's camouflage profitable.

3.10: Larval rearing

Larval rearing has involved all the larvae sampled in Mar del Plata sites, thus they have been grouped into two groups, depending on both sites where they have been collected and their instars. For example, the four larvae collected from San Patricio were an early stage of growth, as they were found on the plants and not buried in the soil. Therefore, they needed suitable breeding conditions, including an appropriate environment and food supply.

A temporary terrarium was set up for initial maintenance in captivity, in which corn and lettuce leaves were provided and kept fresh by submerging them in a cup of water. It is important to point out that, due to the unavailability of a fully equipped laboratory, the terrarium was assembled using some elements brought from the museum and others obtained near the hotel (Fig. 32).

Figure 32: an initial temporary terrarium was constructed with a plastic box in which a cup of water and lettuce leaves inside was placed. The larvae were then gently placed on the leaves.

To avoid the risk of drowning in the glass of water, the larvae were then moved to a larger terrarium, where the leaves were positioned directly on the soil taken from the sampling site (Fig. 33). To reduce excessive moisture, drainage holes were made in the lower outcrops of the terrarium. The terrarium measured 21 cm high, 19 cm wide and 12 cm deep, with a soil stratum of approximately 6 cm in height.

Figure 33: the terrarium built subsequently in which corn leaves were placed directly on the sediment taken from the same area as the larvae (San Patricio).

During larval rearing, humidity level was controlled by spraying water on the substrate once a day, avoiding excessive humidity that could support fungal growth. Larvae were checked during both days and nights.

The larvae collected at San Eduardo were larger in size than those observed and collected the previous day at San Patricio. To set up the experiment, a significant amount of sand was taken from the collection site, followed by the preparation of experimental soil columns at the accommodation.

Three experimental soil columns (A, B and C) were set up to study underground behavior and construction of the pupation chamber. The soil columns consisted of two thin glass panes placed opposite each other, enclosed by a wooden frame that separated the columns. A mosquito net was used to cover them to avoid the larvae from escaping. Since all larvae presented typical morphological characteristics of the pre-pupation instar (size, location in the soil at the time of discovery and pupation chamber construction behavior), no food was initially supplied in the soil columns. The columns had an overall height of 20 cm, measuring 18 cm in width and 2 cm in depth. After measuring the body size, each larva was placed in its own soil column, which was filled with sand taken directly from the collection site to a depth of approximately 12-13 cm.

Once placed in their respective column, the larvae buried themselves in the exact point where they were laid, using peristaltic body movements to inter themselves (Fig. 34).

To monitor any nocturnal activity, checks were conducted at regular intervals (02:00, 04:00 and 05:00).

Figure 34: the burial of the larva in the soil columns in the exact position where they were placed.

RESULTS

CHAPTER 4:

The Results chapter presents the main findings of the research conducted in Patagonia and in Lanzarote on *Rebuffoichnus* and *Hemicycla* specimens.

4.1: ImageJ analysis

Image analysis was conducted on *Rebuffoichnus* and *Hemicycla* shell fragments collected from the Muñique sand pit. Specimens collected from the three stratigraphic levels, corresponding to facies associations A, B, and C, were compared to check variations in number and size across the different depositional levels.

The following statistical data were analysed and presented in Faedda et al. (2025), in prep. The results of Levine's test on the 4 groups considered (number of *Rebuffoichnus*, number of *Hemicycla* fragments, size of *Rebuffoichnus*, size of *Hemicycla* fragments) indicated p-values greater than 0.05 for all groups. The p-values are as follows: 0.8501 for the number of insect trace fossils, 0.4657 for the number of *Hemicycla* fragments, 0.9223 for the size of insect trace fossils and 0.7567 for the size of *Hemicycla* fragments.

Results allowed the one-way ANOVA to be applied, since there were no significant differences in variances and the data were normally distributed. The results are presented below in ordered sections for each of the 4 groups considered.

Number of *Rebuffoichnus*

Regarding the statistical analysis, the first step consisted in performing a Shapiro-Wilk test, to be sure that the data followed a normal distribution. Its results showed a p-value of 0.4285, well above the 0.05 level. Therefore, the normal distribution of the data was confirmed. A one-way ANOVA was then applied to show that the number of *Rebuffoichnus* was different for each Facies Association of the sand pit. Based on results of ANOVA (F (2,6) = 24.52, p = 0.0013) between the number of insect trace fossils among the sand pit levels there are statistically differences. Subsequently, a Tukey's post-hoc test was performed, which showed that there were no significant differences between Facies Associations A and B (p value = 0.9911) and between Facies Associations B and C (p value = 0.5267). Differences exist between Facies Associations A and C, however (p value = 0.0163), and Facies Association C has more insect trace fossils than Facies Association A.

As shown in the boxplot (Fig. 35), the distributions vary notably, with group C showing greater dispersion due to outliers.

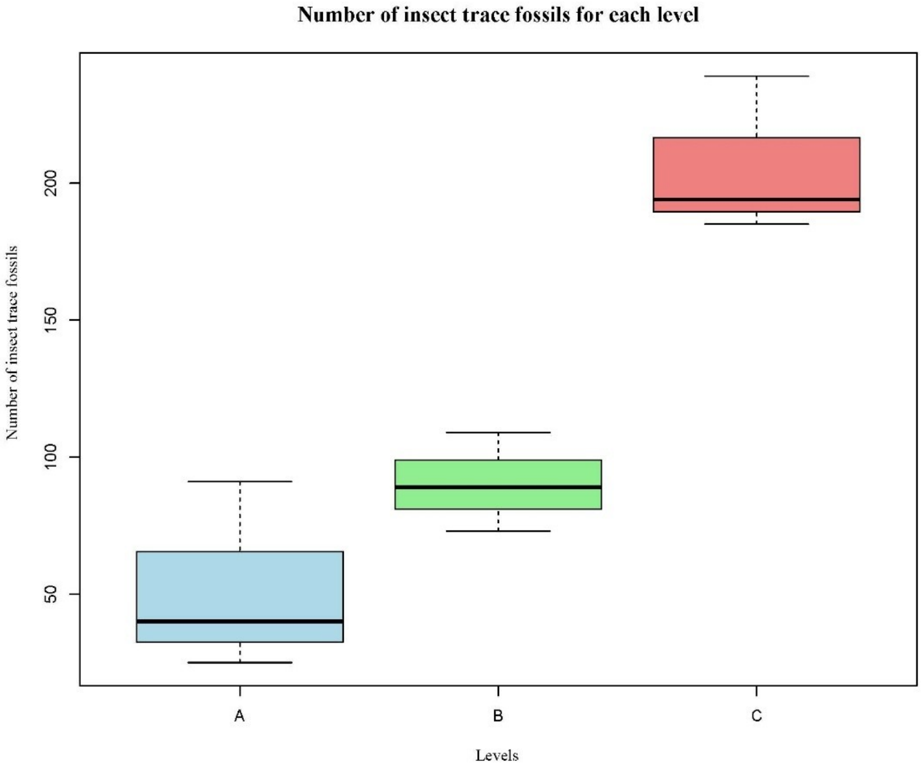

Figure 35: The boxplot expressing the number of insect trace fossils in Facies Associations (levels) A, B and C showed significant differences in the distributions of the data. In group A, the box is the largest, indicating variability in the number of traces, with a median positioned toward the lowest values. Group B has a smaller box, suggesting that the data are more concentrated around the median, which is positioned at half the height of the other groups. Lastly, in group C, extremely high values are present pushing the group upward, resulting in a larger number of insect trace fossils.

Size of insect trace fossils

As in the former case, firstly a Shapiro-Wilk test was conducted. Its results showed a p-value of 0.675, indicating that data follow a normal distribution. Later, a Kruskal-Wallis test on the size of insect trace fossils ($p = 0.03899$) confirmed significant differences.

Therefore, *Rebuffoichnus* sizes vary across sand pit Facies Associations A, B, and C. This result was also confirmed by a one-way ANOVA (F (2, 6) = 10.02, p = 0.0122).

Finally, a post-hoc Tukey test was conducted to find out which Facies Associations differed. The results showed no significant difference between groups A and B (p = 0.1061) or between groups A and C (p = 0.1933). However, a significant difference was found between Facies Associations B and C (p = 0.0101), with *Rebuffoichnus* in Facies Association B larger than in C. Results are shown in a boxplot (Fig. 36).

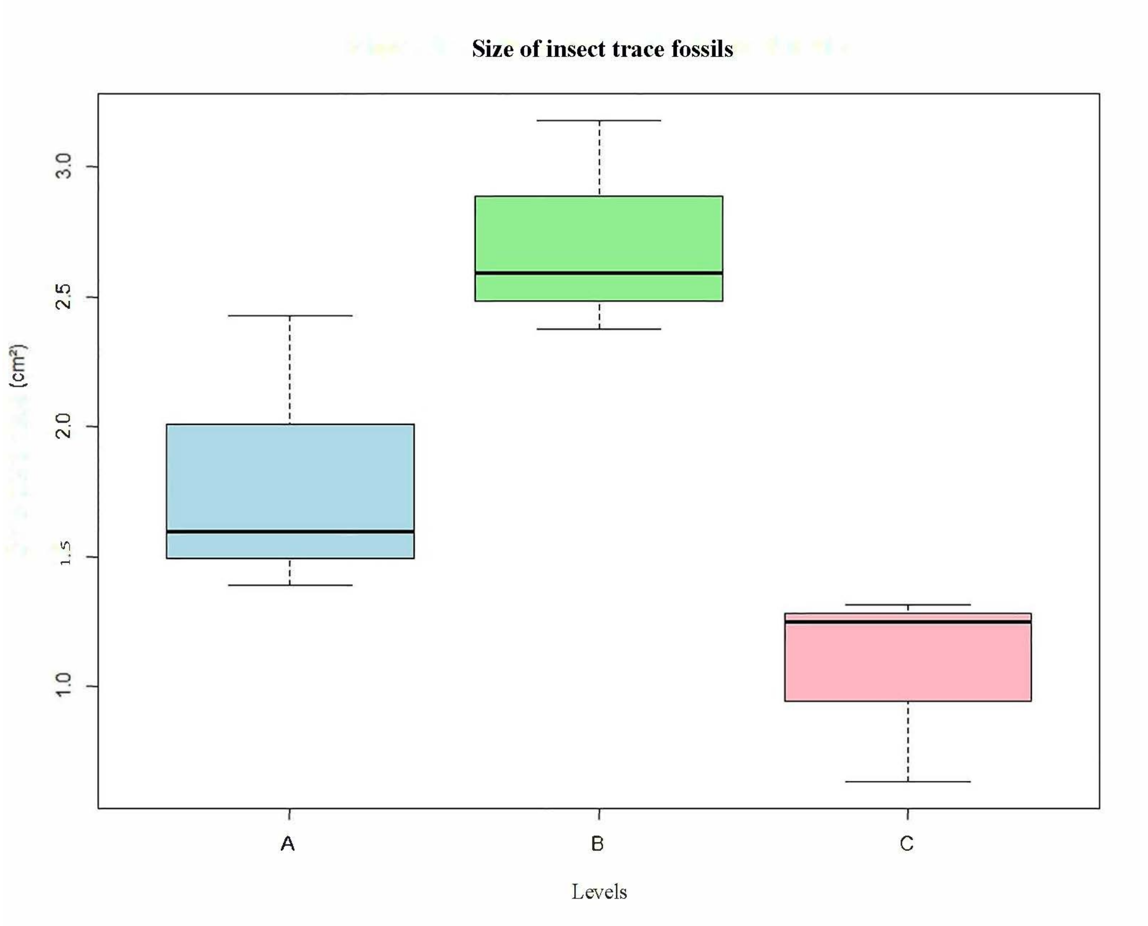

Figure 36: The boxplot illustrates the differences between the sand pit Facies Associations (levels). It shows that groups A and B exhibit greater variability in trace fossil sizes, whereas group C has a more concentrated distribution, with some values classified as outliers. *Rebuffoichnus* in Facies Association B are larger than in C.

Number of *Hemicycla* shell fragments:

Before applying ANOVA, a Shapiro-Wilk test was performed (p= 0.6195), and it showed that the data followed a normal distribution. The ANOVA showed a statistically valid difference between the groups (F (2,6) = 12.91, p-value = 0.00671), indicating that the number of *Hemicycla* fragments varied between Facies Associations A, B and C. Later, a Tukey's post-hoc test showed that between level A and B there were no differences (p=0.1079), and neither were there differences between level A and C (p=0.0872). However, there was a significant difference between level B and C (p=0.0054), with a significantly higher number of *Hemicycla* shell fragments in Facies Association C, as shown by the bar graph (Fig. 37).

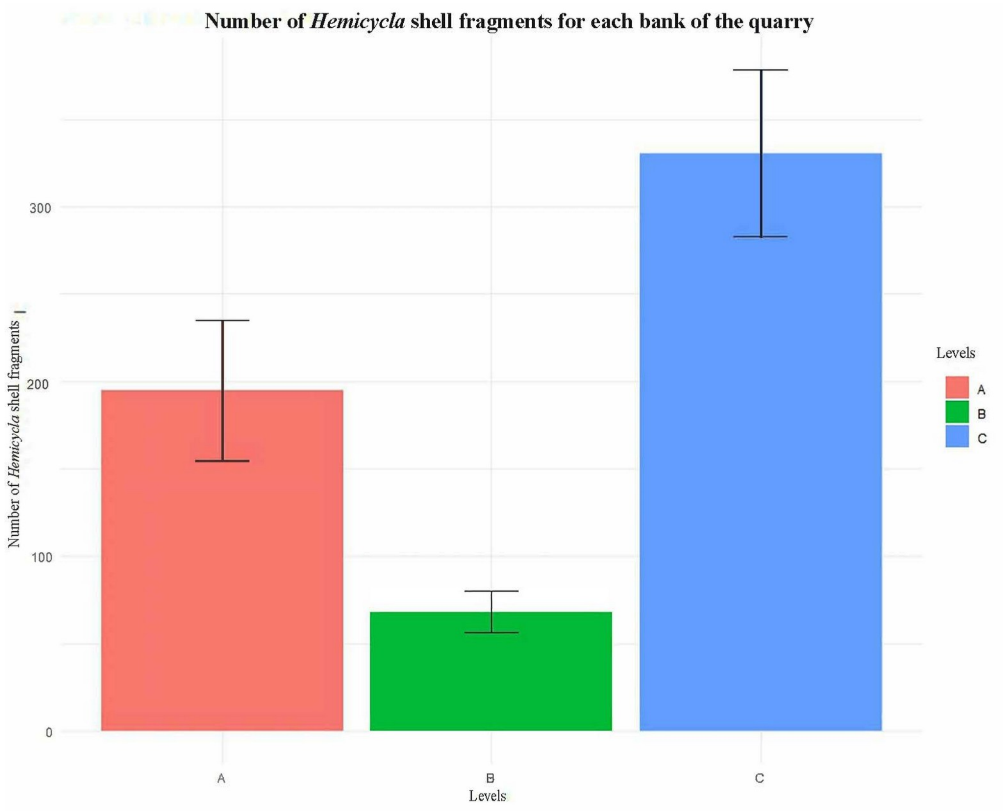

Figure 37: The bar graph shows the mean number of *Hemicycla* for each level (sand pit Facies Associations A, B, C). The differences in the means between Facies Associations are visible, with the standard error showing the variability of the data within each level.

Size of *Hemicycla* fragments

Even for mean sizes of *Hemicycla* shell fragments, after conducting Levene's test, which, as mentioned at the beginning of the chapter, showed the normal distribution of the data, a one-way ANOVA was applied to find out if the mean size of *Hemicycla* fragments changed within the different sand pit Facies Associations (A, B and C). The ANOVA results (F (2,6) = 0.227, p-value = 0.803) did not present any significant difference for this variable among the three levels. Although a bar chart (Fig. 38) visually suggests some differences, the ANOVA p-value confirms that these differences are not statistically valid.

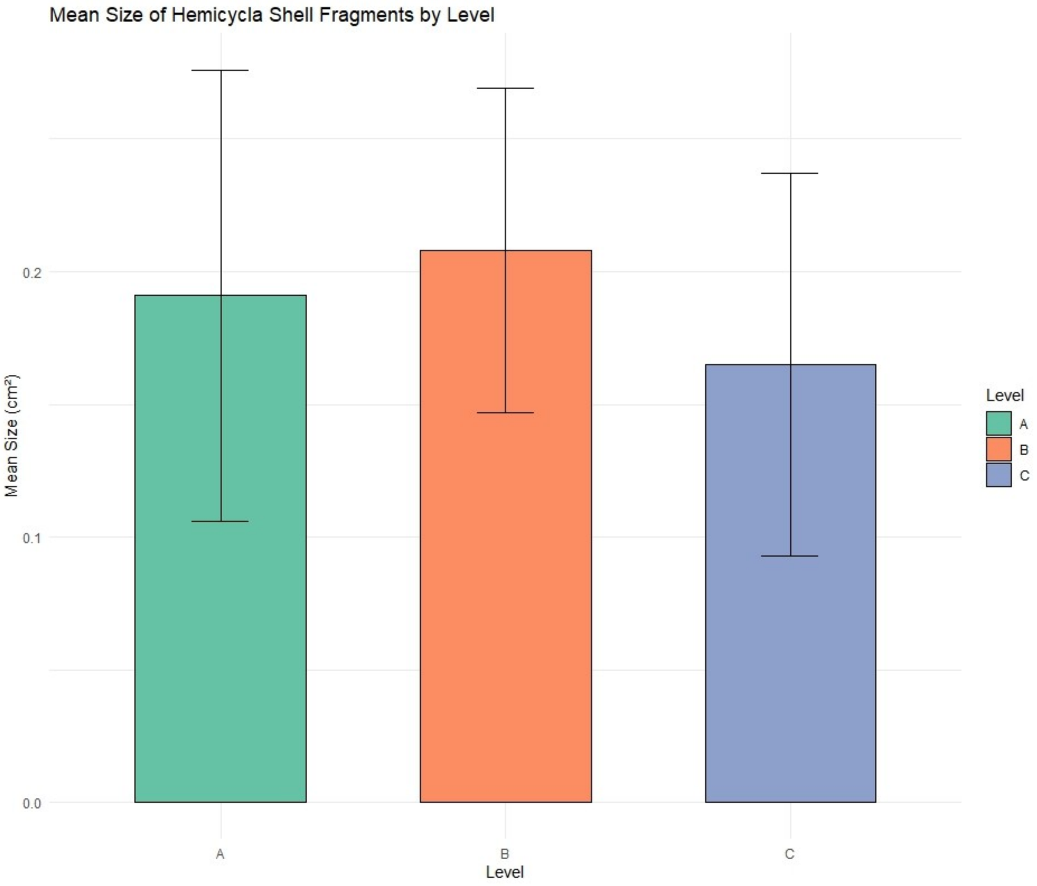

Fig. 38: Bar chart of the average size of *Hemicycla* shell fragments for each level (sand pit Facies Associations A, B, C). While visual differences can be observed in the distributions, the ANOVA analysis did not detect statistically significant differences between the levels (p-value = 0.803).

4.2: Dating of the larva and taxonomic classification

The larva found in the accidentally broken pupation chamber belongs to Noctuidae family. Radiocarbon results show that the larva has an age between 1954 and 1956 ce (radiocarbon of 100.25 ± 0.37 pMC).

4.3: Ichnology and statistical analysis

A statistical analysis was performed on the *Rebuffoichnus* found both in the Muñique sand pit and in the Famara outcrops, particularly at the Piletas, Falls, and Horca sites (Fig. 6), in order to verify if the comparison of their dimensions across these localities revealed noticeable variations.

Statistical analyses were performed on every fossil specimen but considering only two parameters, major axes and minor axes: these were the only ones that could be measured in all of the complete specimens collected. Other variables were not measurable in all of them. Analysis of variance (ANOVA) showed that there was a significant difference between insect trace fossils from different locations for both the major and minor axes. The analysis on the major axes showed that there was a significant difference between the groups ($F(3, 69) = 22.38$, $p < 0.0001$), with Piletas having the highest mean (28.46 mm), followed by Horca (28.26 mm), and Falls showing the lowest mean (20.41 mm). The results on the variance show that Falls had the highest (22.42) and that there was therefore a lot of dispersion within this group. The minor axes analysis similarly showed differences between specimens from different groups ($F = 3, 68) = 18.97$, $p < 0.0001$). The means ranged from Falls (13.00 mm) to Piletas (20.31 mm), with Falls also having the highest variance (9.99), suggesting biggest variability in this group than in the others.

Furthermore, a two-way ANOVA without repeats was also performed, which indicated differences between the groups for both parameters, major axes and minor axes. Thus, the morphological characteristics of the specimens vary according to geographical area ($F = 5.58$, $p < 0.05$) and the measurements of the minor axes and major axes are not correlated with each other ($F = 284.55$, $p < 0.05$).

4.4: Comparison of present-day and fossil chambers

The distinctive morphological features observed in the specimens allowed the traces to be classified according to the ichnotaxonomic guidelines proposed by Genise (2017). Most of the specimens show an elongated sub-ellipsoidal shape, with a sub-circular inner chamber cross-section and a rough-textured outer wall (Fig. 19). Among the most frequently found features, the end corresponding to the exit hole is truncated, with the upper portion slightly protruding from the lower one, while the opposite end appears more rounded. In addition, one of the side faces is flattened, giving the structure a tendency to lean to one side. Many specimens have a passive posterior cemented filling, which in some cases occludes the exit hole or other secondary cavities. Bioclast inclusions and small fragments of land snail shells embedded in the structure are also common. Some specimens show surface incisions or secondary perforations, probably due to parasitism or other biotic interactions. The grain size of the sediment ranges mainly from medium to fine grained sand, with a few exceptions characterized by a coarser sandy matrix.

The six specimens of modern pupation chambers of Noctuidae showed the following results: their structure is fragile and are made of medium-coarse sand which forms recognizable laminations in the inner walls. One of the closed chambers, when shaken, produces a soft vibration and a clanging sound, indicating the presence of an insect remaining inside. One open chamber has an almost perfectly circular hole, is externally rough and shows a layered structure (Fig. 15). Some of the chambers of Noctuidae have coarse materials with some pieces of residual vegetation, while others are more homogeneous.

Statistical Analysis on fossils and modern chambers

Statistical analyses were performed on only two parameters, major axes and minor axes, because they were the only ones that could be measured in all the specimens collected. Other variables were not measurable in all of them. Analysis of variance (ANOVA) showed that there was a significant difference between fossil nests from different locations for both the major and minor axes.

Comparison of modern and fossil chambers

The criteria used to compare the fossil and modern chambers were the major axes and minor axes, as these were the only two parameters that could be measured in all specimens. The number of fossil specimens was larger than the number of modern specimens, and for this reason a simple random sampling was conducted between the fossil ones to equilibrate the numerosity of specimens: 6 fossil and 6 moderns were considered.

Major axes: The homogeneity of the variances between the groups was checked through an F-test (with a p-value higher than 0.05), which means that the variances were similar between the fossil and modern specimens. For independent specimens with comparable variances, a T-test was performed. For the major axes, the mean of *Rebuffoichnus* specimens was 21.6 mm and for the Noctuidae chamber was 22 mm, and according to the T-test performed, their variances were of 11.792 and 20.516 respectively.

The T-value result was -0.17, with a p-value of 0.87 (two-tailed), much higher than the level 0.05. Therefore, there is no significant difference between the fossil and modern major axes means.

Minor axes: For the minor axes, the same T-test was applied, as the F-test which revealed no significant differences between the variances of the *Rebuffoichnus* and modern specimens ($p > 0.05$). The minor axes mean of the fossil specimens was 15.42 mm, while the modern specimens one was 11.72 mm, with variances of 9.64 and 5.61. The t-value results in 2.32, with a p-value of 0.042 (two tails), below the significance level of 0.05. Thus, in contrast to the major axes, *Rebuffoichnus* have larger minor axes compared to Noctuidae pupation chambers.

In conclusion, these results suggest a morphological variation between the two groups over time.

4.5: Micromorphology results

In this study the internal cavities and the wall thickness of *Rebuffoichnus* specimens have been measured through micromorphology. The following results were obtained and presented in Faedda *et al*. (2025), in prep.

Two specimens were cut throughout the longitudinal section: the ones from facies **Sa** (ELJ10, ELJ12) show an external diameter of 16.4 mm and an internal diameter of 12.2 mm, with an external length of 24 mm and an internal length of 21.5 mm. The wall thickness ranges from 1.5 mm to 2.7 mm; the one from facies Wcg (ELJ3) exhibits an external diameter of 15.5 mm and an internal diameter of 11.1 mm; the external length measured 20.7 mm, while the internal length measured 17.5 mm. The wall thickness measured ranges from 2.5 mm to 3 mm. Other two specimens were cut throughout the transversal section: ELJ8 shows an external diameter of 17.6 mm and an internal diameter of 11.8 mm, with a wall thickness ranging from 2.3 mm to 3.1 mm;

ELJ10 exhibits an external diameter of 16.5 mm and an internal diameter of 12.6 mm, with a wall thickness ranging from 1.7 mm to 2.8 mm.

Thin sections of all four specimens revealed the same microstructure and micromorphology. The characteristics observed in all of them are summarised in the description provided herein.

The interior of the chambers is more compacted, as is evident from their observation. This is due to the presence of micritic fine material, which results in lower porosity and greater contact between grains. This heterogeneous distribution of porosity results in two distinct zones within the wall: an internal zone that is more compacted and occupies less than 50% of the wall's thickness, and an external zone that is less compacted.

Analysing the microstructure, specimens show walls characterized by internal massive (Porosity: 5%) microstructure and external single grain and bridge microstructure (Porosity: 35-40%).

The 90% of the wall coarse fraction is represented by elongated to equidimensional, rounded to sub-rounded clasts, and scarce subangular carbonate bioclasts. Bioclasts are mostly whole microfossils (200-500 µ in size) and fragments which have a parallel orientation to the inner surface of the wall and moderate selection. Volcanic rock fragments are common.

The fine fraction constitutes 10% of the wall and consists of micrite (fine-divided carbonate). Some of the bioclasts are covered by amorphous matter (organic or manganese oxide), which also forms bridge structures, mottles and dendrites (Fig. 39). This amorphous matter forms discontinuous lines that are irregularly distributed throughout the wall.

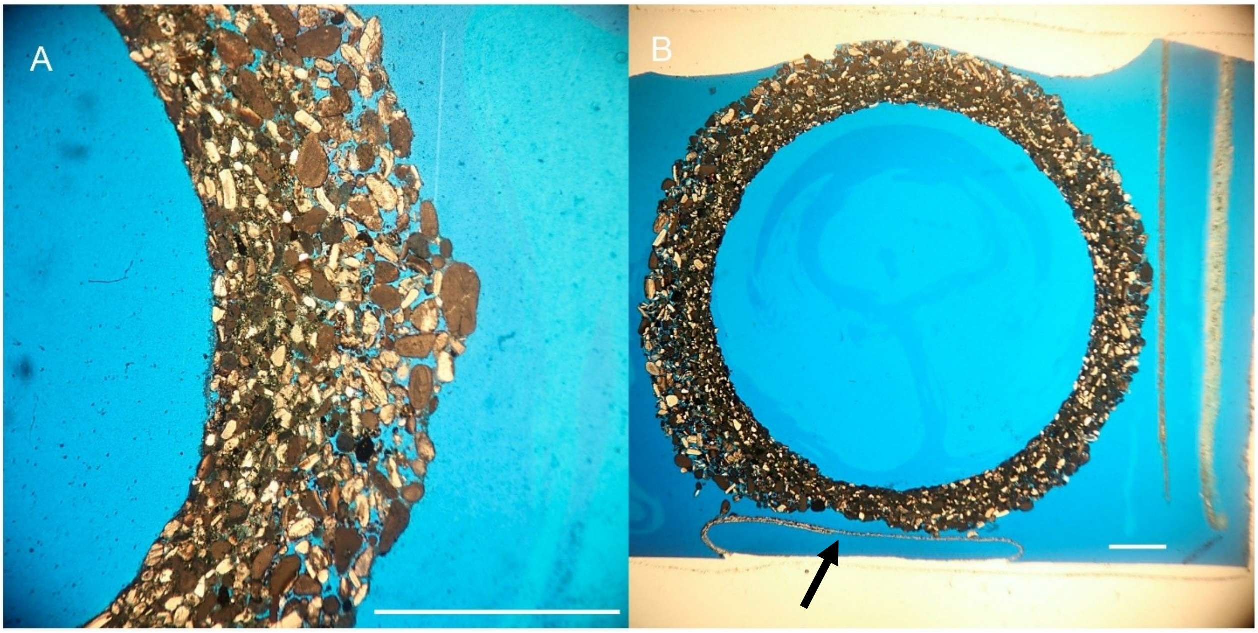

Figure 39: A *Rebuffoichnus* specimen transversally sectioned. A) a detail of the wall showing an internal more compacted zone and an external more porous zone. A parallel orientation of the more elongated grains to the inner surface of the wall is visible. B) cross section of a fossil pupation chamber showing the internal perfectly circular section and the external flattened surface; Taken from Faedda *et al*., 2025, in prep.

4.6: Tomography results

Tomography confirmed the elongated, sub-ellipsoidal external morphology, showed a sub-circular internal cross section and allowed a virtual reconstruction of the *Rebuffoichnus* isp. specimens and that a modern pupation chamber of Noctuidae has a similar structure and wall characteristics (Figs. 40 and 41).

One specimen (MACN-Icn 1015) is filled with passive sediment and shows a perfectly circular inner section, despite the external outline is interrupted by a flatter part (Fig. 40). A second sample

(MACN-Icn 1016) shows the same general features but, in this case, the internal cavity remains unfilled. Tomographic analysis of the fossil chambers allowed noticing an important feature in the wall: there are two distinct areas that can be identified, an inner zone that is more compact and a more porous outer zone, composed of grains and finer material distributed in a different way (Fig. 40).

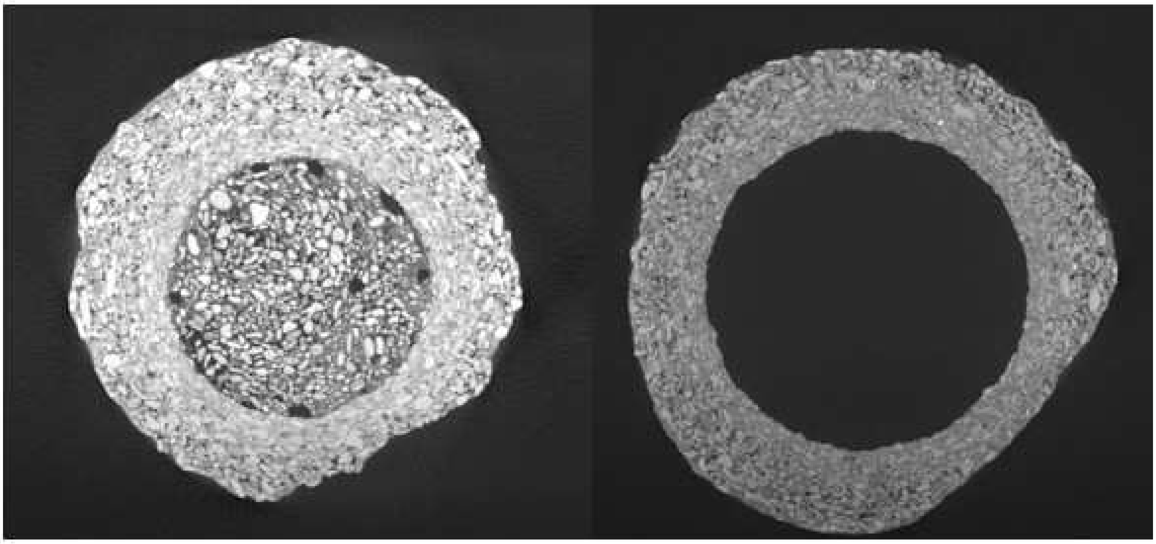

Figure 40: tomography images of two *Rebuffoichnus casamiquelai* specimens, one showing the inner cavity filled with sediment (A) and another with an empty cavity (B). Both examples show the perfectly circular internal cross section, an internal more compacted zone and an external more porous zone of the wall, and the external flattened surface. Taken from Faedda *et al.*, 2025.

The chamber attributed to Noctuidae also has a circular inner section with a flattened portion, and its wall reveals the same dual disposition of grains and fine material (Fig. 41). A 3D video rendering of the tomographic scans is provided in the supplementary material (Video S1).

The Noctuidae pupation chamber shows a circular inner cross-section as well and a flatter outer part and also reveals the same distribution of grains and fine material in the wall.

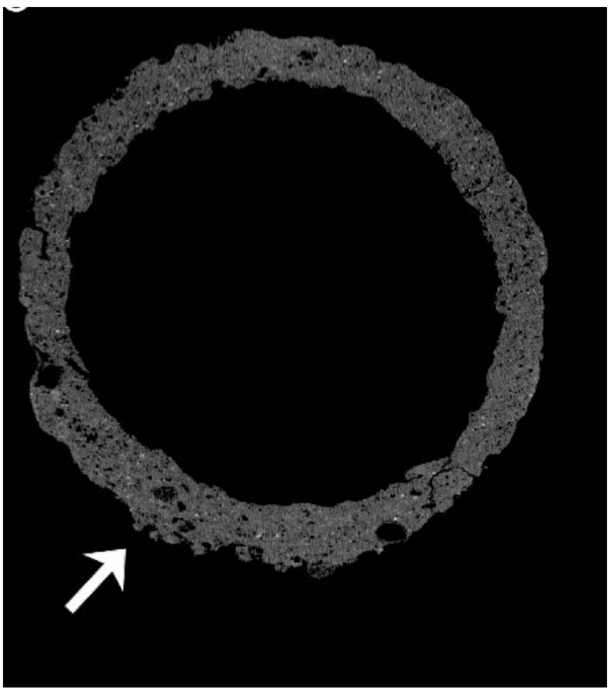

Figure 41: the modern pupation chamber displaying the flattened ventral surface indicated by an arrow. Taken from Faedda *et al*. (2025), in prep.

4.7: Dating specimens and sedimentary deposit

Results of Muñique sand pit

According to Heinrich *et al*. (2021) and Faedda *et al.* (2025) and starting from the lower outcrops to the upper outcrops of the sand pit, the dates range from 108 ka at the base of Facies Association A to about 12 ka at the upper outcrops of Facies Association C (Fig. 16). These ages indicated that the Muñique sand pit formed during Marine Isotope Stages (MIS) 5d to 1, including sub-stages 5d, 5c, 5b, 5a, and the MIS 4, 3, 2, and the onset of MIS 1.

The following description is presented after the stratigraphic and chronological framework defined by Faedda *et al.* (2025).

The lowermost deposits of the Muñique pit (DepoType 1 of Heinrich *et al*., 2021) consist of ~2 m of grey, poorly cemented medium sandstone with large-scale planar and trough cross-bedding (facies Sa), interpreted as aeolian dunes. These grade upwards into brown, bioturbated sandstones (facies Sb; DepoType 2), which locally contain scattered insect traces and shells of *Hemicycla*. An erosive boundary separates this unit from the overlying DepoType 3, corresponding to facies Wlg: dark brown, well-cemented, laminated, normally graded sandstones with thicknesses varying from 20 cm to 1 m. Within this unit, a horizon rich in land snail shells and insect traces divides the deposit into two distinct layers. Where preserved, the upper surface exhibits desiccation cracks. These sandstones are interpreted as distal alluvial fan deposits dominated by unconfined sand sheets and ephemeral streams. Luminescence dating by Heinrich *et al.* (2021) showed an age of 71.6 ± 4.6 ka for these facies (Fig. 16). These deposits represent the unit of Facies Association 1.

Facies Association 2 begins with up to 2.5 m of cross-bedded sandstones (Sa), overlain by 1 m of bioturbated sands (Sb). A sharp erosional contact truncates this sequence, above which occur channelized, cemented medium- to fine-grained sandstones (Wcg) bearing abundant insect traces. A thin (~20 cm) Wlg layer overlies this, again with insect traces and desiccation cracks. The AMS ^{14}C ages reported for facies Wcg is 30.677±637 ka, which is consistent with the 36.3±2.3 ka and 23.6±1.5 ka luminescence ages previously obtained by Heinrich *et al.* (2021) (Fig. 16).

The uppermost Facies Association C starts with nearly 4 m of cross-bedded sandstones (Sa), truncated by a sharp erosional surface, and overlain by poorly cemented, channelized medium sands (Wcg). These deposits contain both insect trace fossils and land snail shells, in some cases with the traces preserved in life position. A *Hemicycla sp.* shell from this Wcg unit was dated using AMS ^{14}C, yielding an age of 12.7 ± 0.05 ka (Fig. 16).

A humid episode between MIS 5 and MIS 4 (probably 71 kyr, corresponding to Heinrich event 7A) led to the stabilization of underlying dunes and the formation of mud cracks at the base of the sand pit, between the facies Sb and Wlg (Fig. 42).

These dunes (facies Sb of Facies Association A) seemed to remain stable until approximately 52 ka. Dune stabilization likely occurred progressively, beginning at the margins of the El Jable plain and advancing toward its center. Ongoing analyses of other specimens continue to support this pattern.

Figure 42: mud cracks found on the upper outcrops of Facies Association A, between facies Sb and Wlg.

Results of Famara Cliff

The stratigraphic work carried out for each chosen site in the alluvial fan area (LZ403, Horca, Las Piletas and Falls) led to the recognition of five main depositional environments: talus cone, proximal fan-head, medial fan, distal fan, and aeolian system (Fig. 43).

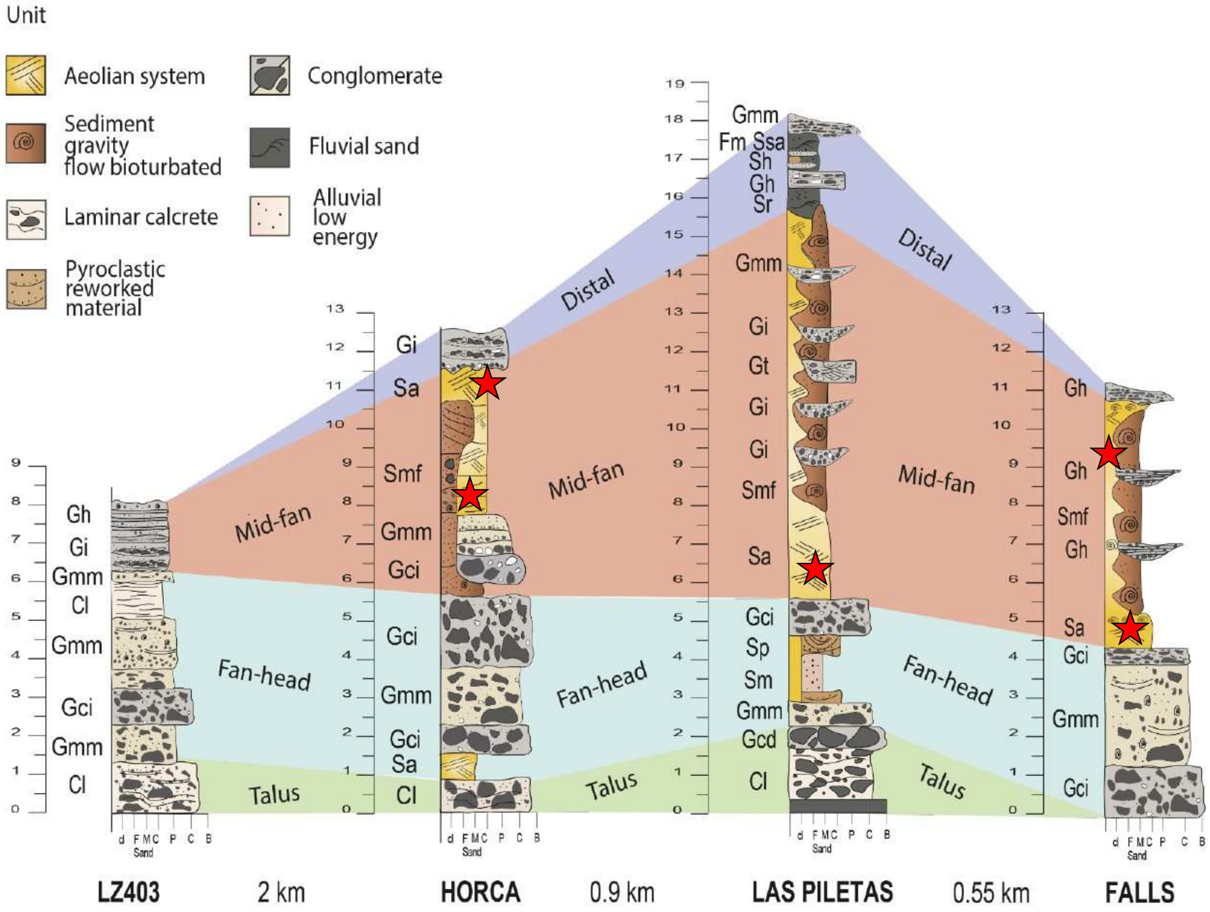

Figure 43: Simplified stratigraphic logs from four barrancos (LZ403, Horca, Las Piletas, and Falls) within the alluvial fan complex depict the different depositional zones (talus, fan-head, mid-fan, and distal fan) distinguished based on lithofacies characteristics. Taken from Stelletti (2024). Red stars indicate the presence of *Rebuffoichnus* ispp.

Research on the four barrancos reveals a north–south evolutionary trend. The succession evolves from steep sectors dominated by gravity-driven deposits to gentler areas where fluvial and aeolian sediments alternate. In the northern sites, such as LZ403 and Horca, the deposits mainly consist of coarse, debris-flow and breccia units typical of the upper fan zones. Southward, in Las Piletas and Falls, these are progressively replaced by finer fluvial sands and aeolian dune facies that mark the transition towards the El Jable plain.

Overall, the alternation between alluvial and aeolian deposits reflects changes in surface processes and environmental conditions through time. Periods of higher water activity led to the development of fluvial channels and debris flows, while drier phases favoured the accumulation of wind-blown sands and dune migration. Aeolian deposits often cap or truncate the fluvial units, indicating moments of reduced sediment supply and surface stabilization.

Fossil traces assigned to *Rebuffoichnus* were found within these upper levels, as shown by the red stars in Figure 43. They occur mainly in the aeolian facies of Las Piletas and Falls, and locally in the uppermost layers of Horca. Their presence points to brief intervals of soil formation and colonization by insects, suggesting that even within this highly dynamic system, short-lived stable surfaces developed across the fans.

Stratigraphy of barrancos

Each site considered in this study has already been investigated in detail by Ostera (2025).

For the purposes of this work, the descriptions are presented following a north–south geographical order (Fig. 6).

The first site is the LZ403 barranco, located at the northernmost position and characterized by the steepest gradient. The uppermost portion of its alluvial fan is dominated by carbonate-rich clast. Within the exposed stratigraphic succession, two main lithotypes can be identified: conglomerates, which occur both at the lower and at the upper outcrops of the sequence, and intervening levels of sandstone (Fig. 44). The overall matrix of the deposits consists of carbonate sand with an average grain size.

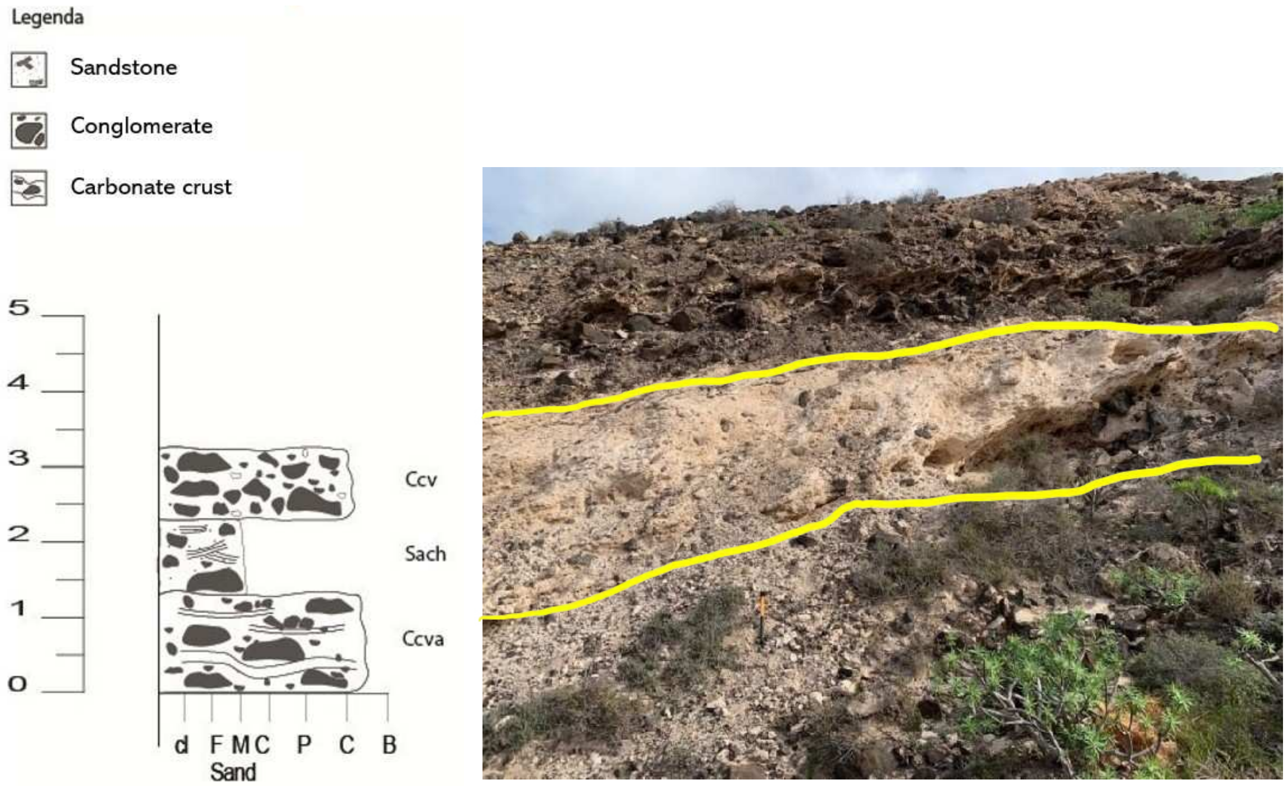

Figure 44: on the left, the stratigraphic column of the part of the fan LZ403 closest to the source, the proximal deposit; on the right, the deposit with the subdivision of the layers. Taken from (Ostera et al. 2025).

Proceeding towards the south, the second barranco studied is HORCA (Fig. 6).

This is the longest of all the gullies examined. As in the previous case, a carbonate crust forms the basal unit; however, this one is characterised by the predominance of boulders embedded in the carbonate matrix. Above this level there is a clast-supported conglomerate composed largely of boulders, with only a few pebbles scattered within the carbonate matrix (Fig. 45). Thick conglomeratic bodies and cross-bedded sandstones indicate the reactivation of an alluvial fan under variable flow energy. The alternation of sandy and gravelly intervals suggests short-lived but intense episodes of sediment transport, followed by more stable depositional conditions.

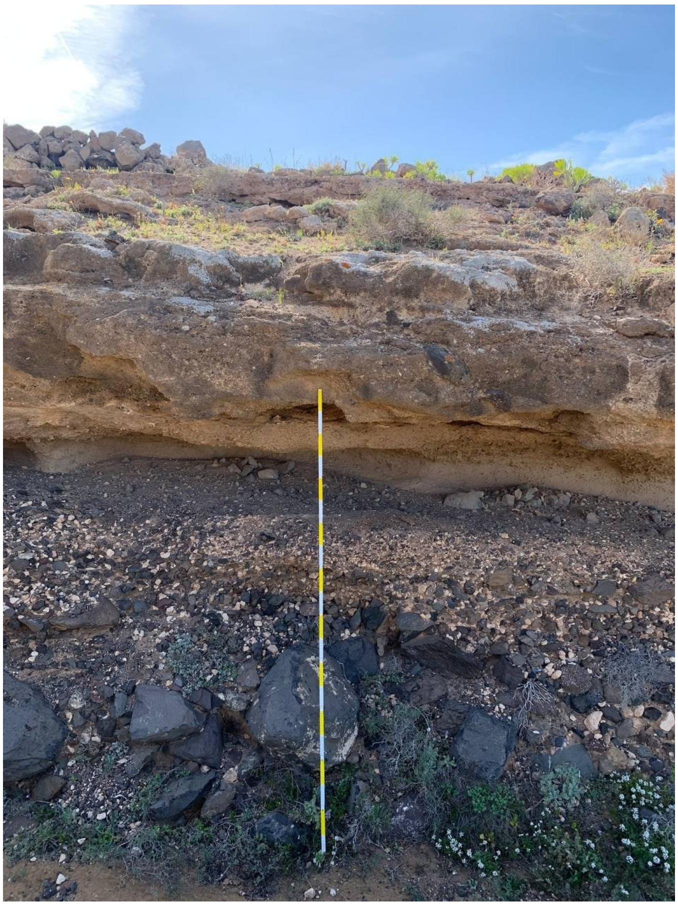

Figure 45: Proximal HORCA barranco deposit. Taken from Ostera (2025).

The barranco named Falls is the shallowest among the systems studied. Its main characteristic is the presence of a small waterfall of about 5 metres high (Fig. 46), which gives the barranco its name. Another important feature of this barranco are the markedly deeper incisions along its course, with walls reaching 6 metres in height (Figs. 47 and 48).

Figure 46: the small waterfall which gives the name to the barranco.

Figure 47: incisions in the intermedium part of barranco FALLS.

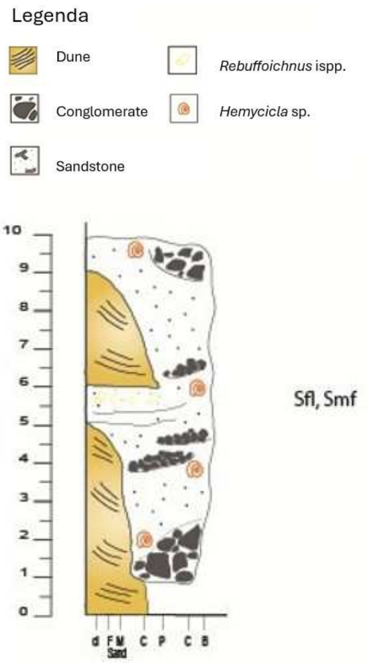

Figure 48: on the left, the stratigraphic column of the part of the barranco FALLS more distal to the source; on the right, the deposit with the subdivision of the layers. *Hemicycla sp.* and *Rebuffoichnus* ispp. are present. Taken from Ostera (2025).

Here, the stratigraphic succession includes a well-defined conglomeratic base overlain by sandstones that host abundant *Rebuffoichnus isp.* and *Hemicycla* shells. (Figs. 49 and 50). The fossil-bearing levels occur near the top of a conglomeratic unit interpreted as the reactivation phase of the alluvial fan, dated between 44 and 40 ka. This section provides the clearest evidence linking biogenic structures with the sedimentary dynamics of the fan system.

The *Rebuffoichnus* level (Figs. 49, 50 and 51) begins *in situ* (they are well oriented, and the exit hole faces between 87°E and 11°N).

Figure 49: bioturbated deposit near the waterfall of the same name in the FALLS barranco.

Figure 50: detail of bioturbation caused by the presence of *Rebuffoichnus* ispp.

Figure 51: the orientation of *Rebuffoichnus* ispp. is particularly visible in this deposit near the waterfall.

Finally, the southernmost site, Las Piletas, displays a progressive transition from debris-flow and fluvial deposits to fine-grained sands and aeolian layers. This evolution marks the gradual shift from alluvial to dune environments across the central plain.

Piletas barranco was investigated less extensively than the previous ones, mainly due to logistical constraints and time limitations. The stratigraphy and facies analysis presented here are taken from the work of Stelletti (2024) (Figs. 52 and 53).

In the proximal area of Piletas, the stratigraphy shows alternating high-energy debris flow events with episodes of fluvial deposition. The deposits are dominated by poorly sorted conglomerates, sometimes supported by clasts and sometimes by matrices, which mainly contain basaltic fragments together with carbonate and pyroclastic clasts (Fig. 52). The interbedded sandy bodies, which locally show planar crossbedding, indicate the contribution of short-lived but powerful channelled flows. In this context, the presence of well-developed crossbedding is particularly significant, as it probably formed in the convergence zone of neighbouring cones, marking one of the most distinctive sedimentary features in the proximal section of this barranco.

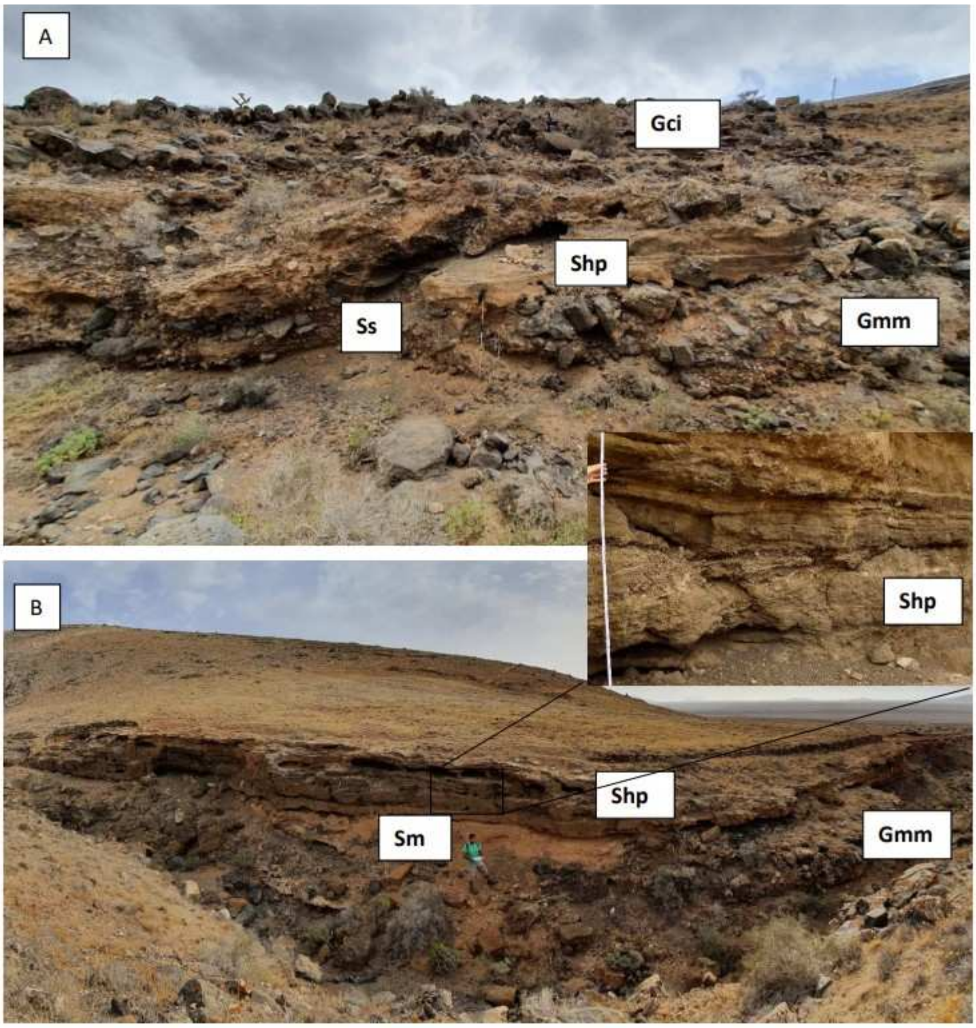

Figure 52: the proximal part of the PILETAS barranco. A: debris flow deposits, with matrix supported and open work conglomerates; B) colluvium deposits. Taken from Stelletti (2024).

Continuing downhill, the deposits undergo a clear transition to a different: thick intervals of massive sands are alternated with gravelly bodies, recording a shift to more sustained fluvial activity. Gradually, the system evolves into finer-grained deposits, where laminated rippled sands indicate shallow, low-energy flows (Fig. 53).

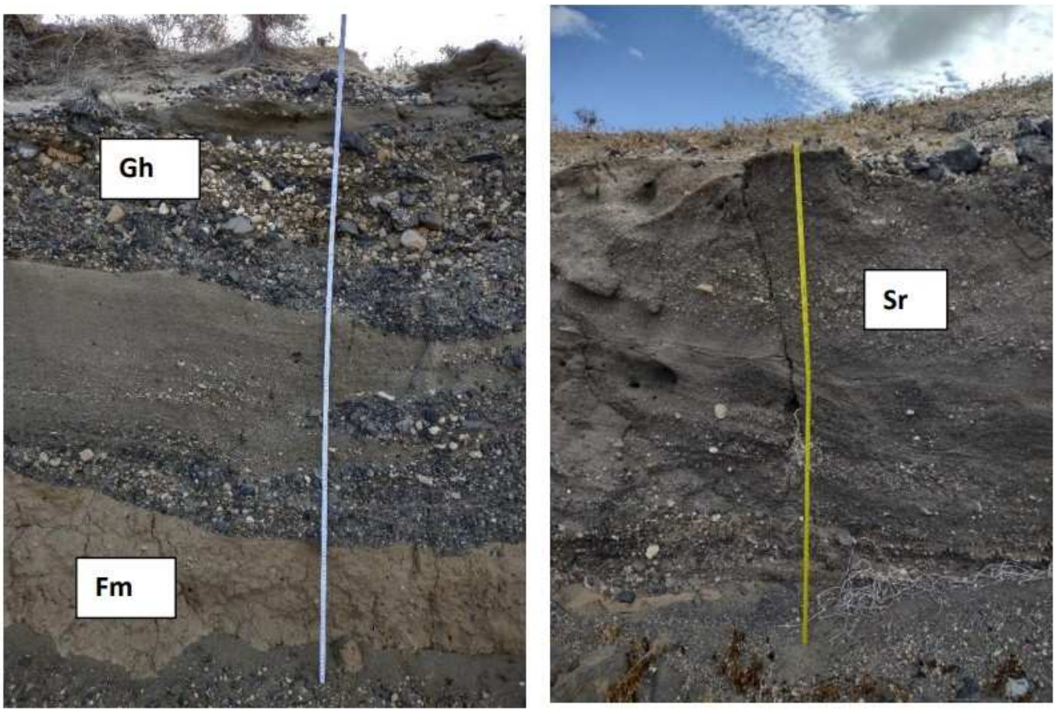

Figure 53: fluvial deposits in PILETAS barranco. Taken from Stelletti (2024).

What distinguishes Las Piletas from other barrancos is the development of stagnant water sequences, composed of alternating mud, laminated sands and thin aeolian interbeds. Finally, the distal part of the alluvial fan captures the gradual transition from alluvial sedimentation to the dune fields of the surrounding plain (Fig. 54).

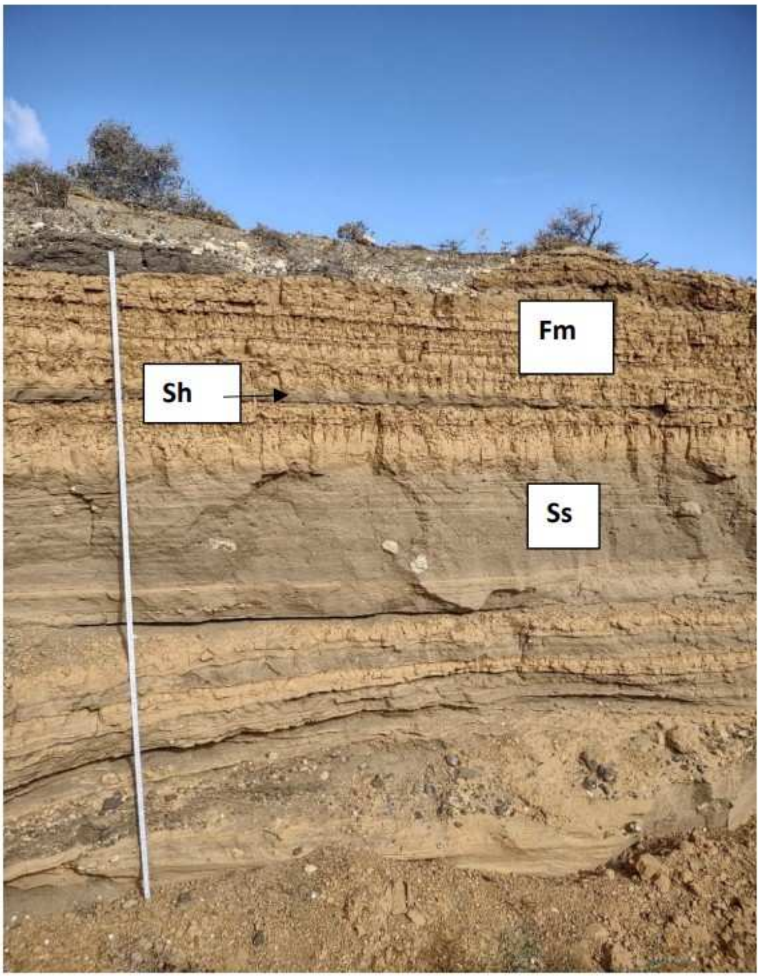

Figure 54: the transition from subcritical to supercritical flow or during initial sand bed movement at low flow speeds. Taken from Stelletti (2024).

The stratigraphic documentation of the barrancos conducted by Stelletti (2024) and Ostera (2025) shows a north-south variation. In the northern sectors, where the slopes are steeper, gravitational deposits prevail, while further south, sediments deposited by water become more common, interspersed with wind dune systems (Fig. 55).

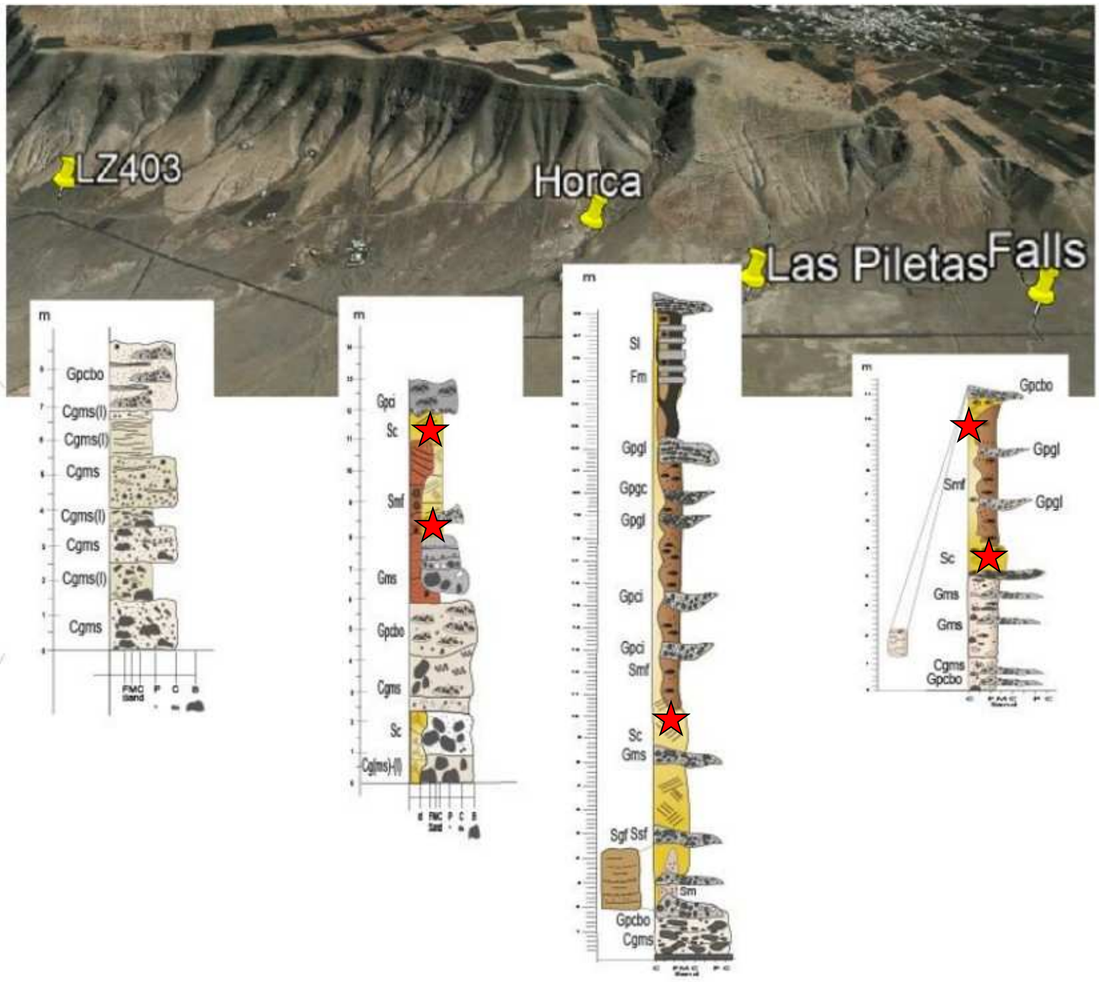

Figure 55:

Modified after Stelletti (2024). Red stars indicate the presence of *Rebuffoichnus* ispp.

Stratigraphic correlation of the barrancos

Starting with barranco LZ 403, no absolute ages were obtained. According to the inclination of the deposit and the permanence of the main carbonate crust along the barranco, it is possible to recognise two different systems of debris cones above it. The lower one, which developed in contact with the carbonate layer, shows clear reworking of the matrix under the influence of water and is relatively limited in extent. Within this debris cone, it is possible to separate a proximal part with few clasts from a distal portion where channelling is evident. A second fan overlaps the first and, although it reworks part of the underlying material again, it is less extended. The grain size suggests stronger erosion: pebbles and boulders predominate in the upper part, while in the valley the deposits are characterised by well-embedded pebble-sized clasts without matrix (Fig. 56).

The HORCA barranco is longer and provides evidence of three deposition systems. At the base, there are gravitational deposits covered by alternating aeolian and alluvial systems (Fig. 56). The latter two systems are relatively balanced in terms of thickness and distribution. It is particularly clear that the dune deposits are often eroded by alluvial events, which cut into them and form lenses and, in some cases, small channel fills.

LAS PILETAS area is the best dated, due to both radiocarbon and luminescence samples. PILETAS ages range from about 13 ka to more than 90 ka, thus including both glacial and interglacial intervals. The most recent levels (13-25 ka) correspond to the upper dune and soil levels, while the intermediate ages (circa 39-46 ka) are associated with interbedded aeolian sands and palaeosols. Finally, the oldest ages, between 67 and 95 ka, come from the lower part of the sequence, where several palaeosols are preserved. Overall, the dated horizons show repeated alternations of aeolian deposits and soil development phases (Fig. 56).

In the FALLS barranco, dune deposits are dominant but are interrupted by alluvial deposits that truncate and remodel the sequence. The compact sands are interbedded with lenses of conglomerates, interpreted as channel fills (Fig. 56). These channels do not follow the current geometry of the barranco but cross it. The compact sands are interspersed with lenses of conglomerates, interpreted as channel fillings (Fig. 56). These channels do not follow the actual geometry of the barranco, instead they cross it, in some cases almost perpendicularly. Radiocarbon and luminescence dating of this section (approximately 10-44 ka) confirm its correlation with the other sequences studied.

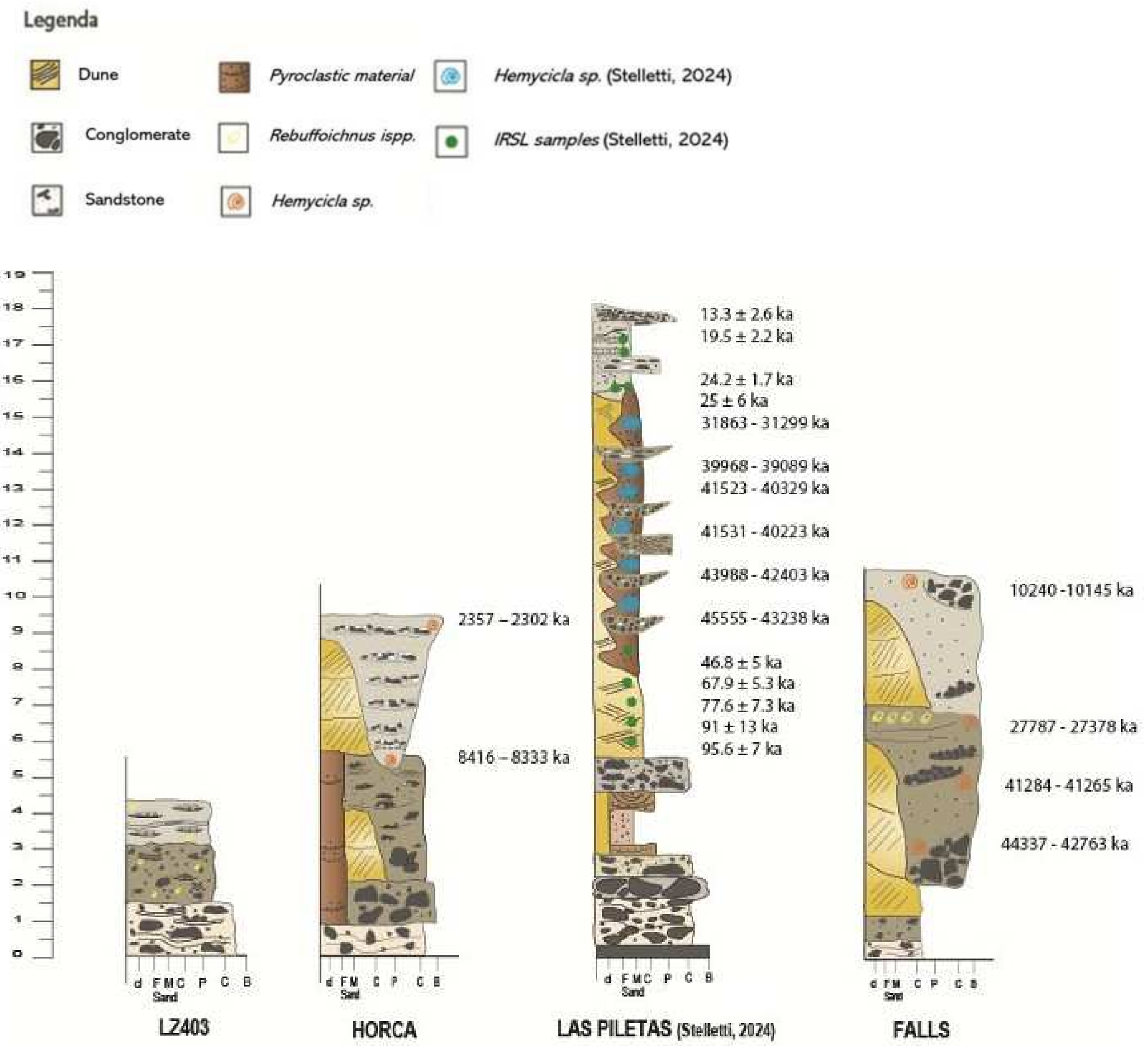

Figure 56: the stratigraphic correlation of the four barranco sections (LZ403, HORCA, LAS PILETAS and FALLS). Radiocarbon and luminescence samples (Stelletti, 2024) are reported with their respective ages. Modified after Stelletti (2024) and Ostera (2025).

4.8: Field trips during the period abroad

In keeping with the order followed in the Materials and Methods chapter, the Patagonian results are presented at the end of the Results chapter.

4.8.1 Patagonia

The field trip conducted in the province of Rio Negro, Argentina, allowed increasing knowledge in the field of ichnoentomology thanks to field observations of numerous insect trace fossils such as *Coprinisphaera akatanka* and *Teisseirei* isp. (Fig. 57). During investigations in Patagonia, *Rebuffoichnus* traces have not been found.

Figure 57: some of the insect trace fossils found during the field trip in Patagonia. On the left: *Coprinisphaera akatanka*; on the right: *Teisseirei* isp.

Near the Parque Nacional Nahuel Huapi (41.15724° S; 70, 37553° W), near the town of San Carlos de Bariloche, a fossil bee nest (Fig. 58) was discovered.

Figure 58: Left: the moment of the excavation; right: the bee nest with its shared and contiguous cell walls, a feature typical of Hymenoptera clustered traces.

During the field trip, a deposit with very particular insect trace fossils whose chambers are interconnected were also discovered (Fig. 59). The producers of this bioturbation are probably social insects such as termites.

Figure 59: a particularly bioturbated deposit, probably a social insects fossil nest. A) general view of the outcrop showing the distribution of chambers and tunnels; B) close-up of a surface with a high number of chambers; C) oval-shaped chamber, with a well-developed tunnel; D) detail of an elongated tunnel, highlighted with a scale coin.

4.8.2: Mar Del Plata:

In Mar Del Plata a Noctuidae pupation chamber has been found under a plant (*Melilotus albus*, Medikus 1787) belonging to the Fabaceae family. The pupation chamber (measuring 1.9 cm in length and 1.3 cm in diameter) contained remnants of the pupation exuvial inside (Fig. 60).

Figure 60: the modern pupation chamber of Noctuidae found in Mar Del Plata. Exuvial remnants are visible.

Regarding the rearing experiment, conducting an experiment involving biological processes and ecological features always has its challenges. The major ones have been maintaining an appropriate humidity level, cleaning the terrarium of their feces and correctly guessing the larvae's food preferences. For example, the specimens collected in San Patricio, they have showed a marked preference for corn leaves over lettuce (Fig. 61).

Figure 61: the terrarium where San Patricio specimens have been placed with corn leaves. The terrarium has been closed with a plastic bag to preventing larvae escape.

Other difficulties that occurred during the experiment included the finding of a larva outside the terrarium, on a plastic bag, actively consuming the material (Fig. 62).

Figure 62: A plastic bag was not enough to prevent some larvae from escaping, and one was found outside the bag feeding on plastic.

The larva was immediately put back into the terrarium. The rest of the larvae also showed inclination to escape. Their activity levels seemed low, with limited movement. However, the presence of fecal pellets on the leaves (Fig. 63) confirmed that they were feeding.

Figure 63: white arrows indicate fecal pellets of the larvae, a clear sign that the feeding was ongoing.

Three out of four larvae were found in the terrarium on 16 December, which suggested that one may have pupated in the terrarium substrate. However, this hypothesis was later dismissed, as no pupation chambers were discovered when the terrarium was disassembled.

Unfortunately, on 18 December all the larvae were found dead. The main cause of death is not known for sure.

Regarding the larvae collected in San Eduardo site, it has been assumed that these specimens were in the prepupation instar, as they were already found embedded in the sandy substratum, probably preparing for pupation. Compared to the San Patricio individuals, these larvae showed higher vitality and reactivity, moving around inside the containers in which they had been temporarily placed during the sampling.

The length and width measurements of the San Eduardo larvae were as follows: Larva 1 measured 4.8 cm in length and 0.8 cm in width, Larva 2 was 4.1 cm long and 0.8 cm wide, Larva 3 measured 5 cm in length and 0.7 cm in width and Larva 4 measured 4.5 cm in length and 0.8 cm in width. Larva 1 was placed in column A, Larva 2 in column B and both larvae 3 and 4 in column C. Once placed in their respective columns, the larvae tended to bury themselves in the exact point where they were laid, using peristaltic body movements to inter themselves (Fig. 64).

Figure 64: the stages of larval burial in the sediment through peristaltic movements.

All specimens buried themselves quickly, except for Larva 1, which took about 15 minutes before dipping into the substrate. During this time, Larva 1 assumed a rolled-up position on itself, following the cryptic mimicry strategy described for Noctuidae. It was only after a light stimulation that the specimen began the burial process.

4.9: Larval rearing

Observations conducted during the larval rearing showed the following results.
All the larvae except one specimen, “Larva 1” progressively become more lethargic in their behavior and then died. The only surviving specimen that reached the adult stage was kept under controlled humidity conditions by daily spraying of water directly on the substrate. Larva 1 showed no signs of activity in the days following sampling, so it was decided to introduce lettuce leaves into the column. This change was successful: during the night, the larva emerged from the substrate to feed. Larva 1 was seen feeding by keeping the posterior part of the body submerged into the soil and only projecting the anterior portion towards the surface, without climbing directly onto the leaf. Moreover, unlike the larvae from San Patricio, Larva 1 showed a preference for lettuce over corn leaves, preferring the thicker part of the leaf stem. During the experiment, it was observed that the larva responded to light stimulation, moving away quickly after exposure to a direct light source. Moreover, along the walls of the columns were visible deposits of darker material arranged in a wavy or scalloped pattern (Fig. 65), attributed to excretions or glandular secretions. However, no obvious excretions were found on the surface of the substrate.

Figure 65: the white arrow points to deposits of darker material arranged in a scalloped pattern.

As previously mentioned, Larva 1 was the only specimen to complete the development cycle up to the adult stage, while the other individuals all died due to uncertain reasons.

During the days immediately after sampling and moving into the experimental soil column, Larva 1 did not show any noticeable activity, remaining mainly buried. To track its behavior, a red-light source was used at a frequency of approximately once a day, as a red light is less disturbing to the insect. Food was provided approximately every two days, and the experimental diet included lettuce, rocket, chard and corn leaves. These observations revealed that larvae had a preference over corn leaves rather than fresh lettuce and showed a nocturnal habit since they came out to feed only during the night, usually between 23.00 pm. and 01.00 am.

After each meal, the larvae returned to bury itself. This behavior remained constant until 2nd of January, when a drastic reduction in the individual's activity was observed until death.

Larva 1 remained buried for 41 days, only coming out at night to feed on corn leaves. During this period its activity gradually decreased until it entered the pupation stage (Fig. 66) on January 24th.

Figure 66: the pupa, only partially visible in the sediment.

The camber measured 2.9 cm in length, 1.3 cm in width and 0.8 cm of the exit hole. The adult emerged on February 24th as *Agrotis fausta* (Kohler, 1958) (Fig. 67), and it has been deposited at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina).

Figure 67: on the left, dorsal part of *Agrotis fausta*, with its forewings and hindwings differing in pattern and color; on the right, the ventral part of the specimen. The pectinate antennae, typical of Noctuidae individuals, are recognizable.

4.10: Field observations

Atypical wet meteorological conditions have been recorded in April 2025 in Lanzarote: an average of 50.3 mm of rainfall was recorded, which is 329% of the expected value (http://www.aemet.es). During a field trip in May 2025, the activity of Sphingidae (Lepidoptera) larvae on the soil surface has been observed (Fig. 68).

Figure 68: traces left by Sphingidae in Lanzarote. Scale is 5 cm.

It has been possible to study their behaviour only during the field work, since they cannot be transported out of the island for studies in laboratory conditions. The following observations are reported in the study by Faedda *et al*. (2025), in prep.

Larvae had different sizes, ranging from 1 to 7 cm in length, since they were probably at different larval instars, and they have been found feeding on different types of plants including *Euphorbia sp*.

If molested, Sphingidae specimens showed a different defensive strategy compared to Noctuidae specimens from Argentina: they kept moving unbothered and did not show a curling position.

Also, the mimicry of Sphingidae specimens was aposematic rather than cryptic, with their colors warning potential predators (Fig. 69).

Figure 69: Sphingidae specimens found in Lanzarote. They display their typical aposematic mimicry with brightful colors such as light green and yellow.

Another significant difference was that the Noctuidae larvae were found near the base of the host plant, unlike the specimens from Lanzarote.

During the observations, last-instar larvae were seen constructing burrows into the soil.

The construction of a burrow consisted of entering inside a cavity and moving sand sideways with the head and through peristaltic contractions of the body and then placing the sand outside (Fig. 70).

Figure 70: Sphingidae constructing burrow into the ground.

A burrow was measured and had an inner depth of 8 cm, with an entrance 3 cm wide and 2 cm in height (Fig. 70).

DISCUSSION

CHAPTER 5:

5.1: Interpretation of statistical analysis of *Rebuffoichnus* ispp.

Interpretation of statistical analysis of *Rebuffoichnus* ispp.

Based on the results, it seems that the environmental conditions present at the time of the formation of the sand pit caused a change in the size of the *Rebuffoichnus*. In particular, statistical results show that Facies Association B is bioturbated by *Rebuffoichnus* with a significantly larger size than Facies Associations A and C. (Fig. 36).

Performing a statistical analysis based on ImageJ software may be useful not only for obtaining ecological and palaeoenvironmental information related to the traces, but also for the characterization of the levels themselves that compose the deposits. A larger size of the *Rebuffoichnus* ispp. present in Facies Association B can be interpreted in two ways. The first is that these are traces produced by a different species than those who have been found in Facies Associations A and C. Indeed, the discovery of an adult weevil inside a larger but comparable *Rebuffoichnus casamiquelai* specimen from Quaternary limestones in Australia supported this theory. Also, the position of its exit hole was coherent with weevil pupation chambers (Lea, 1925; Ellis & Ellis-Adam, 1993; Genise et al., 2013). Another hypothesis that would explain the higher size of *Rebuffoichnus* ispp. in Facies Association B could be due to climatic conditions that acted as selective factors on the size of the insects. FA C is distinguished by a greater number of traces (Fig. 35), although of a smaller average size, suggesting a higher population density but with smaller individuals, while level A shows intermediate values in terms of abundance and size. In parallel, the distribution of *Hemicycla* shells follows a similar pattern, with higher abundance in level C and more constant size between levels (Figs. 37, 38).

5.2: Ichnology and Neoichnology

Insect trace fossils attributed to the ichnogenus *Rebuffoichnus* are consistently found in these depositional systems and mostly horizontal or sub-horizontal orientated. It was not possible to determine the ichnogenus, due to the lack of sufficient distinguishing features.

Some specimens have a flattened ventral surface (Fig. 71). This morphological detail could depend on the *in situ* orientation of the moths, as they construct their pupation chambers horizontally, with an exit hole located at one end of the chamber.

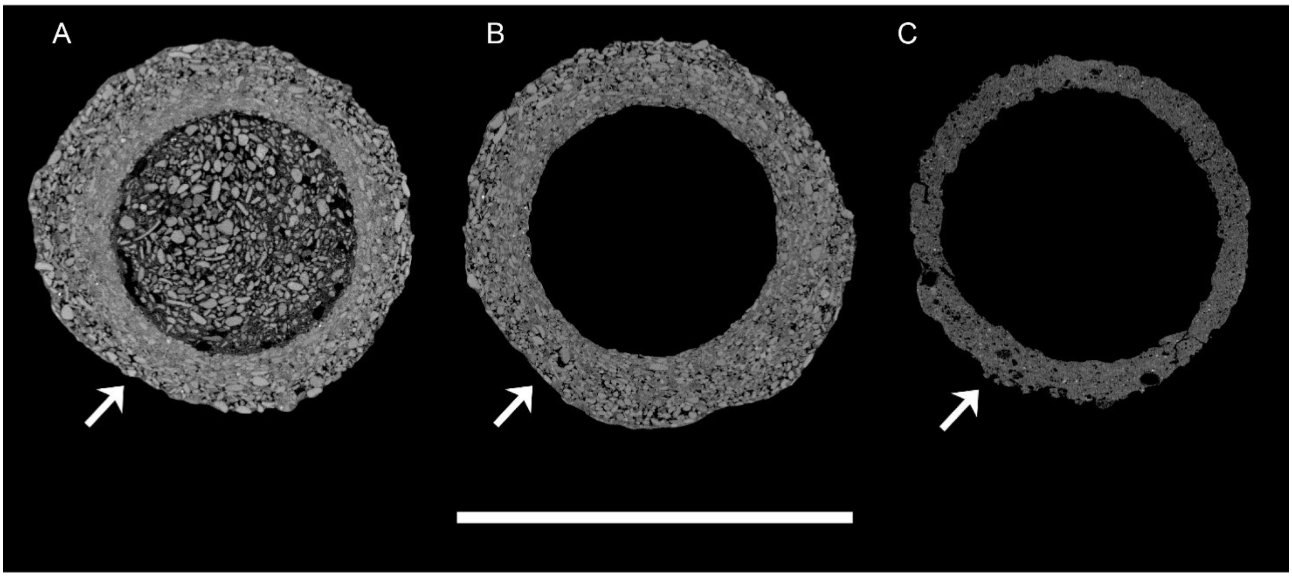

Figure 71: Two specimens of fossil chambers (on the left) and one modern pupation chamber (on the right) displaying the flattened ventral surface indicated by arrows. Taken from Faedda *et al.* (2025), in prep.

The results demonstrate that the morphological traits of *Rebuffoichnus* ispp. vary significantly between the locations, as the measured major and minor axes differ significantly between the groups. The traces with the largest dimensions were specimens in Piletas and Horca, while the smallest in Falls. Specimens from El Jable have intermediate values, probably due to a potential transitional pattern in trace fossils morphology. The results show that environmental conditions, substrate composition and other behaviors, which will need to be studied in more detail, may influence the size of trace fossils. The highest variance is held by the Falls group for both variables, indicating greater variability: different trace sizes could be attributed to different strategies or other producers. The two-way ANOVA confirmed that the minor axes and major axes are two distinct traits and are not correlated with each other. Differences in traces size could therefore be derived from different adaptive ecological strategies or simply from different producers. This high variability could suggest a diversity of behavior linked to environmental factors or evolutionary strategies of the different species.

Additional investigations are necessary to find out if these differences are mostly due to the species taxonomy, habitat characteristics or a combination of both.

From the statistical analysis comparing the modern and fossil chambers, it is interesting that no significant differences emerged for the major axes, but the fossil chambers show significantly larger dimensions for the minor axes than the actual ones, indicating possible morphological variations between the two groups over time. Indeed, the fact that the actual chambers have maintained the same size for the major axes compared to the past ($p > 0.05$) suggests that there has been a remarkable stability and morphological constancy over time. The size of the chambers appears to be linked to similar biological characteristics, which (in addition to the finding of a specimen of Noctuidae at the larval stage) support the hypothesis that the producer of the fossil chambers was indeed an insect belonging to the same family. The constancy in the size of the major axes suggests evolutive conservative adaptation within the family Noctuidae. Regarding the significant difference emerged from the statistical analysis on the minor axes, however, this difference is not necessarily indicative of taxonomic diversity between actual and fossil chambers. It could in fact result from ecological or environmental factors such as variations in resource availability, which could have led to actual chambers with smaller diameters than fossils.

5.3: Micromorphology and Tomography

Both tomography and micromorphology have revealed similarities between the *Rebuffoichnus* specimens and the modern pupation chambers of Noctuidae. For example, the cross-section is perfectly circular in both fossil and modern chambers. In addition, the general morphology corresponds, and both have a sub-ellipsoidal chamber with similar dimensions of the minor and major axes.

Another remarkable similarity is that both fossil and modern specimens have a flatter part (Fig. 71). This last morphological feature can be interpreted because of the *in situ* orientation of the chamber, which is consistent with the behaviour of moth larvae, which construct horizontal pupation chambers. The micromorphological analyses of the thin sections confirmed the existence of pattern: a grainy outer surface and a smooth inner wall (Fig. 39). These two features are interpreted as the result of an active selection of material by the larva during the construction of the chamber, probably to provide mechanical protection and insulation from the surrounding substrate.

5.4 Sperimental Neoichnology

5.4.1: Taxonomic classification

The lepidoptera fauna of Canary Archipelago has never been described in detail as one may have thought (Falck & Karsholt, 2022), and this is demonstrated by the fact that the number of species is unsure, as mentioned in the Introduction section.

The larva discovered inside a broken specimen of *Rebuffoichnus* during the sampling process has been identified as an insect belonging to the order Lepidoptera and more especially to family Noctuidae (Latreille, 1809), due to its morphological traits (Fig. 21). Firstly it seemed that the larva was probably at the 7th instar or at pre-pupation stage, because the pupation chamber could be constructed only at the end of the larval development.

However, after dating through radiocarbon method it is evident that the larva has not passed through any fossilization process, despite its brownish-yellowish color. The two dark brown dorsal bands may be the result of a cuticular thickening. Thick and cuticular bands are typical of Noctuidae and are useful for their hypogeal life when they bury into the sediments, or a form of mimicry, which serves for their life in the substrate. The prolegs are located in segments following the 4+1 formula, which means that prolegs can be found in pairs in 4 abdominal segments and in 1 anal segment: this is another morphological trait of Noctuidae family which helps distinguish it from other Lepidopetera larvae. Spiracles conservation is extraordinary considering their nature as structures of epidermal origin, which are often not preserved in fossil specimens. The ventrally oriented head indicates that it is a hypognathic larva, a typical characteristic of Noctuidae family.

Some species of wasps often prey on Noctuidae larvae, and they generally carry their prey inside structures (such as fossil pupation chambers) and then feed on it later. This could explain why a Noctuidae larva was found inside a *Rebuffoichnus* specimen.

5.4.2: Larval rearing

A rearing experiment has several issues such as maintaining optimal temperature and humidity parameters. During the experiment all the larvae except one collected in Mar del Plata died. Given that this type of lepidopteran larvae are very sensitive, the cause of their non-survival could be probably stress or an unsuitable environmental condition. The larvae observed *in situ* inside the soil columns showed irregular behaviors, and even Larva 1, the only one to reach the adult stage, did not build a pupation chamber. The stress was probably due mainly to the substrate. Even if the same sand from the collection site was used, the stability of the substrate proved to be a critical factor. In fact, even small movements of the soil column can have a negative impact on the pupation process, as the individuals need a stable environment to complete their pupation transition. If exposed to stress, the larvae could pupate without building a pupation chamber, which could affect its survival and developmental success.

Since there has been a high larval mortality, sampling a larger number of larvae would be recommended to increase the probability of success.

Another important point regards the timing of metamorphosis. For example, Larva 1 was found underground, which suggested an imminent transition to the pupation stage. However, pupation did not occur until approximately one month after sampling, far beyond initial predictions. The timing of metamorphosis changed from that recorded in the natural environment, and this delay could be attributed to stress conditions, although measures were taken to minimize it. It is another point that proves larvae sensitivity to environmental variations.

During the larval rearing, along the walls of the columns were visible deposits of darker material arranged in a wavy or scalloped pattern were visible, which could potentially be attributed to excretions or glandular secretions. In fact, Noctuidae larvae constantly expel a liquid substance while moving in the sand, in contrast to Sphingidae specimens, which expel the excretion once during chamber construction (Genise, Farina, et al., 2013). The expulsion of liquids was evident from the signs left in the soil present inside the columns (Fig. 72).

Figure 72: The soil column where Larva 1 was placed. The white arrow indicates the sign of liquids left from Larva 1. Scale is 2 cm.

5.5: Chronostratigraphy and palaeoclimate

Famara barrancos

No traces of *Rebuffoichnus* ispp. were found in the LZ 403 barranco. This could be due to the fact that this area is characterised by very coarse deposits, and even the grain size itself suggests greater erosion, as explained in the Results section. Regarding the other barrancos (HORCA, LAS PILETAS and FALLS), *Rebuffoichnus* ispp. were found in levels corresponding to approximately 10 ka, 40 ka, 44 ka and 46 ka (Fig. 55).

The discovery of *Rebuffoichnus* specimens in these layers is significant; however, it is necessary to examine the paleoclimatic context in which these deposits were formed.

The period between 40 and 12 ka corresponds to the Late Pleistocene, thus including part of Marine Isotope Stage 3 (MIS 3, ca 60–29 ka BP), MIS 2 (29–14 ka BP), and the possibly early stage of MIS 1 (Holocene around 11.7 ka BP).

During this period climatic events occurred. One example is represented by DO events. These are rapid warming and cooling cycles recorded in Greenland ice cores that have had a strong global impact. Other are the Heinrich events (massive iceberg released and melted into the North Atlantic) that also had an impact on ocean circulation and the European climate. The ecological niches of many species were strongly influenced by these climatic events of the time, for example by changing their distribution and survival strategies.

Lepidoptera are some of the organisms that have evolved or migrated to adapt. Several studies on this subject have been published in the literature. For example, studies on species such as Taiwanese Saturnidae moths and Thitarodes (Hepialidae) show that cold oscillations have facilitated the genetic differentiation of species and subspecies through habitat fragmentation and glacial refuges (Wang & Pierce, 2023; Yeh et al., 2022). This differentiation is linked to cyclical expansions/reductions in vegetation, especially in temperate refuge areas during glacial periods (Du et al., 2023; Ramos et al., 2023).

Plant diversity increases significantly during warm interstadial phases and in the post-glacial period, with forest/temperate species retaking territories; these processes lead to recolonisation by lepidoptera and other phytophagous insects. (Emre & Arıkan, 2025; Ramos et al., 2023; Yang et al., 2021).

Muñique Sand Pit

The Facies Associations (A-B-C) have been recognized stratigraphically and represent an alternation of dry and wet phases that allowed the formation of a dune-wadi dominated alluvial fan system. Dates performed on the facies levels (Wlg, Wcg, Sb, Sa) both through luminescence and radiocarbon methods, permit a correlation between sedimentary facies and Late Pleistocene climatic fluctuations, particularly those linked to both marine isotopic stages (MIS) and DO events.

The presence of *Hemicycla* shells associated with the same levels as *Rebuffoichnus* makes it possible to confirm the palaeoenvironmental interpretation and to provide an indirect temporal constraint for the insect trace fossils, since the same shells have been radiocarbon dated with AMS. The lower outcrops of Facies Association (FA) A (cross-bedded sandstones) have been dated to 108.4 ka, while the normal-graded sandstones facies of the same Facies Association to 76.6 ka (Heinrich *et al*., 2021). Therefore, the deposition of the bioturbated sandstones facies occurred in this time interval. This period falls between late MIS 5 and the beginning of MIS 4. Thus, DO 21 (~87 ka) and DO 20 (~82 ka) events fit well. The presence of terrestrial gastropod shells, such as *Hemicycla sp*., is generally associated with arid environments (Yanes *et al*., 2008), although they are active organisms during wetter periods such as the rainy season. Their presence in sandpit deposits could indicate a vegetated landscape (or at least sufficient vegetation to support both moths and land snails), but dependent on seasonal and climatic variations probably associated with DO 21-

20. However, the environmental conditions present during the formation of depositional system B favored the formation of larger *Rebuffoichnus* specimens.

The most significant record in terms of *Rebuffoichnus* size, however, falls in Facies Association B, and particularly in the bioturbated sandstones and normal-graded sandstones facies. Dates are correlated with MIS 3 (ca. 59-28 ka), a period known for its climatic variability with repetitive cooling and warming events. In fact, during MIS 3, a series of DO events occurred in the northern hemisphere, resulting in alternating wet and dry conditions on a millennial scale. In particular, the dated levels consistently correspond to DO 8 (~38 ka), DO 7 (~34 ka) and DO 6 (~31 ka) events.

Facies Association C, which is dated between ca. 23.6 ka and 12.7 ka and includes an intermediate date of 16.6 ka, falls between the end of MIS 2, which includes the last glacial maximum (LGM, ~21 ka) and the following transitional events towards more stable climatic conditions. Thus, climatic conditions at that time were still cold, but with periods of higher local humidity probably related to fluctuations in Atlantic atmospheric circulation and the activation of ephemeral water systems (wadis).

In Facies Association C *Rebuffoichnus* specimens are more abundant in number but smaller in size than in FA 2. This suggests a less intense and shorter duration of humid events, not sufficiently strong to favor higher plant availability, in line with an environment still in post-glacial transition.

CONCLUSION

CHAPTER 6

The purpose of this doctoral thesis was originally to investigate if insect trace fossils could be considered trustworthy proxies for studying the paleoclimate. Over the course of three years, the objective expanded to include reinterpreting the origin and ecological implications of *Rebuffoichnus* specimens found in Lanzarote. The origin of *Rebuffoichnus* is still under debate, but since there are no mentions in the scientific literature of Noctuidae as possible producers of these insect trace fossils, this represents a new approach.

One of the difficulties encountered during the study was the gap in the scientific literature on the lepidoptera fauna of the Canary Islands, a topic that surely needs more attention in the future. Another challenge was not being able to directly date the traces, but only through luminescence and radiocarbon on the *Hemicycla sp.* shells. Although these are reliable dating methods, it would be interesting to approach future studies using more refined dating methods. Another difficulty was trying to reproduce natural conditions in the soil columns used to rear the larvae, and due to the high mortality rate, it will be necessary to specimen a larger number of larvae in the future. Despite these methodologies' difficulties, the research goals have been met.

The fieldworks revealed that the activity of Lepidoptera (Noctuidae and Sphingidae) was surprisingly high both in Lanzarote and in the comparable research area in Argentina. The section of the study dedicated to larval rearing also underscored important behavioural aspects, such as the expulsion of liquid by the larvae to move through the sand.

The stratigraphy of the Muñique sand pit has been described along with the insect trace fossils and has provided a better definition of the chronology of the El Jable deposits. The ages provided by Heinrich *et al*. (2021) are confirmed, and it is pointed out that the insect nests were formed during a wetter period, between 70 and 12 ka. In addition, a comparison and description of both fossil and modern pupation chambers of Noctuidae has been conducted: this study supports the hypothesis that Noctuidae may be the producers of at least some of the trace fossils in Lanzarote.

Notably, the Australian *Rebuffoichnus* specimens are larger in size and have a rougher texture than those found in Lanzarote, supporting the idea that multiple producers may have built similar traces. Therefore, it is reasonable to assume that those from Lanzarote are the result of another producer, and probably not Coleoptera. Based on morphological comparisons with modern chambers, the cross-section of the Lanzarote *Rebuffoichnus* is perfectly circular, just like that of the family Noctuidae (Lepidoptera). It is not elliptical as that of the family Sphingidae (Lepidoptera) which produce the *Teisseirei* trace: this excludes them as possible producers of the traces and leaves Noctuidae as the only plausible Lepidoptera producer.

Regarding the significance of *Rebuffoichnus* as a proxy for improving the knowledge of the Pleistocene paleoclimate, their investigation, integrated with an accurate stratigraphy and dating of the deposits, led to the following conclusions.

Firstly, a key climatic factor is humidity, which is linked to precipitation: the frequent presence of wetlands, ephemeral lakes and swamp forests supported Lepidoptera reproduction and larval development. In Pleistocene deposits, alluvial fans represent phases of active flow and sediments rich in organic matter. These are excellent conditions for the proliferation of Lepidoptera and the preservation of insect trace fossils. The presence of wady dominated alluvial fans (fossil/intermittent river channels) in the Pleistocene levels where *Rebuffoichnus* is found is therefore clearly linked to paleo-humidity conditions and thus to periods when the local climate was significantly wetter than today (Genise et al., 2000; Ghandour et al., 2021; Ramos et al., 2023). Therefore, *Rebuffoichnus* can be considered a reliable and useful proxy for refining paleoclimatic reconstructions and for increasing the knowledge of Pleistocene climatic oscillations.

Future studies will focus on two main points: firstly, to confirm the Noctuidae hypothesis, through a more detailed neo and paleoichnological investigation and by looking for any possible fossilized remains of the producer inside the closed chambers. Secondly, to explore in a more detailed way their role as proxies of Lanzarote's paleoclimate and environmental changes.

However, the main goal of this research has been achieved. In fact, insect trace fossils, which are often underestimated in palaeoenvironmental studies, can provide important information on how climate, substrate and behaviour are related. Besides the specific case of El Jable, the results contribute to an insight on how biogenic structures can act as recorders of Quaternary environmental changes in semi-arid landscapes.

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