Article

Testing the Usefulness of the Surface Collecting Method in a Vertebrate Microfossil Site from the Barremian of Spain (Los Menires, Mirambel Formation)

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Abstract: Surface collecting is the first and sometimes the only type of sampling carried out in many fossiliferous localities, including vertebrate microfossil assemblages. Nevertheless, it is rare to test how representative these surface-collected samples are of the palaeobiocoenosis. A first approach to the palaeontological analysis of Los Menires, a Barremian vertebrate microfossil assemblage, is here performed while testing the usefulness of the surface collection method. New fossil material obtained by surface collection is described, and the resulting data are compared with those obtained by screen-washing. The fossil assemblage of Los Menires is dominated by parautochthonous remains of freshwater aquatic and semiaquatic organisms—i.e., charophytes, ostracods, bivalves, gastropods, testudinatans, crocodylomorphs, lissamphibians, and osteichthyans—although parautochthonous remains of terrestrial vertebrates—i.e., dinosaurs, lacertilians, and mammaliforms—are also present. The accumulation of vertebrate hard parts in Los Menires took place in a low-energy, shallow-water, depositional environment within the alluvial-lacustrine system represented by the Mirambel Formation. Sampling test results indicate that surface collection is effective in recognizing the main fossil groups present in an assemblage. Yet, it is not suitable for capturing delicate and tiny fossils nor for recognizing the abundance of eggshells. In contrast, it can generate an overrepresentation of other hard components such as coprolites or ornithopod teeth.

Keywords: Mesozoic vertebrates; sampling methods; palaeobiodiversity; microfossil vertebrate assemblages; shallow lacustrine; lower Cretaceous; Ladruñán anticline; Maestrazgo basin; Teruel province

1. Introduction

Vertebrate microfossil assemblages can be highly representative of the vertebrate fauna present in the palaeocommunity [1,2]. However, the usefulness of data from vertebrate microfossil assemblages in palaeoecological reconstructions can be questioned if some factors are not considered. A detailed taphonomic analysis is needed before assuming that the recorded taphocoenoses are representative of the original thanatocoenoses before inferring the original paleobiocoenoses, (e.g., [2,3]). However, sampling methodologies can result in a significant sampling bias. Loss and breakage during collection, undesired sorting, and unrepresentative samples are examples of sampling practices that may affect the results obtained [1,4–6].

The sampling of vertebrate microfossil assemblages involves the observation of a fraction of the total community in order to derive an estimation of taxon richness from the original palaeobiocoenosis [5]. Studies carried out using only partial data for reliability

usually require a significant investment of resources and the use of empirical methods (e.g., rarefaction [5]) to ensure that the sample size is representative. However, it is useful to have some quick, reliable criteria to estimate the relative richness of a fossiliferous level or putative assemblage in order to establish comparisons with other previously known deposits when there is no time available for complete, statistically significant sampling. Possible scenarios where this quick test may be needed include (1) when considering the design of future fieldwork surveys, (2) during palaeontological surveys related to environmental impact assessments, and (3) geosite delimitation for effective land use and management. The surface pick-up of fossil specimens during palaeontological surveys constitutes a researcher's first contact with a potential palaeontological site and is a less time-consuming collection method. Still, the number of studies evaluating the quality of the samples acquired by surface collection is scarce [7], specifically regarding vertebrate microfossils [8], despite the extensive literature on the study of vertebrate microfossil assemblages (e.g., [8,9]). Previous studies have reported that there is a correlation between sampling methods and inferred palaeobiocoenosis composition; this is likely related to the fact that surface collection is skewed to the largest bioclast fraction [8]. Nevertheless, all previous studies agree regarding the need for more study cases to test this hypothesis.

The aim of this work is to approach the palaeontological analysis of a Mesozoic vertebrate microfossil assemblage—Los Menires—by testing the usefulness of the surface collection method. For this purpose, we describe new fossil material of a sample obtained by surface collection, and the resulting data are compared with those obtained by means of screen-washing a sample of bulk rock from the same fossil locality. Through this case study, we intend to illustrate how useful information obtained from a subsample can be for the provisional analysis of a vertebrate palaeocommunity.

2. Geological and Palaeontological Setting

The fossil site of Los Menires is located near the small village of La Algecira (Castellote municipality, NE Teruel province, NE Spain) in the eastern part of the Iberian Chain (Figure 1). The fossiliferous level crops out in the southern area of the Ladruñán anticline, an N-S-trending fold with periclinal closure to the north [10]. Palaeogeographically, this area belongs to the north-western margin of the Morella sub-basin (Figure 1B), within the Maestrazgo Basin [11–13]. The local series ranges from Upper Jurassic to Upper Cretaceous, with Los Menires included within the Barremian Mirambel Formation (Figure 1C). The unit is formed by an alternation of detrital alluvial intervals and carbonate-rich palustrine-lacustrine intervals [14]. In the area of Los Menires, the Mirambel Formation is well exposed in its lower part, overlaying the lacustrine limestones of the Herbers Formation. The layer of the vertebrate microfossil site studied here is located 30 m above the base within a succession of sandstones, lutites, marls, and limestones (Figure 1D). The facies association of the Menires section represents a distal alluvial to the lacustrine system, including sub-environments of floodplain, palustrine plain, and shallow lacustrine indicated by lithofacies and fossil content (see Appendix A).

Los Menires is a microfossil bonebed—sensu Eberth et al. [15]: a relative concentration of fossils where most component elements (>75%) are ≤5 cm in maximum dimension—from the Mirambel Formation. This microfossil assemblage is located in a lenticular bed of dark grey marls (Figure 2), which represent shallow lacustrine sedimentation, as indicated by the presence of abundant charophytes and ostracods, but also scarce agglutinated benthic foraminifera. The latter would be indicative of a location near the ancient coastline. The charophyte flora from the Mirambel Formation—and specifically from the Los Menires assemblages—are dominated by the clavatoraceans *Atopochara trivolvis triquetra*, *Globator maillardii trochiliscoides*, and *Globator maillardii biutricularis* [14]. Non-marine ostracod remains are present in the Mirambel Formation but they are less frequent than those of charophytes. Cyprideans are the most frequent ostracods but non-cyprideans (*Macrodentina* sp. And *Theriosynoecum* sp.) are also represented [14].
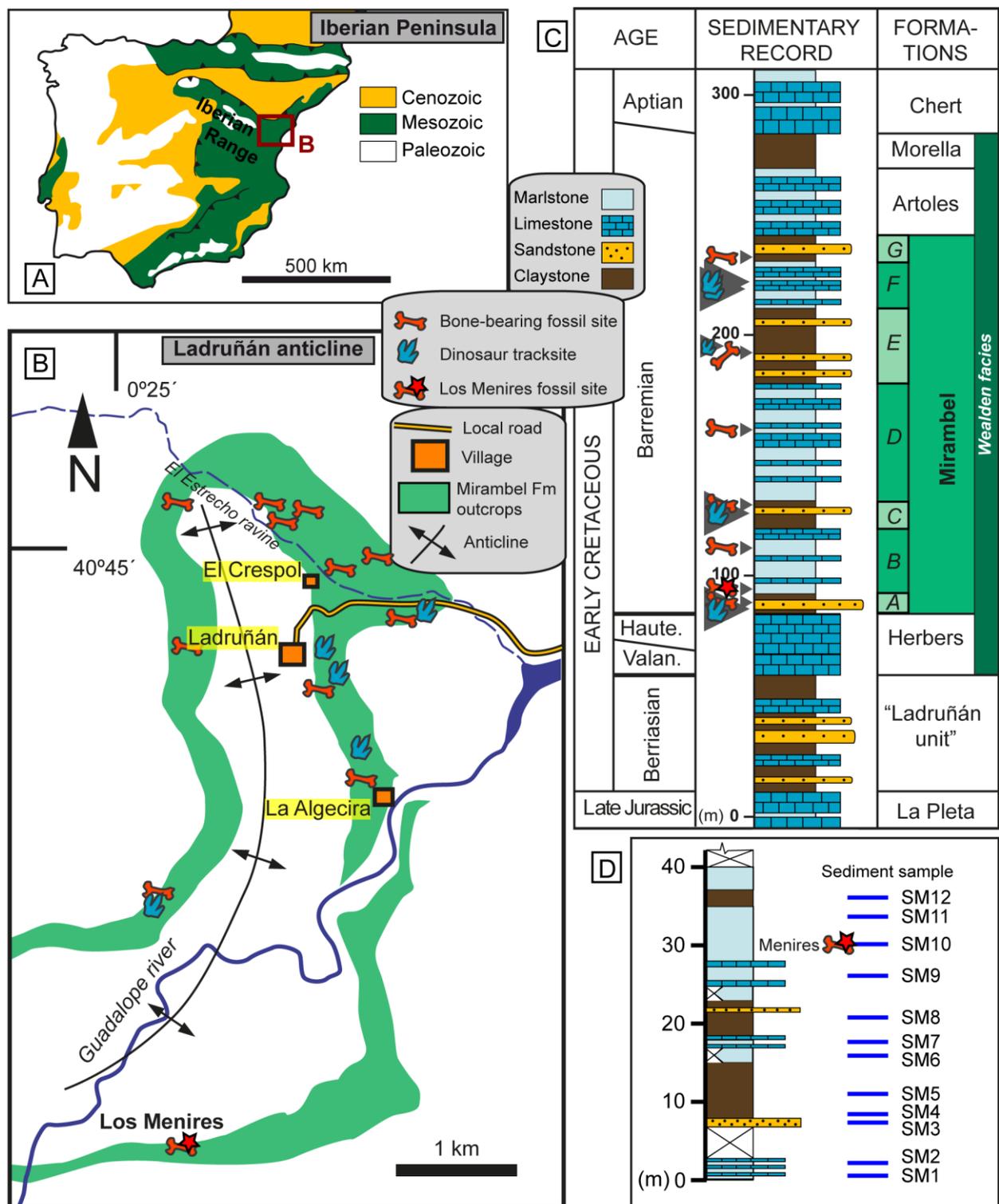
Figure 1. Geographical and geological location of the Los Menires fossil site from the Lower Cretaceous Mirambel Formation (Teruel Province, NE Spain), partially from [14]. (**A**) Geological setting of the studied area (B) within the Iberian Peninsula. (**B**) Outcrops of the Mirambel Formation in the Ladruñán area with the location of the main vertebrate fossil sites. (**C**) Synthetic log of the uppermost Jurassic-Early Cretaceous sedimentary units in the study area. Within the Mirambel Formation, A to G indicate successive detrital- and carbonate-rich intervals. (**D**) Stratigraphic location of the Los Menires site and sediment samples within the local reference section.

Figure 2. Los Menires fossil site: general view to the North of the outcrop where the lenticular bed of fossiliferous dark grey marls is well exposed.

Gasca et al. [14] preliminarily reported a remarkably diverse vertebrate fossil assemblage from the Los Menires locality, including lissamphibians, squamates, testudinatans, crocodylomorphs, dinosaurs, and mammaliaforms (see Appendix B). This record is composed of a high concentration of teeth and disarticulated cranial and postcranial remains. Concerning the dinosaur record, tooth morphology allowed for the recognition of theropods, including spinosaurids, several maniraptoriform morphotypes, and ornithopods.

Eggshell records from Los Menires have been partially studied by Moreno-Azanza et al. [16]. Some eggshell fragments have been related to the ootaxon *Mycomorphoolithus kohringi* [16]. These eggshells are characterized by their mushroom-shaped shell units comprising radiating, wide crystals and may represent eggshells of non-eusuchian crocodylomorphs [16].

3. Materials and Methods

3.1. Selection of the Locality for the Case Study

In order to test the reliability of surface collection as a method to address the richness and diversity of a fossil locality, a series of prerequisites were considered for the locality subject of this case study: First, in the evaluated fossil locality, there would have to be an important bioclast concentration and outcrop conditions that allowed sediment erosion and fossil exhumation—i.e., fine-grained and/or poorly cemented sediments and limited existence of vegetation cover—as necessary conditions to make feasible the collection of sufficient remains on the surface. In addition, the locality would have to be either new or have remained unexplored for a sufficient period since the last palaeontological survey to avoid any effects of previous selective collections. All these requirements apply to the Mesozoic vertebrate microfossil site of Los Menires.

The fossil locality of Los Menires was discovered during a fieldwork survey performed by the Aragosaurus-IUCA research team in 2009. It was found in a small area of badlands cleared of vegetation. The fossiliferous outcrop is a band of approximately 1-m thick dark grey marlstones that extends laterally less than 20 m (Figure 2). It is located 795 m above sea level within the climatic division "wet submediterranean" and has 500 mm of annual rainfall and 13 °C annual average temperature (data available at https://www.aragon.es/-/atlas-climatico-de-aragon; Atlas Climático Digital de Aragón; accessed on 15 December 2022).

This rugged area was affected by a major wildfire in 1994 that destroyed a good part of the pine forest that occupied this slope of the Guadalupe River valley. From then until the discovery of the palaeontological site in 2009, it is presumed that this territory experienced an increase in the erosion process due to surface runoff.

The palaeoenvironmental reconstruction of Los Menires is based both on detailed stratigraphic and micropaleontological analyses performed in the section of Los Menires (Figure 1D) and the study of its successive palaeontological assemblages [14]. Bulk rock samples were collected and microfossils were extracted by washing and sieving samples along the entire series of the Mirambel Formation. Samples of 2 kg were systematically taken (see Appendix A) from successive soft horizons (lutites, marltones, and poorly-cemented sandstones), and these were processed using 2% hydrogen peroxide and sieves of 2.0, 1.0, and 0.5 mm mesh. The skeletal remains and eggshell fragments were sorted under a binocular microscope. To complete the micropaleontological study, other microfossils of palaeoecological or biostratigraphic significance were identified, such as charophyte and ostracod remains (see Appendix A). From the systematic sediment sampling of the unit, it could be confirmed—by comparison of the fossil richness in each individual and size-equivalent sample of equal weight—that the greater skeletal concentration was present in the Los Menires bed (Figure 2). All this research is part of the integrative study of the vertebrate record from the Mirambel Formation, from which a first preliminary publication has already been conducted, documenting the Barremian alluvial-lacustrine system of the Ladruñán area [14].

3.2. Sampling Methodology

We designed a sampling protocol for both surface collection and screen-washing sampling of microfossils (Figure 3). Surface collection was conducted after a period of four years without visiting the Los Menires site. The entire outcropping surface was then systematically surveyed by a crew of four trained paleontologists to recover all observable vertebrate fossil remains, which were subsequently identified and counted (Table 1) (Figure 3C–E). Additionally, 15 kg of bulk rock from the fossiliferous layer was washed and sifted—using the same process described above (Figure 3A)—but for five separate subsamples. The latter was with the purpose of determining the robustness of some observations (e.g., abundance ranks, see [5]). The smallest mesh size used during screen-washing, with aperture diameters of 0.50 mm, was the most used to screen microvertebrate Mesozoic assemblages (e.g., [17]).

Table 1. Vertebrate fossil remains from the Los Menires fossil site collected during a surface collection survey. The different fossil categories are ordered by their abundance.

Number	Element	Higher Taxonomic Group	Taxa	Labels	Size (Maximum Dimension)
56	Plate fragment	Testudinata	Pleurosternidae and Helochelydidae	MENI-A-1 to 56	Up to 20 mm
54	Undetermined bone fragment	Vertebrata	-	MENI-A-57 to 109 and 148	From 20 to 41 mm
11	Coprolite fragment	-	-	MENI-A-110 to 120	Up to 23 mm
10	Osteoderm fragment	Crocodylomorpha	-	MENI-A-121 to 130	Up to 12 mm
7	Tooth	Ornithopoda	Styracosterna	MENI-A-131 to 137	More than 9 mm
5	Tooth	Crocodylomorpha	Goniopholididae	MENI-A-138 to 142	From 4.6 to 9.7 mm
3	Tooth	Crocodylomorpha	Bernissartiidae?	MENI-A-143 to 145	From 3.7 to 4.5 mm
1	Vertebrae	Crocodylomorpha	-	MENI-A-146	8.7 mm
1	Vertebrae	Testudinata	-	MENI-A-147	5.4 mm
1	Scale	Osteichthyes	-	MENI-A-149	7.5 mm
1	Tooth fragment	Dinosauria	Saurischia	MENI-A-150	15.4 mm
1	Eggshell fragment		-	MENI-A-151	6.5 mm
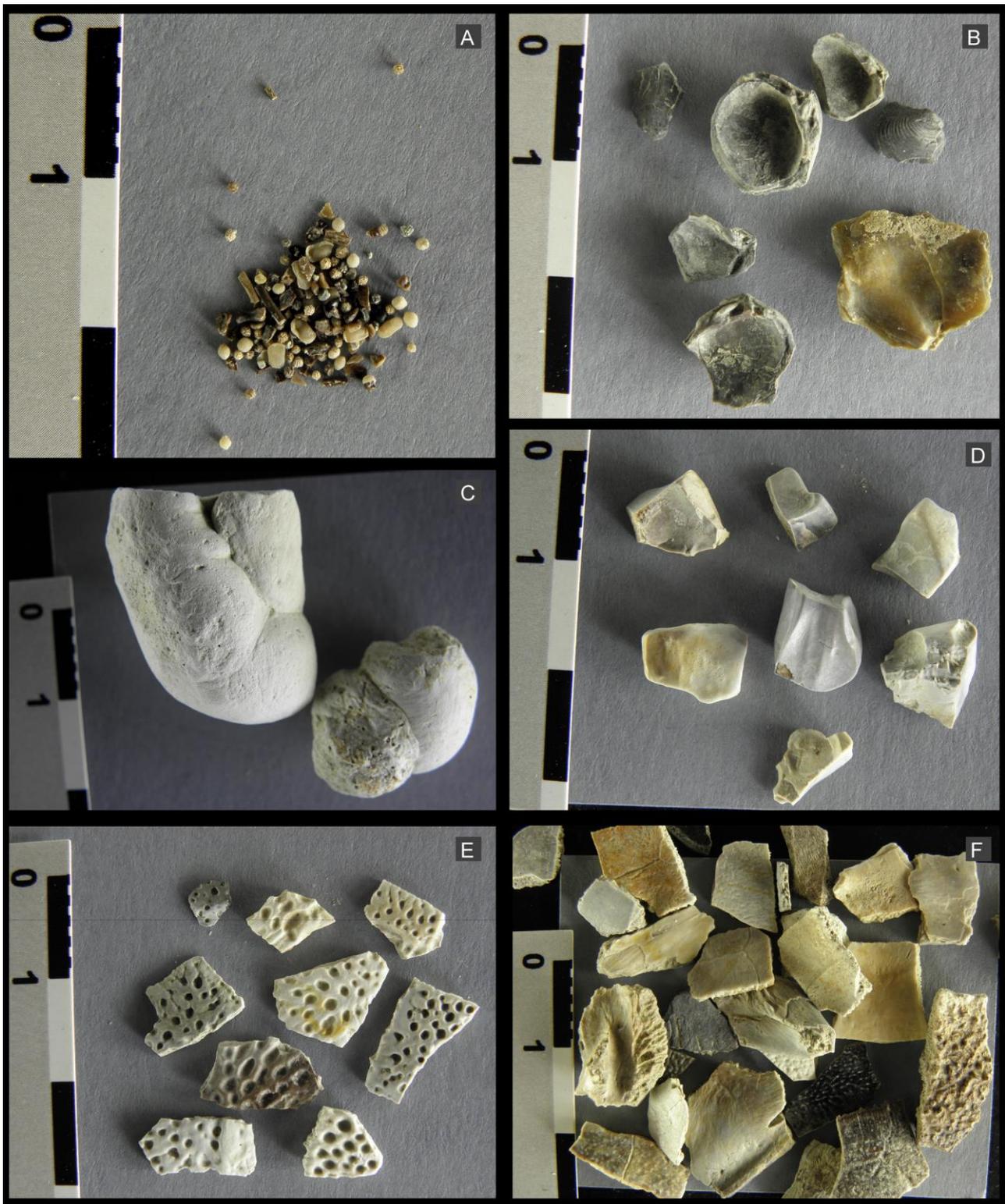
Figure 3. Fossil remains from the Los Menires fossil site. (**A**) Assorted microfossil remains after picking; (**B**) mollusks; (**C**) coprolites; (**D**) ornithopod shed teeth; (**E**) crocodylomorph osteoderms; (**F**) turtle plates. Scale bars are centimetric.

All materials were recovered with permission under the national and local administration (Gobierno de Aragón). All materials included in this study are housed at Museo de Ciencias Naturales de la Universidad de Zaragoza.

4. Results

4.1. Vertebrate Record: Sample Obtained by Surface Collection

The studied sample included a total of 151 specimens (labeled MENI-A-1 to 151). The vertebrate sample (Figures 3B–F and 4) described here is shown in Table 1, with components ranked by abundance. Undetermined fragmentary bones were the most common vertebrate remains. The rest of the identifiable vertebrate remains are described below, including teeth, postcranial bones, eggshell fragments, and coprolite fragments. Along with the vertebrate material, other collected fossils included shell remains of invertebrates (Figure 3B) such as freshwater gastropods (*Viviparus* sp.) and bivalves. The recovered material was mostly well preserved except for the breakage that occurred during recent post-exhumation subaerial exposure. The breakage affected turtle plates and larger bones more than other more resilient elements such as teeth. Abrasion and weathering stages observed on the remains were frequently low.

Figure 4. Vertebrate fossil remains recovered by surface collection from the Los Menires fossil site. (**A**,**B**) MENI-A-151, eggshell fragment in internal (**A**) and external (**B**) views. (**C**,**D**) MENI-A-149, osteichtyian scale in external (**C**) and internal (**D**) views. (**E**,**F**) MENI-A-146, Crocodylomorpha indet. Vertebra in dorsal (**E**) and ventral (**F**) views. (**G**) MENI-A-56, Helochelydridae indet., plate fragment in dorsal view. (**H**) MENI-A-1, Pleurosternidae indet., plate fragment in dorsal view. (**I–K**) MENI-A-138, Goniopholididae indet., in lingual (**I**), apical (**J**), and basal (**K**) views. (**L**,**M**) MENI-A-139, Goniopholididae indet., in lingual (**L**) and mesial or distal (**M**) views. (**L**,**M**) MENI-A-143, Bernissartiidae? Indet., in apical (**N**) and lingual (**O**) views. (**P–R**) MENI-A-131, Styracosterna indet., right maxillary tooth in lingual (**P**), distal (**Q**), and labial (**R**) views. (**S**) Saurischia indet., tooth fragment.

4.1.1. Osteichthyes

A small ganoid scale (MENI-A-149) was recovered. MENI-A-149 was slightly rectangular. Its anatomical position was inferred to be on the right flank by comparison with the squamation described in other lepisosteiform fishes (e.g., [18]). The surface and borders of the scale were smooth. The anterodorsal corner and dorsal peg were slightly broken. The anteroventral process was poorly developed. In the internal face, there was a triangular ventral socket for the peg-and-socket articulation of the adjacent scale (Figure 4C,D).

4.1.2. Testudinata

Fifty-six turtle plate fragments (MENI-A-1 to 56) were collected. Twenty-two of them were extremely fragmentary and undiagnostic beyond a diploe structure, typical of turtle shell bones (e.g., [19]). However, the ornamentation pattern of some shell fragments allowed for the assignment of these remains to Pleurosternidae indet.—33 fragments (MENI-A-1 to 33)—and, to a lesser extent, Helochelydridae—1 fragment (MENI-A-56). Among the remains of pleurosternids, caparace elements corresponded to a complete neural bone and fragments of three costal bones; three peripheral plates were also recognized. The external surface of all these elements was ornamented by small, regular, and clearly defined pits, with fine striations perpendicular to the margins of the plates. Other turtle fragments were ornamented with vermiculation.

Helochelydridae (Solemydidae, see [20] p. 5) was diagnosed by the presence of distinct tubercles that decorated the surface of the cranium, shell, and osteoderms [21]. MENI-A-56 was an undetermined caparace fragment assigned to Helochelydridae by its external surface ornamented with distinctive tubercles or pustules (Figure 4G). These pustules were approximately 0.6 mm in diameter and arranged mostly individually, but sometimes coalesced in groups of two or three elements. The internal surface was rather flat but with a median ridge, suggesting that the fragment belonged to a coastal plate. The specimen was highly fragmentary and intensely weathered and eroded, i.e., some individual tubercles were broken, preserving only its bases. However, the distinctive ornamental feature typical of helochelydrids was verifiable and sufficient to establish its taxonomic affinities [22].

An isolated vertebra (MENI-A-147) tentatively related to Testudinata was recovered. MENI-A-147 was a centrum slightly longer (5.7 mm) than wide (4.2 mm), and dorsoventrally low (2.4 mm). The anterior articular face was concave and wider than the posterior end, which was less well preserved but seemed to also be concave. Ventrally, a median keel and pair of foramina were present. Articulation with chevron bones was absent (Figure 4E,F). This overall morphology resembled that of the anterior caudal vertebrae of other chelonians (e.g., [23] Figure 7).

4.1.3. Crocodylomorpha

Crocodylomorphs were well represented by 19 elements, including teeth and remains of the dermal skeleton, along with an isolated vertebral centrum.

The teeth recovered by surface collection can be differentiated into two morphotypes which can be respectively related to Goniopholididae (Figure 4I–M) and (tentatively) to Bernissartiidae (Figure 4N,O). Specimens MENI-A-138 to 142 assigned to Goniopholididae indet. were broad, conical, lingually curved teeth. Their cross sections were subcircular and slightly labiolingually compressed. They exhibited mesial and distal carinae, basioapical ridges—eleven to fifteen on the lingual face, eight to eleven on the labial face—and enamel striations, which were mostly vertically oriented in central areas and inclined to the margins. The contact of the striae with the carinae generated the appearance of false serrations. This tooth morphology is congruent with the generalist dentition of goniopholidids, a group widely represented in the Lower Cretaceous of Spain (e.g., [24,25]).

Specimens MENI-A-143 to 145 were low crowned, bulbous, less labiolingually compressed, single-cusped, and lacking mesial and distal carinae. Crowns bore tiny apicobasal striations, resulting in a braided enamel texture, along with a set of wider, faint ridges. This distinctive morphology corresponded to the tribodont dentition described in

small crocodyliforms belonging to the Bernissartiidae family (e.g., [26,27]) but also to hylaeochampsids such as *Unasuchus* from the upper Barremian of Cuenca province, Spain [28].

The dermal skeleton remains (MENI-A-121 to 130) consisted of some fragments of osteoderms (Figure 3E) that were ornamented by an irregular net of deep surrounding pits on the external surface, whereas they were smooth on the internal face. However, one of the fragments (MENI-A-122) bore a smooth anterior edge to allow for the overlapping articulation with the preceding osteoderm, as is observed in the dorsal osteoderms rows of other neosuchian dermal skeletons (e.g., [29] Figure 7K; [25] Figure 5D,E). MENI-A-121 bore remnants of a subtle median keel, polygonal outline, and edges without sutures, resembling nuchal osteoderms (e.g., [25] Figure 5L). The rest of the fragments were rather flat, but not complete enough to infer their corresponding anatomical position.

MENI-A-146 was a complete, unfused, sacral vertebra centrum, which was amphicelic, elongated, and more wide than high. It had a faint anteroposterior median groove on the ventral surface. The ventral margin was gently concave when observed in lateral view. In dorsal view, the neural canal was broad and hourglass-shaped but became wider at the anterior part of the vertebra. The unfused sutures revealed the corresponding immature condition of the individual ontogeny. The overall morphology of the specimen resembled that of the first sacral of crocodylomorphs (e.g., [29] Figure 6F,G).

4.1.4. Dinosaurs

Identifiable dinosaur remains consisted of seven ornithopod shed teeth (Figure 3D) and a tooth fragment (MENI-A-150) with a small portion of enamel preserved and a morphology reminiscent of saurischian dinosaurs (Theropoda?) (Figure 4S).

Ornithopod teeth (MENI-A-131 to 137) were terminally resorbed and without preserved enamel. However, the morphology of the crowns still allowed us to appreciate distinctive features of the dentition of the iguanodontian dinosaurs such as the pattern of longitudinal ridges (Figure 4R). The overall morphology of the collected specimens (Figure 3D) was reminiscent of that of the styracosternans, which are also frequently found in other Barremian localities within the Maestrazgo basin [24,30,31].

4.1.5. Eggshells

Eggshell remains are quite difficult to identify by surface prospection and, in the absence of complete eggs or nests, only relatively large fragments are recognizable. In this regard, only an undetermined eggshell fragment was recovered (Figure 4A,B).

4.1.6. Coprolites

Eleven coprolite fragments from 5 to 23 mm in size were collected. Some fragments preserved at least one complete end, which was rounded (Figure 3C). The coprolite overall morphology was cylindrical and subcircular in sections, and some of them bore circumferent constrictions. The color of the specimens was whitish—likely a result of alteration by recent subaerial exposure—and the outer surface was either smooth or slightly rough and showed irregular microfractures. The smooth sectors showed a polished look, bearing occasionally tiny striations which were arranged parallel or crossed with each other. The rugged sectors showed small pits and other greater rounded hollows partially filled by marly, bioclastic sediment. There was no evidence of individual layers nor identifiable inclusions and, from what could be observed on broken surfaces, the coprolites were apparently structureless inside.

Vertebrate coprolites display a wide range of morphological variation, although the majority are elongate and sub-cylindrical; thus, identifying the exact producer of a coprolite is a challenging task [32]. A plausible morphological match for the only coprolite morphotype of the studied sample was a crocodylomoph. Crocodylomorph coprolites are generally sausage-shaped and circular in cross sections, with few structures visible on their outer surface except for occasional striations or traces from coprophagous organisms. They bear circumferent constriction marks (e.g., [33]). In addition to the size of the specimens, this hy-

pothesis is coherent with the common presence of crocodylomorphs within the osteological record of the fossil assemblage. Furthermore, a fecal matrix without recognizable inclusions would be in accordance with what is observed on the coprolites attributed to crocodiles and with the fact that modern crocodiles have a very effective digestive system [34]. However, the fragmentary nature and scarcity of the sample prevented the drawing of unequivocal conclusions. Likewise, further analyses—which are outside the objectives of this work—are required to relate these coprolites to a particular clade of crocodylomorphs or discard other tetrapod affinities or producers (e.g., testudinatans and theropod dinosaurs can also produce cylindrical coprolites with rounded ends and constant diameters [32]).

4.2. Screen-Washing Subsampling

A detailed description of the 668 specimens recovered by screen washing is outside the scope of this work. Nevertheless, we identified all the recovered specimens in order to compare the screen-washed and surface-collected samples in terms of richness and faunal diversity. The detailed results of the count of the different types of microfossils (i.e., eggshells, unidentifiable bony remains, and identifiable remains) and major vertebrate groups in each subsample are shown in Table 2, specifying the count for each mesh size (0.5, 1, and 2 mm).

Table 2. Number of vertebrate microfossil remains collected from 15 kg of bulk rock from the Los Menires site.

Sample and Size (kg)	Mesh Size (mm)	Osteichthyes	Lissamphibia	Squamata	Testudinata	Crocodylomorpha	Bone Remains Indet	Eggshell Fragments
A (3.372)	0.5	4	0	0	0	5	31	24
	1	1	2	1	0	7	19	3
	2	0	0	0	0	0	0	0
	Total A	5	1	2	0	13	53	27
B (2.911)	0.5	2	0	3	0	9	55	40
	1	1	1	0	15	4	11	5
	2	0	0	0	4	0	1	0
	Total B	3	1	3	19	13	67	45
C (2.680)	0.5	0	2	3	0	3	50	47
	1	0	0	0	2	0	19	3
	2	0	0	0	5	0	0	2
	Total C	0	2	3	7	3	69	52
D (3.300)	0.5	1	0	6	0	8	55	43
	1	1	0	0	4	1	13	3
	2	0	0	0	2	0	9	0
	Total D	1	0	6	6	9	77	46
E (2.700)	0.5	0	7	2	0	3	50	38
	1	0	0	0	5	1	14	9
	2	0	0	0	5	0	0	0
	Total E	0	7	2	10	4	64	47
TOTAL (14.963)	0.5	7	9	14	0	28	241	192
	1	3	3	1	26	13	76	23
	2	0	0	0	16	1	13	2
	All remains *	**10**	**12**	**15**	**42**	**42**	**330**	**217**

* 668 fossil specimens obtained by screen washing (see Section 3).

A marked difference in this second sampling was the presence of tiny fossils from some microvertebrate groups such as lissamphibians, squamatans, and atoposaurid crocodylomorphs, which were not recovered in the surface sample. These remains were highly broken and consisted of osteoderms, teeth, and isolated bones. Teeth attributed to atoposaurids had crowns with mesial and distal carinae and were ornamented with apicobasal ridges. These also showed a wide morphological variability comprising conical, lanceolate, and broad leaf-shaped crowns in relation to the position in the dental arcade (e.g., [35,36]). Osteichthyans are scarce, but remains have been identified in addition to scales, such as some lanceolate teeth with smooth carinae belonging to Amiiformes indet. Eggshell fragments were much more abundant in these samples, representing almost a third of

the specimens collected. Along with vertebrates, other microfossils were relatively common, such as mollusks (e.g., planorbid freshwater gastropods), ostracods (cyprideans), charophytes (clavatoraceans), and small plant fragments.

Regarding the size distribution (Figure 5), the most abundant remains were less than 1 mm in size. The fraction 0.5–1 mm was the most optimal to record eggshell fragments, squamatans, and lissamphibians. Otherwise, turtle remains were found only in size fractions greater than 1 mm.
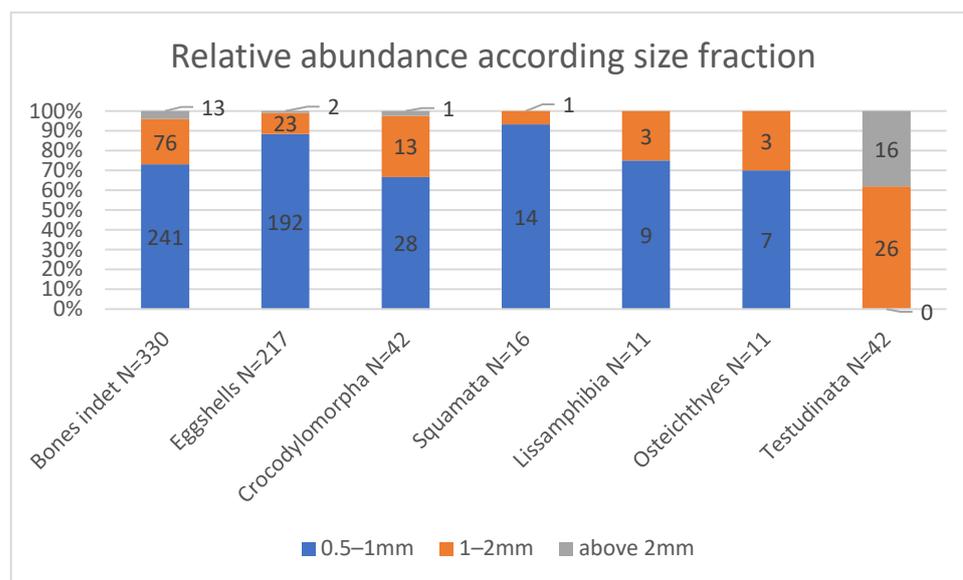
Figure 5. Bar graphic with the results of the screen-washed sample of Table 2.

5. Discussion

5.1. Comparison between Samples: Surface Collection vs. Screen Washing

Vertebrate microfossil bonebeds are localized concentrations of small resilient vertebrate hard parts (e.g., [8]). The inherent size bias of the sampling method of surface collection is manifested in the absence of small-bodied vertebrate groups such as lizards or lissamphibians, as reported in previous studies [8]. Our data show that other remains, such as eggshell fragments, are also highly skewed toward the thin fractions of the screen-washed samples, and may remain unnoticed in surface collection. However, leaving aside the impossibility of validating the presence of the most minute and delicate vertebrates, some common patterns can be observed in both samples.

To characterize the general compositional structure of a fossil assemblage, a parameter that can be provided from the data described in this work is the relative abundance rank. It is commonly considered useful when the analysis of a vertebrate microassociation is carried out (e.g., [5,8]). Thus, the results for the Los Menires fossil site, which are shown in Table 3 and Figure 6, reveal some considerations of interest.

Unidentifiable bone fragments were the most abundant remains recovered both on the surface and through screen-washing but were more abundant at the <1 mm fraction. This may be due to breakages or bone modification, which can significantly affect fossil association. The breakage could originate before burial but may also influence the exhumation of fossils and processing of samples.

Concerning the diversity of the fossil assemblage, a few observations can be highlighted: (1) Testudine plates are the most common identifiable elements that can be collected on the surface but also in the size fraction of screen-washed sediment > 1 mm. (2) Both sampling methods reveal a clear predominance of pleurosternids over helochelydrids. (3) The important representation of crocodylomorphs in the fossil association was detected in both types of sampling, at least for goniopholidids and bernissartiids. (4) The two sampling

methods reveal the scarcity of osteichthyans compared to other groups of semi-aquatic or terrestrial vertebrates.

Table 3. Relative abundance rank of fossil specimens included within the different categories of remains recognized in this study of the Los Menires locality.

Sampling Methods:	Surface Collection		Screen Washing	
Rank	Fossil Category	Number of Specimens	Fossil Category	Number of Specimens
1	Testudinata	59	Bone remains indet	330
2	Bone remains indet	53	Eggshell fragments	217
3	Crocodylomorpha	18	Testudinata	42
4	Coprolite remains	11	Crocodylomorpha	42
5	Dinosauria	8	Squamata	16
6	Osteichthyes	1	Lissamphibia	11
7	Eggshell fragments	1	Osteichthyes	10
-	Squamata	0	Coprolite remains	0
-	Lissamphibia	0	Dinosauria	0
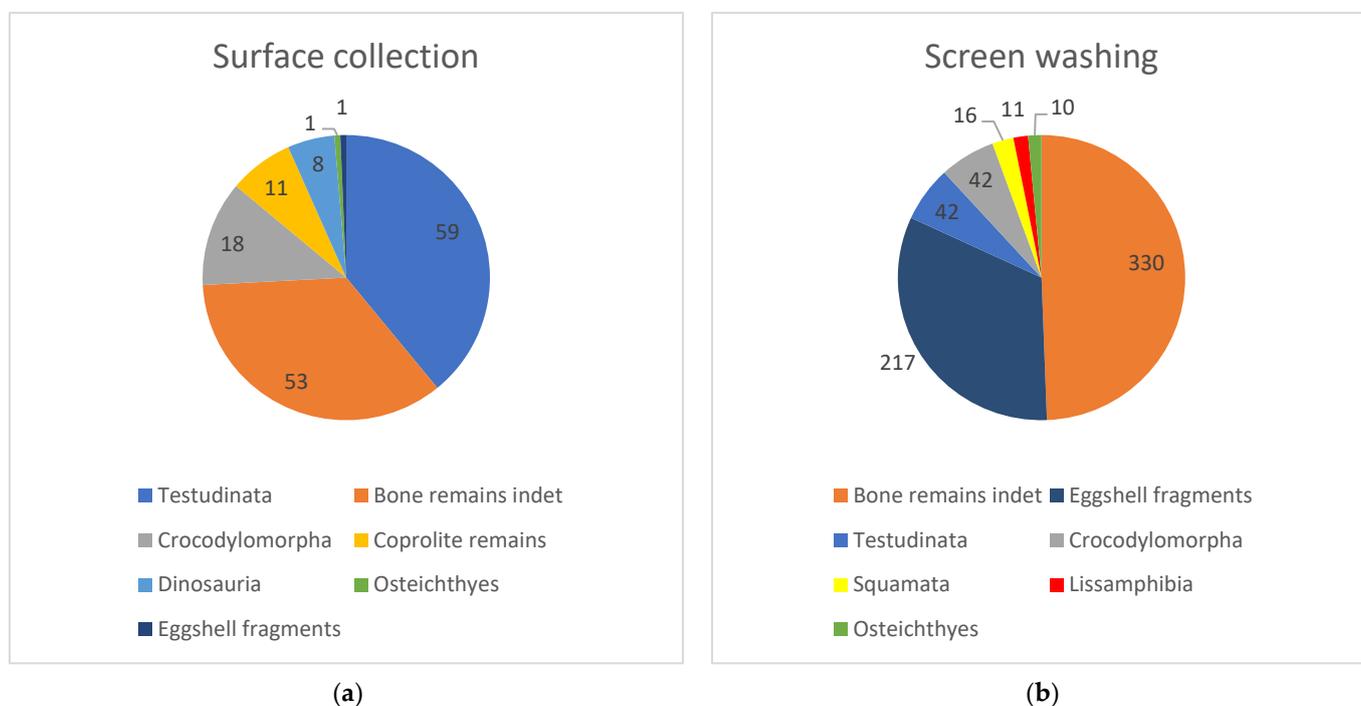
Figure 6. Relative abundance of the fossil remains (including number of specimens) based on the different sampling methods performed at the Los Menires fossil site: (**a**) Specimens obtained by surface collection; (**b**) Specimens obtained by screen washing.

From this comparison of sampling methodologies, it can be concluded that surface collection is reasonably effective in recognizing the main fossil groups that can constitute an association. However, the collection of remains on the surface is not suitable for capturing delicate and tiny fossils, such as those of some small vertebrates (e.g., lizards, lissamphibians), nor for recognizing the abundance of eggshells. In contrast, it can generate an overrepresentation of other components such as coprolites or ornithopod teeth that a 15 kg sediment sample may fail to detect. Lastly, according to the available data about the locality of Los Menires, some rare components of the fossil assemblage—i.e., dromaeosaurid and mammaliform teeth—could not be identified using the sampling methods described in this study.

The number of specimens obtained in this study seems to be low compared to the quantities that have been necessary to document robust analysis in other Mesozoic lo-

calities (e.g., [2,6,37]). However, the processing of the sediment divided into subsamples (Table 2) has allowed us to recognize the stability of some patterns in relation to the relative abundance rank that serves as a guarantee that data are representative (see [5] Figure 4). Rank orders are stable in subsamples regarding the dominance of unidentifiable bones and eggshell fragments within the microassociation and the abundance of crocodylomorphs. The rest of the considerations, relative to the less common fossil groups, would be more inconsistent. In order to broaden these data and consolidate interpretations, future work must focus on the successive repetition of samplings in this locality and make comparisons with samplings in other different fossiliferous localities.

5.2. Origin of the Microfossil Site and Palaeoecological Approach to the Biota of Los Menires

Attending to the fine-grained nature of the hosting layer, the accumulation of vertebrate hard parts in Los Menires took place in a low-energy setting [2,14]). This, in turn, corresponds to a distal sub-environment within the alluvial-lacustrine system represented by the Mirambel Formation as a whole [14].

Concerning vertebrates, the bioclast concentration of Los Menires (45 microfossil remains per kilogram) is high in comparison with other Iberian localities (see [38]), being a rate similar to that of the richest levels from the lacustrine El Castellar Formation of Galve (Teruel province) or those of vertebrate microfossil-rich Lower Cretaceous deposits from distant paleogeographical regions (e.g., [39]).

As stated previously [14], there is no evidence of catastrophic events or biogenic concentrations in the Mirambel Formation but rather the evidence is suggestive of attritional accumulations. The genetic framework for the vertebrate skeletal sites was physical concentrations, with sedimentology as a key factor. The source of the different bone concentrations fits with a passive attritional model. The concentrations were derived from a set of processes in which autochthonous to parautochthonous remains were accumulated [40]. When sediment accumulation is slow relative to bone input, fossil-rich deposits can occur, as in the case of Los Menires, whereas, most of the time, moderate sedimentation rates prevent significant bone concentrations.

Given the depositional environment inferred for the Los Menires bed, the abundance of remains from semiaquatic vertebrates such as turtles and crocodiles is unsurprising. However, the turtle's bony shell is very robust, and its fragments are more durable than most other bones; thus, an overrepresentation of Testudinata in the fossil assemblage can partly reflect a positive preservational bias. Furthermore, their very characteristic shape and diagnostic histology make testudinate plates very easy to identify, even with broken fragments, which is not the case with most other postcranial elements of other vertebrates, which can result in an identification bias. Yet, in any case, pleurosternids are the best-represented turtles, in contrast to helochelydrids, which are sparingly present. Non in vain Pleurosternidae are freshwater turtles widely represented in the Iberian biotas from the Late Jurassic to the Albian [41]. Otherwise, based on some anatomical features, i.e., limbs covered with osteoderms, secondary palate, jaw morphology, shell bone microanatomy, and histology, helochelydrids are large-bodied turtles interpreted as terrestrial dwellers, with a rather molluscivorous diet [21,22]. Interestingly, in addition to being more abundant, remains of freshwater pleurosternids are better preserved than those of likely-terrestrial helochelydrids, which is coherent with the respective conditions of parautochthony for the first and parautochthony or allochthony for the latter.

In accordance with what is observed in other Lower Cretaceous assemblages of Iberia, crocodylomorph taxa of Los Menires are ubiquitous clades represented by relatively small body-size specimens. Size restriction at the crocodylomorph assemblages has been explained as evidence of a community of dwarf species or an age segregation behavior (e.g., [25,42]). Goniopholididae were common semiaquatic predators in freshwater ecosystems of Laurasia during the latest Jurassic and Early Cretaceous [43] periods, which are also well represented in the faunal assemblage of Los Menires. However, the atoposaurids are more terrestrial crocodylomorphs [44] and were recovered at the site mainly by screen washing.

Dinosaur remains are scarce, with ornithopod shed teeth being the most abundant identifiable elements. The remarkable accumulation of ornithopod shed teeth supports the existence of a favorable area where phytophagous dinosaurs lost resorbed teeth from their dental rows during feeding [45].

Eggshell fragments are also abundant vertebrate fossil remains in Los Menires that are mainly obtained by the micropaleontological analysis of sediment. Eggshell accumulations are more common in palustrine and lacustrine levels from the Mirambel Formation [14], as in other non-marine Barremian units from nearby sub-basins [16,24,46].

The new results along with the previously known data (see [14]) allow us to consider which fossil assemblages of Los Menires are mostly demic, i.e., organisms that died and accumulated in the same environments where they lived, with a predominance of remains of freshwater aquatic and semiaquatic organisms, i.e., charophytes, ostracods, bivalves, gastropods, turtles, crocodilians, lissamphibians, and osteichthyans. Therefore, the remains, e.g., utricles, shells, disarticulated bones and teeth, eggshell fragments, and coprolites, of these groups are autochthonous or, more likely, parautochthonous fossils that accumulated in a low-energy, shallow-water, depositional environment. Likewise, remains of terrestrial vertebrates, i.e., dinosaurs, lacertilians, and mammals, are also present and would be parautochthonous rather than allochthonous, given the low-energy sedimentary context and absence of obvious biostratinomic signals of hard transport, e.g., high degree of roundness and abrasion.

The presence of marine, ademic, and allochthonous elements, i.e., benthonic foraminifera, whose accumulation in the depositional system would occur during storm events, indicates a clear geographical proximity of the shallow freshwater depositional environment with respect to the coastline. This is in agreement with the proposed model for the Mirambel Formation [14]. Moreover, the relative abundance of semiaquatic vertebrates—testudinatans and crocodylomorphs—and the scarcity of both fully aquatic fishes or vertebrates of terrestrial lifestyle—dinosaurs and mammaliforms—highlights Los Menires assemblage as fossil evidence for an ancient wetland, i.e., lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water, see [47]. The sedimentological and taphonomic features of Los Menires are, in turn, evidence of a lentic system.

The recorded time of bioclast accumulation of the Los Menires assemblage is unknown, but a time-averaging of thousands of years is proposed in similar depositional settings with attritional mortality taking place [48,49].

This first approach to the palaeoecology of Los Menires must be taken with caution as, firstly, the analyzed sample was not large enough to be representative of the fossil association. Secondly, further work is required to determine how representative the vertebrate fossil assemblage of Los Menires is of the vertebrate fauna present in the paleobiocoenosis. Since most observations presented in this work are coherent with the palaeoenvironmental context assignable to the fossil locality of Los Menires and the Mirambel Formation, the extension of the study on a larger sample may reinforce and refine our results.

6. Conclusions

The fossil assemblage of Los Menires is dominated by autochtonous or parautochthonous remains of freshwater aquatic and mainly semiaquatic organisms, i.e., charophytes, ostracods, bivalves, gastropods, turtles, crocodylomorphs, lissamphibians, and osteichthyans, whereas parautochthonous remains of terrestrial vertebrates, i.e., dinosaurs, lacertilians, and mammaliforms, are also present. The accumulation of vertebrate hard parts in Los Menires took place in a low-energy, shallow-water depositional environment within the alluvial-lacustrine system represented by the Mirambel Formation.

From the comparison of subsamples respectively obtained by surface collection and screen washing methods, it can be concluded that surface collection is reasonably effective in recognizing the main fossil groups that can constitute an association. However, the collection of remains on the surface is not suitable for capturing delicate and tiny fossils,

such as those of some small vertebrates (e.g., lizards, lissamphibians), nor for recognizing the abundance of eggshells. In contrast, it can generate an overrepresentation of other components such as coprolites or ornithopod teeth.

Results and interpretations of this work must be endorsed with repeated sampling and should be tested in other vertebrate microfossil assemblages.

Appendix A

In addition to the new palaeontological data reported in this work, the local stratigraphic series of the Los Menires outcrop was logged and sampled in order to recognize the fossil richness and palaeoenvironmental significance of the unit. From this systematic bed sampling, it is concluded that the Los Menires horizon (=SM10) hosts the highest bioclast concentration for the series.

Table A1. Systematic sediment sampling of the Mirambel Formation in the local series, which includes the Los Menires fossiliferous bed (=SM10), from [14] (S3).

Samples (2 kg)	Lithology	Stratigraphic Location (m)	Eggshells (Fragments)	Skeletal Remains	Charophytes	Ostracods	Depositional Environment
SM1	Gray and ochre marls	0.2	yes (30)	no	yes	yes	Shallow lacustrine
SM2	Gray and ochre marls	2	no	no	no	no	Alluvial-palustrine
SM3	Gray sandstones	7.5	no	no	no	no	Fluvial channel
SM4	Ochre lutites with red tones	8.5	no	no	no	no	Floodplain
SM5	Purplish lutites	11	no	no	no	no	Floodplain
SM6	Gray marls with red patches	16	no	no	no	no	Floodplain
SM7	Gray marls with ochre patches	17.5	no	no	no	no	Floodplain
SM8	Ochre lutites	21	yes (12)	no	yes	yes	Palustrine
SM9	Dark-gray marls	26.5	yes (50)	yes	yes	yes	Shallow lacustrine
SM10 *	Very-dark-gray marls	29.5	yes (63)	yes	yes	yes	Shallow lacustrine
SM11	Gray marls with ochre tones	34	yes (2)	no	yes	no	Palustrine
SM12	Reddish and ochre marls	36	yes (5)	no	yes	no	Palustrine

* = Los Menires bed.

Appendix B

The Barremian Mirambel Formation is a Cretaceous sedimentary unit in the Iberian Chain (NE Spain) that preserves different types of dinosaur and other vertebrate fossils (skeletal, eggshell, and ichnological remains [14,16,50]). Here is shown a comparative overview of the vertebrate record from the Barremian Mirambel Formation, including the complete faunal list [14] and references therein, the taxa recorded in the fossil locality of Los Menires [14], and the taxa identified from the subsample obtained by surface collection and described in this work. The taxonomic diversity identified in the Mirambel Formation (17 vertebrate taxa) is provisionally low in comparison with other Barremian units from the Iberian Range (e.g., [24]) as most of the vertebrate material from the Ladruñán anticline has not been studied in depth.

Table A2. Vertebrates recorded in the Mirambel Formation.

Higher Taxa	Taxa	Los Menires Assemblage	Surface Sample of Los Menires
Chondrichthyes			
	Hybodontidae indet.		
Osteichthyes		x	x
	Pycnodontiformes indet.	x	
	Lepisosteiformes indet. [1]	x	
	Amiiformes indet.	x	
Lissamphibia			
	Lissamphibia indet.	x	
Squamata			
	Squamata indet.	x	
Chelonia			
	Helochelydridae indet. [2]	x	x
	Pleurosternidae indet.	x	x
Crocodylomorpha			
	Goniopholididae indet.	x	x
	Atoposauridae indet.	x	
	Bernissartiidae indet.	x	x
Ornithopoda			
	Styracosterna indet.	x	x
Sauropoda			
	Titanosauriformes indet.		?
Theropoda			
	Spinosauridae indet.	x	
	Carcharodontosauridae indet.		
	Maniraptoriformes indet.	x	
Mammalia			
	Spalacotheriidae indet.	x	

[1] = Semionotiformes, in [14]; [2] = Solemydidae, in [14].

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