Dinosaurs and other vertebrates from the Papo-Seco Formation (Lower Cretaceous) of southern Portugal

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Abstract

New vertebrate remains reported from the Papo-Seco Formation (Lower Barremian, Lower Cretaceous) of Areias do Mastro, in Cabo Espichel, SW Portugal, south of Lisbon. The marine, lagoonal, and estuarine limestones, marls, sands and gravels have yielded remains of dinosaurs and other reptiles since the 19th century. Recent paleontological prospecting produced several vertebrate remains, including turtle shell fragments, crocodilian teeth, fish and pterosaurs. Research identified both bones and teeth of fish, crocodiles, dinosaurs Baryonyx and iguanodontian, as well as a ctenochasmatoid pterosaur, and a possible ornithocheirid pterosaur. These new disclosures are an important contribution to the knowledge of vertebrate diversity from the Portuguese Cretaceous. Faunal species combination proven to be similar to other faunal associations of Barremian formations in the Iberian Peninsula.

Keywords: Early Cretaceous, vertebrates, dinosaurs, pterosaurs, Espichel, Portugal

1. Introduction

The Early Cretaceous was a key time in the evolution of terrestrial biota, marking the changeover from floras dominated by cycads and other gymnosperms to those dominated by angiosperms (Barrett and Willis, 2001; Lloyd et al., 2008). The rise of angiosperms was associated with the diversification of various insect groups, including butterflies, ants, bees, and wasps, as well as of insect-eating animals such as lizards, birds, and mammals. This modernisation of terrestrial biota seems to have occurred without much dinosaur involvement, which continued as the major large-sized terrestrial animals (Barrett and Willis, 2011; Lloyd et al., 2008), but the time in retrospect was crucial in marking the initiation shift from marine dominance to terrestrial biodiversity (Vermeij and Grosberg, 2011).

The Early Cretaceous vertebrates of the Iberian Peninsula are of scientific knowledge for some time, especially...
in eastern Spain sites such as Galve (Teruel), Uña and Las Hoyas (Cuenca), Golmaya (Soria), for example (e.g. Estes and Sanchiz, 1982; Sanz et al., 1984; Buscalioni and Sanz, 1987; Ruiz-Omeñaca et al., 2004; Fuentes Vidarte et al., 2005; Ortega et al., 2006; Torcida Fernández-Baldor, 2006; Sánchez-Hernández et al., 2007; Buscalioni and Fregenal, 2010; Canudo et al., 2010; Pereda Suberbiola et al., 2012a), showing close similarity to the well-documented faunas from the Wealden of England, France, and Germany (e.g. Benton and Spencer, 1995; Batten, 2011). Reports of such faunas from the Cretaceous in Portugal have been more sporadic.

Portuguese Cretaceous vertebrates were first reported in the 19th century, from the Cabo Espichel area, south of Lisbon, however the remains were rare and fragmentary. The Portuguese geological survey (Sauvage 1897, 1898) reported dinosaur and crocodile teeth from the Papo-Seco Formation, at Boca do Chapim’s quarry. Later, Lapparent and Zbyszewski (1957) reported turtle remains and crocodile teeth and bones, as well as dinosaurian remains. Among the latter are two teeth fragments referred to megalosauridae (Lapparent and Zbyszewski, 1957), later classified as carnosauria. incertae sedis (Galton, 1994). Some herbivorous dinosaur remains were also reported: teeth, caudal vertebrae and the distal end of a right femur identified as Iguanodon and teeth of Astrodon (=Pleurocoelus) valdensis (Lapparent and Zbyszewski, 1957; Dantas, 1990; Galton, 1994). According to Antunes and Mateus (2003) these sauropod teeth are insufficient to assign a specific classification. A tooth from Boca do Chapim (MGIGM.10), displayed in Museu Geológico’s inventory to an Iguanodon, was in 2000, identified as a cf. Pelorosaurus tooth (Figueiredo, 2000). These sauropod designations, whether Pelorosaurus or Astrodon, are in line with descriptions of material from various locations in the European Early Cretaceous, such as the English Wealden, despite affinities between these taxa being uncertain (Taylor, 2010).

Recently, a preliminary analysis of a new discovery of several bones of an ornithopod dinosaur in Boca do Chapim’s quarry was reported (Figueiredo, 2010, 2014). Fragments of jaws found at Boca do Chapim by Sauvage (1897-1898) were identified as being from a crocodile (Suchosaurus girardi); they were later analysed by Buffetaut and classified as spinosaurid Baryonyx, based on similarities with the holotype of Baryonyx walker from the English Barremian (Buffetaut, 2007). Recently, Mateus et al. (2011) reported skull and post-cranial bones also attributed to Baryonyx walker in a place they named Praia das Aguncheras (Mateus et al., 2011), being the real topology Praia do Guincho.

Since 1999, Centro Português de Geo-História e Pré-História carried out research in the Papo-Seco Formation, during which a set of vertebrate remains (bones and teeth) were found: turtles, fishes, tetanuran theropods (including derived maniraptorans/birds) and iguanodontian ornithopods among dinosaurs (Figueiredo, 2002, 2004, 2005, 2007, 2008, 2014). The purpose of this paper is to publish the findings of Areias do Mastro location. Although several vertebrate remains of the Papo-Seco Formation are known, this the first report of remains found at Areias do Mastro’s quarry. The remaining quarries of Papo-Seco Formation enclosed the remains of vertebrates published from Boca do Chapim (Lapparent and Zbyszewski, 1957) and Praia das Aguncheras (= Praia do Guincho) (Mateus et al., 2011).

Institutional abbreviations: CPGP, Centro Português de Geo-História e Pré-História, Lisbon, Portugal; LAP – Laboratório de Arqueozoologia e Paleontologia do CPGP, Golegá, Portugal; MGLNEG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisbon, Portugal.

2. Geology

Areias do Mastro is situated about 40 km south of Lisbon, in the SW of the Setúbal Peninsula, near Sesimbra (Fig. 1). It is a small beach at the bottom of the coastal cliffs of the Cabo Espichel anticline.

The Papo-Seco Formation was previously referred to as ‘Grès marneux à grands sauriens’ (Choffat, 1904-1907, p. 13), ‘Grès aux dinosauriens’ (Rey, 1972, p. 174), and ‘Ca-madas com Iguanodon mantelli’ (Ferreira, 1961, p. 255), the source of previously reported bones and teeth, as noted. It is dated as Lower Barremian (Rey, 1972; Manupella et al., 1999), 127 to 129.4 million years old, according to the International Chronostratigraphic Chart, 2015. This formation is about 18.5 m thick, characterized by its marls and greenish silty clays with lignite and gypsum. It presents intercalations of sandstones with horizontal stratification (Manupella et al., 1999). The fauna of this formation comprises remains of dinosaurs and invertebrates (bivalves and gastropods) in the coarse sandstone layers, and ostracods in the marls. At the upper boundary of this formation can be observed bioturbated silty limestone layers with oyster remains. The overall sedimentary setting is a mix of lagoonal and estuarine sediments (Manupella et al., 1999; Dinis et al., 2008).

The Papo-Seco Formation lies between Areias do Mastro and Boca do Chapim formations. The older layers, by the seashore, still belong to the Areias do Mastro Formation, showing marine carbonate limestone facies. On top of these layers sandstones can be clearly observed, indicator of an estuarine environment, which correspond to the beginning of the Papo-Seco Formation (Fig. 2). Above these lay marly beds, which contain marine and terrestrial vertebrate remains.

The lowest layers of the Papo-Seco Formation, from Boca do Chapim at the southernmost entrance to Areias do Mastro, two faults of about 2m thick of light-coloured marine limestone (Fig. 2), in terms of fauna, yield some fragments of turtle and gastropods shells, as well as some fish teeth. These initial layers are topped by a further two layers of thin yellowish sandstones.

Sedimentological analysis of the interbedded layers (Table 1) demonstrates evolution from a lagoon-like (cat’s-eye
pond) environment, more closed, witnessed by the prevailing fine fraction, to a coastal marine environment, as shown by the marly clays of the carbonate layers. Between these two phases, the increase in the sandy fraction indicates the opening of the lagoon and, possibly, an estuarine episode (with over 65% of sand). While carbonates increase progressively with increasing influence of marine processes, the concentration of organic matter could be related either to interplay of aerobic/anaerobic conditions during deposition, or to post-depositional processes.

3. Materials and Methods

The study is based on a collection of 22 vertebrate fossils from Areias do Mastro, curated in the palaeontology collection of CPGP. These materials result from prospecting at the cliffs of Areias do Mastro (1998-2003) and the excavation of four clay layers in the lower part of the cliffs (2004-2009). The palaeontological research coordinated by SF as part of a wider project that includes the pre-historic archaeology of the whole Cabo Espichel area.
In the laboratory (LAP), the materials were cleaned and measured followed by a taxonomic study, through a comparison, analysis of the main characteristics of the studied fossils, and biometric studies. The measurements used for tooth analysis CPGP.1.06.2 followed Smith et al.’s (2005) methodology. For the measurement of fish teeth, only three dimensions were considered: length, width and crown height. In Hospital de Seia and in laboratory of Setpet was made a radiographically study of CPGP.01.99.1.

4. Systematic palaeontology

4.1. Actinopterygians

OSTEICHTHYES Huxley 1880
ACTINOPTERI GII Cope 1871
SEMIONOTIFORMES Arambourg & Bertin 1958
Genus: LEPIDOTES Agassiz 1832
CF. LEPIDOTES SP.

Table 1.- Basic sedimentological characterisation of the lowest layers of the Papo-Seco Formation, in Areias do Mastro (Cabo Espichel, Portugal).

<table>
<thead>
<tr>
<th>Description</th>
<th>Sand fraction</th>
<th>Organics</th>
<th>Carbonates</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1 Clay</td>
<td>10%</td>
<td>1.1%</td>
<td>Residual</td>
<td>Lagoon/Coastal lake</td>
</tr>
<tr>
<td>C2 Sandy clay</td>
<td>27.6%</td>
<td>0.6%</td>
<td>3.9%</td>
<td>Transition to open environment?</td>
</tr>
<tr>
<td>C3 Sandy loam (slightly marly)</td>
<td>65.02%</td>
<td>2.9%</td>
<td>8.55%</td>
<td>Estuarine</td>
</tr>
<tr>
<td>C4 Marly sandy clay</td>
<td>35.69%</td>
<td>0.4%</td>
<td>20.64%</td>
<td>Marginal marine carbonate facies</td>
</tr>
</tbody>
</table>

Fig. 2.- The Areias do Mastro locality, summary sedimentary log, showing vertebrate-bearing units (top left), diagram of cliff section, showing the two faults, and the Papo-Seco and Areias do Mastro formations (top right), and (bottom) photographs of the surveyed sites, showing fossiliferous beds highlighted.
Material: CPGP.1.05.3; 4; 5; 6; 7; 8 and 24; and CPGP.1.07.5; and 21. 9 teeth.

Description: 11 hemi-ellipsoid or round and flattened teeth (Fig. 3: 1-9), from 3-6 mm in diameter, and with smooth occlusal surfaces and flat bases on the insertion side. The sedimentary analyses and the few fish remains identifiable indicate the presence of the shallow seas inhabitant Lepidotes, which present very characteristic of this genus: The material of Areias do Mastro shows that the marginal teeth are compressed and the inner teeth are smooth and less elongated than the teeth of Pycnodus.

4.2. Crocodyliforms

CROCODYLIFORMES Hay 1930
NEOSUCHIA Benton and Clark 1988
GONIOPHOLIDIDAE Cope 1875
ANTEOPHTALMOSUCHUS Salisbury and Naish, 2011
Cf. ANTEOPHTALMOSUCHUS SP.

Material: CPGP.1.03.1 (Fig. 3, 10 to 13); PGP.1.03.7 (Fig. 3: 14-17); CPGP.1.05.9 (Fig. 3: 18-21); CPGP.1.06.71 (Fig. 3: 22-25); CPGP.1.06.81 (Fig. 3: 26-29). 5 teeth.

Description: Five caniniforms teeth, conical and curved towards the lingual side, with sharp crowns, and with very fine longitudinal striations, further marked on the lingual side when compared with the labial surface. The carinae are not serrated or jagged. The base is circular, but the crown is subcircular in cross section.

These teeth exhibit characteristics of the goniopholidid group described by Andrade et al.: The crown is subcircular in cross section, without evident lateral compression, but the lingual and labial surfaces are asymmetric. The labial face is strongly arched, whereas the lingual is not as much. Enamel ornamentation is present on both lingual and labial surfaces, in the form of basi-apical ridges. These are well defined, conspicuous, and closely packed, however low. Overall, the ornamentation is non-anastomosed. A distinct keel runs on mesial and distal faces of the crown (Andrade et al., 2011, p. 82). We found also the characteristics described by Puértoas-Pascual et al. (2015) to the G anteophtalmosuchus specimen of Teruel (Spain): they are conical, relatively short and robust, with the labial surface more convex than the lingual surface. The posterior surface is slightly shorter and slender. Two carinae are well developed in the anterior and posterior surfaces of the teeth; these carinae are basoapically straight (Puértoas-Pascual et al., 2015, p. 46). In CPGP.1.03.1 and PGP.1.03.7, the apex is broken, CPGP.1.05.9 has its apex worn, and the base and the labial face broken in the mesial area, CPGP.1.06.71 consists only of the apex, while CPGP.1.06.81 has the apex broken and the face worn.

4.3. Pterosaurs

PTERODACTYLOIDEA Plieninger 1901
ORNITHOCHERIROIDA Seeley, 1870
ORNITHOCHERIIDAE Seeley 1870
ORNITHOCHERIIDAE indet.

Material: CPGP.1.03.2 (Fig. 3: 30-33). One tooth.

Description: Sharp tooth, concave on the distal and curved in the mesial edge, slightly bent in the apical, to the lingual side. It presents some of the characteristics of plesiosaur teeth: the cross-section is compressed enough buccolingually, with smooth carinae, not serrated and pronounced in the medial and apical portions; the enamel has fine grooves which branch off towards the base. Slender recurved teeth are present in ornithocheirid pterosaurs and elasmosaurid plesiosaurs, but in ornithocheirids the enamel surface is generally smooth, restricted to the apex of the tooth, and asymmetrically distributed (Averianov, 2007; Sweetman and Martill, 2010).
Descriptions: The more complete tooth (CPGP.1.09.1; Fig. 3: 34-36) is needle-like, 35.8 mm long, and measuring 4.6 mm x 4.3 mm at the base. The specimen is a single tooth crown, covered from bottom to top in enamel. At the base, the tooth wall is thin and the interior is filled with sediment, suggesting a deep pulp cavity, but the extent of this pulp cavity cannot be determined. The degree of curvature is modest, amounting to an offset of only 2.3 mm from the tip to a horizontal line projected from the base of the preserved tooth. The tooth is more or less circular in cross section from tip to base, but the cross section becomes slightly extended distally, marked by a posterior carina that runs for 80% of the length of the tooth from below the tip to the base. The surface of the enamel is generally smooth, and only lightly pitted, but with some slight longitudinal ridges, each 0.05 mm wide, and running for much of the length of the tooth, on the labial face.

The less complete specimen (CPGP.1.04.3) is 11.7 mm long and measures 4.2 mm x 3.2 mm at one end. According to its general appearance and following cues from measurements, it is likely a broken middle section from a needle-like tooth, as described. It shows the same dimensions, cross-sectional shape, and surface texture as the complete tooth crown.

4.4. Dinosaurs

4.4.1. Saurischians

THEROPODA Marsh 1881
SPINOSAURIDAE Stromer 1915
BARYONYX Charig and Milner 1986
BARYONYX sp.

Comments: As already mentioned, in the 19th century, in the Papo-Seco Formation, in deposits from the Boca do Chapim, fragments of a maxilla and a jaw were found by the French palaeontologist H. E. Sauvage, who attributed them...
to a crocodile, *Suchosaurus girardi*, (Sauvage, 1898). However, these remains were revised in 2007 by H. Buffetaut, who attributed them to *Baryonyx* based on similarities with the holotype of *Baryonyx Walkeri* from the English Barremian (Buffetaut, 2007). More recently, O. Mateus and collaborators reported the discovery of a set of bones (from the cranial and post-cranial skeleton) from about 1 km to the north of Areal de Mastro, in Praia do Guincho, and assigned the material to *Baryonyx Walkeri* (Mateus et al., 2011).

Material: CPGP.1.06.2 (Fig. 3: 37-40). One tooth.

Description: Ziphodont conical tooth, curved, with the crown narrow and pointed, with longitudinal grooves in the apical and medial areas. The base has no ornamentation. It has a worn apex. The distal carina is sharp and micro-serrated (Fig. 5.2). The mesial carina has a long and wide longitudinal groove, which seems to result from normal wear of the tooth. This tooth is identified as *Baryonyx* sp., based on its overall shape and surface ornaments, further confirmed by the biometric study: our measurements of CPGP.1.06.2 are within the range of values obtained by Smith et al. (2005) for *Baryonyx* from the British Wealden (Table 2). Furthermore, this tooth shows the characteristics of the *Baryonyx* teeth described in several studies (Charing and Milner, 2007; Smith et al., 2005; Fowler, 2007; Buffetaut, 2007, 2012; Alonso and Canudo, 2015; Alonso et al., 2015). These characteristics are: subcircular cross section, moderate lingual curvature, carina located on the mesiodistal axis of the crown, six ridges. The CPGP.1.06.2 does not have fluted enamel on the labial surface or any microgranular ornamentation on the edges, but it has very fine denticles, from the apex to the base, with very high density, with 7 denticles per mm (Fig. 5.2). These last three characteristics are present in the morphotype of *baryonychine* teeth but not in other spinosaurids (Alonso and Canudo, 2015).

SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
SAUROPODA indet.

<table>
<thead>
<tr>
<th>Material</th>
<th>CPGP.1.06.2</th>
<th>BMNH R9951</th>
<th>BMNH R9951a</th>
<th>BMNH R9951D</th>
<th>BMNH R9951E</th>
<th>BMNH R9951F</th>
<th>BMNH R9951G</th>
<th>BMNH R9951H</th>
</tr>
</thead>
<tbody>
<tr>
<td>CBL</td>
<td>12.20</td>
<td>13.06</td>
<td>10.49</td>
<td>11.69</td>
<td>15.76</td>
<td>13.18</td>
<td>12.12</td>
<td>16.42</td>
</tr>
<tr>
<td>CBW</td>
<td>10.80</td>
<td>11.24</td>
<td>7.90</td>
<td>11.19</td>
<td>12.05</td>
<td>10.88</td>
<td>10.35</td>
<td>15.19</td>
</tr>
<tr>
<td>CH</td>
<td>28.11</td>
<td>31.37</td>
<td>23.72</td>
<td>28.72</td>
<td>34.8</td>
<td>29.67</td>
<td>27.19</td>
<td>38.55</td>
</tr>
<tr>
<td>AL</td>
<td>27.39</td>
<td>32.29</td>
<td>24.77</td>
<td>29.22</td>
<td>37.41</td>
<td>30.52</td>
<td>30.46</td>
<td>43.88</td>
</tr>
<tr>
<td>CA</td>
<td>80.62°</td>
<td>82.96°</td>
<td>80.56°</td>
<td>82.42°</td>
<td>83.39°</td>
<td>82.60°</td>
<td>81.14°</td>
<td>83.60°</td>
</tr>
<tr>
<td>CBR</td>
<td>0.885</td>
<td>0.860</td>
<td>0.753</td>
<td>0.957</td>
<td>0.764</td>
<td>0.825</td>
<td>0.853</td>
<td>0.922</td>
</tr>
<tr>
<td>CHR</td>
<td>2.304</td>
<td>2.401</td>
<td>2.261</td>
<td>2.456</td>
<td>2.208</td>
<td>2.251</td>
<td>2.243</td>
<td>2.347</td>
</tr>
<tr>
<td>CBL/CBW-R</td>
<td>1.130</td>
<td>1.162</td>
<td>1.328</td>
<td>1.045</td>
<td>1.308</td>
<td>1.211</td>
<td>1.171</td>
<td>1.081</td>
</tr>
</tbody>
</table>

Table 2 - Key measurements of tooth CPGP.1.06.2 and known teeth of *Baryonyx* from the British Museum of Natural History (BMNH). Abbreviations: AL: apical length; CA: crown angle; CBL: crown base length; BR: crown base ratio; CBW: crown base width; CH: crown height; CHR: crown height ratio; CBL/CBW-R: crown base length / crown base width ratio.

Fig. 7. - Tooth of Baryonyx sp., CPGP.1.06.2. In 1: a) labial surface; b) distal surface; c) lingual surface; d) medial surface. 2: Showing micro-serrations.

Material: CPGP.1.06.33 (Fig. 6). One caudal vertebra.

Description: The right side of the centrum of a distal caudal vertebra with the base of the neural arch. It has a subcylindrical shape (length, 11.4 cm; proximal height, 7.5 cm; distal height, 7.4 cm) and it is laterally and ventrally concave. The posterior condyle is slightly displaced dorsally and the cotyle is concave. The central zone of the lateral surface has a large and lower prominence with a horizontal ridge. In Portugal the remains of Early Cretaceous sauropods are rare, however the most represented group of sauropods in the Cretaceous of the Iberian Peninsula are the Titanosauriformes (Ortega et al., 2006, p. 226, Mannion et al., 2013). On
Delapparentia and Proa are only described in Iberian Peninsula (Gasca et al., 2014, 2015).

ORNITHOPODA Marsh, 1881
ORNITHOPODA INDET.

Material: CPGP.1.03.3 (Fig. 3: 41, 42). One tooth Description: Fragment of the lingual part of the crown of a left denture tooth. It is shows some wear on the occlusal surface. It has no kind of ornamentation. In the distal area, the surface is flat, making an angle with the lingual zone. The mesial area is curved.

IGUANODONTIA Dollo, 1888
ANKYLOPOLLEXIA Sereno, 1986
STYRACOSTERNA Sereno, 1986
IGUANODONTS

The remains (a maxilla fragment and a tooth) show features of iguanodonts. However, in recent years the taxa related to Iguanodon have been revised. Despite revision, the current analysis frames the remains in the group of iguanodonts, also describing and grouping the characteristics of these findings within the recently revised genera identified in this group. The study of this material was done by comparison of the
discretion of the teeth and maxilla of Iguanodonts described in the Barremian of Western Europe defined by Carpenter and Ishida (2010), Ruiz-Omeñaca (2011) and Norman (2013). The following species are signed: Dollodon seelyi (nomen dubium, Norman, 2013), Iguanodon bernissartensis, Mantellisaurus atherfieldensis, Proplacopora galtoni and Delapparentia turoliensis. Of these species the Iguanodon bernissartensis, Mantellisaurus atherfieldensis and Delapparentia sp have cranial skeleton elements described (Norman and Weishampel, 2004; Paul, 2007, 2011; Norman, 2011a, 2013; Gasca et al., 2015).

Material: CPGP.1.99.7 (Figs. 8, 9 and 10); CPGP.1.01.2 (Fig. 3 and 6: 43-46). A maxilla fragment and a tooth.

Description: A fragment of the left part of a maxilla, with part of the palate and five teeth (two with the crown completely above the alveolar parapet, one with the apex above and two still within the alveoli). This fossil is 9.8 cm long and it has a robust appearance. It has three foramina, which circumscribes the alveolar parapet, it has two teeth with triangular crown, strongly denticulated and two other teeth with a semi-rectangular crown that have a very large primary ridge (Fig. 6). It has some features of the Iguanodontidae teeth noted by Norman and Weishampel (2004); Paul, (2007, 2011) and Norman, (2011, 2013), such as possessing only one replacement tooth per tooth position, the labial surface of the crown is thickly enameled and has a strongly denticulate margin and is dominated by a very large primary ridge arising from the base of the crown. On the labial surface there are grooves or lines and a less prominent second ridge. The teeth do not display any ornamentation on the lingual surface. In lateral view of maxilla there are tree foramina for alveolar nerve and, in medial view, we can identify two foramina for blood vessels.

From X-ray analysis (Fig. 10), it is possible distinguish the dental alveoli, which are wide and deep, revealing a long root. In this x-ray is clearly observed only one replacement tooth per tooth position.

The estimate length of CPGP. 01.99.7 (approx. 30 cm), considering the size of the teeth, places it between that of a Mantellisaurus atherfieldensis (=Iguanodon atherfieldensis) (27 cm) and that of a Iguanodon bernissartensis (39 cm) (Norman and Weishampel, 2004). The foramen of insertion of the jaw muscles are less prominent than those of I. bernissartensis, and similar to those of Mantellisaurus atherfieldensis (Fig. 8). Considering the length and the characteristics of the foramen of jaw muscles insertion from the CPGP. 01.99.7, it appears closer to Mantellisaurus atherfieldensis than to I. bernissartensis. Furthermore, the CPGP.1.01.2 and the teeth of CPGP.1.99.7 have a different shape and ornamentation of those of Delapparentia sp (Gasca et al., 2014, fig. 2), in particular the shape and position of the ridges.

CPGP.1.01.2 is an isolated tooth. It displays the same dimensions (Table 3) and it holds, from the lingual view, the same characteristics of the cheek teeth of the CPGP.1.99.7. The difference is the presence of 8 accessory ridges, between the primary ridge and the marginal ridges (5 between primary ridge and the anterior marginal ridge and 3 between the primary ridge and the posterior marginal ridge). Identifying some features of the iguanodonts teeth noted by Galton (1994, p. 258) such as a free edge with small marginal denticles and a distinct ridge. From the posterior viewpoint, the marginal edge is curved. The lingual surface is slightly convex and without any ornamentation.

5. Discussion

5.1. Identifications

Most of the identifications, especially those of fish and crocodilian teeth are explained above, and follow standard
procedure, however the pterosaur and dinosaur fossils require more justification and discussion.

As for the teeth assigned to pterosaurs, such long needle-like teeth could be ascribed to a marine reptile such as an ichthyosaur or a plesiosaur, or even to a pterosaur or a crocodilian. In all these groups there are many taxa which jaws were lined with close-packed rows of slender teeth, where maxillary and mandibular tooth sets are interlocked as the jaws closed, a classic adaptation for catching fish (Massare, 1987). We exclude ichthyosaurs and plesiosaurs because no known specimens have such long and slender, needle-like teeth. Further, ichthyosaurs and plesiosaurs are generally rare in the Early Cretaceous, especially so in continental sediments. This leaves crocodilians and pterosaurs as possible candidates. The posterior carina and the full-length enamel covering could indicate that this tooth comes from a crocodilian rather than a pterosaur. In pterosaurs, the enamel ends well above the base of the crown: in a ctenochasmatid pterosaur from the English Middle Jurassic, the enamel extends over 80% of the length of the crown of the tooth, and 63% of the length of the whole tooth, including the crown (Buffetaut and Jeffery, 2012). However, the present tooth shows the same modest curvature and slight ridging identified in ctenochasmatid pterosaur teeth (Buffetaut and Jeffery, 2012, Fig. 4), and our specimen is presumably broken at the base of the enamel covering, so the extent of the non-enamedled crown and root cannot be determined with precision. Furthermore, the needle-toothed crocodilians, such as teleosaurids and metriorhynchids, generally displayed broader, shorter teeth. Only certain species of Steneosaurus and Teleosaurus had such truly needle-like teeth, and yet these teeth were curved in two directions (Distally and labially) and these taxa are restricted stratigraphically to the Middle Jurassic (Buffetaut and Jeffery, 2012).

Among pterosaurs, those that contemplated this kind of teeth tended to have elongated and slightly curved teeth, but the length to maximum breadth ratio of the crown in Triassic and Jurassic forms is generally 0.12–0.50 (Wellnhofer, 1978). Pterosaurs underwent dramatic diversification in morphology in the Cretaceous (Prentice et al., 2011), and that includes their teeth – some clades, notably pteranodontids, lost their teeth entirely, whereas others (pterodactylids, germanodactylids, dsungaripterids, ornithodromes) reduced the dentition to small numbers of short teeth. Only pterodaustriods and ctenochasmatids adopted long, slender teeth, and those of the former clade are hair-like or baleen-like (Wellnhofer, 1978; Martill, 2011). This suggests that the new teeth can be identified as ctenochasmatid, and in particular as gnathosaurine ctenochasmatid, an identification followed in analogous cases for long, slender, needle-like teeth in Early Cretaceous continental sedimentary deposits (e.g. Sánchez-Hernández et al., 2007, Fig. 5; Sweetman and Martill, 2010, Fig. 5). Ctenochasmatoid pterosaurs are well known mainly from the Early Cretaceous period in Asia, with numerous taxa from the Yixian Formation (early Aptian) of NE China (Lü et al., 2011), but with additional reports from South America (Martill, 2011) and Europe. Previous European reports include specimens from the Late Jurassic Solnhofen Limestone Formation (Tithonian) of southern Germany and equivalent-aged rocks of northern France (Bennett, 2007), the Purbeck Limestone Group (Berriasian) of southern England (Howse and Milner, 1995), and the Camarillas Formation (lower Barremian) of Burgos, Spain (Sánchez-Hernández et al., 2007) and the Leza Formation (Lower Cretaceous) of La Rioja, Spain (Pereda Suberbiola et al., 2012b).

The sauropod vertebra (CPGJ.1.06.33) shows the characteristics described in other caudal vertebrae of sauropods. As in the vertebrae described by Mantel on Pelorosaurus, it presents a Subcylindrical form and slightly concave facet (Mantel, 1850); and, as in the caudal vertebrae of Lusotitan described by Mannion et al. (2013), it has the posterior face of the centrum predominantly flat (Fig. 6.1) and it has a horizontal ridge
on the lateral surface of the centrum (Fig 6.2) that divides it into an upper and lower regions (Mannion et al., 2013).

The assignment of a tooth (CPGP.1.06.2) to the genus *Baryonyx* is consistent with biometric studies of other teeth of this genus (Smith et al., 2005). This confirms the presence of *Baryonyx* in the Cabo Espichel, as reported earlier by Buffet-taut (2007) and Mateus et al. (2011), one of them quite close to Praia das Agunechiras (Mateus et al., 2011) in concordance with our findings. The presence of a groove in the mesial carina can be explained by the way theropods gnawed the flesh and bones of prey, after applying the bite, dragging the teeth through the flesh and bones, which produced long grooves (Erickson and Olson, 1996).

During the Early Cretaceous the ornithopod faunas suffered some changes: the camptosaurs were gradually replaced by more derived iguanodontians and the smaller forms maintaining close species of *Hypsilophodon*, among others (Ortega et al., 2006, p. 226). Specimen CPGP.1.99.7 was initially assigned to an indeterminate *Hypsilophodon* (Figueiredo, 2002, 2004, 2005), and after to cf. *Camptosaurus* (Mateus, 2007; Figueiredo, 2008). However, after a more carefully comparative study, it appears that this fossil does not belong to this genus. The teeth are totally different from those of *Hypsilophodon*, and are bigger and wider (cheek teeth) than those of *Camptosaurus*. On the other hand, despite the wide geographic distribution of iguanodonts in the Early Cretaceous (Europe, North America, Asia, Africa and Australia) (Norman and Weishampel, 2004; Paul, 2007, 2012; Norman, 2011a, 2013; Carpenter and Ishida, 2010), the presence of *Camptosaurus* in the Barremian of Europe seems unlikely (Carpenter and Ishida, 2010; Paul, 2008). The teeth and maxilla bone have several similarities with the iguanodonts. The maxilla’s labial surface is curved, like that of the iguanodonts and not flat, like *Camptosaurus*. As previously mentioned, it holds only one replacement tooth per tooth position, the labial surface of the crown is thickly enameled and has a strongly denticulated margin with a very large primary ridge arising from the base of the crown, on the lingual surface, the teeth do not display any ornamentation.

Pterosaurs frequented coastal and estuarine areas, *Baryonyx* fed primarily on fishes and small animals in habitats near the coast, the crocodile *Goniopholis* also lived in coastal environments, and the fish *Lepidotes* are characteristic of lagoon habitats. These observations are in concordance with the sedimentological analysis.

5.2. Comparison of fauna

The fauna of the Papo-Seco Formation of SW Portugal, consisting of fishes (*Lepidotes*), crocodilians (cf. *Anteophthamosuchus*), pterosaurs (stenochasmatoid and a possible ornithocherid) and dinosaurs (*Baryonyx*, sauropods, iguanodonts) is very comparable with those of similar age (early Barremian) from England (e.g. Vectis Formation, Upper Weald Clay) and from Spain, in Galve, Uña, Burgos, Golmayo and Las Hoyas, (e.g. Estes and Sanchez, 1982; Sanz et al., 1984; Sanz et al., 1987; Buscalioni and Sanz, 1987; Ruiz-Omeñaca et al., 2004; Fuentes Vidarte et al., 2005; Ortega et al., 2006 Sánchez-Hernández et al., 2007, Sweetman and Martill, 2010; Serrano et al., 2013; Buscalioni et al., 2013; Puértolas-Pascual et al., 2015). *Lepidotes* and Goniopholidids are ubiquitous throughout the world in the Early Cretaceous. Goniopholidids are one of the most common taxa of the crocodylomorph European Mesozoic fossil record (Buscalioni et al., 2013) and teeth and osteoderms are dominant remains in fossil assemblages (Schwarz, 2002; Salisbury and Naish, 2011). G. baryglyphaeus occurred in the Iberian Peninsula, in the Upper Jurassic (Kimmeridgian) of Portugal in the Alcobaça Formation (Brinkmann, 1989; Cre-spo, 2002; Schwarz, 2002; Malafaia et al., 2006). In different formations of Spain of chronologies between the Berriasian and the Aptian several taxa of goniopholidids were identified (Buscalioni and Sanz, 1987; Buscalioni et al., 2013). The European goniopholidids are composed of three genera (*Goniopholis*, Hulkepholi and *Anteophthamosuchus*) and there is also another goniopholidid, the “Dollo specimen”. The genus *Goniopholis* has a biochronological distribution between the Kimmeridgian and the Berriasian. The others goniopholidids are known from the Valengianian to the Aptian (Andrade et al., 2011). The Papo-Seco Formation dates from the Barremian, therefore within the period of occurrence of the genera Hulkepholi and *Anteophthamosuchus*. The materials from Areais do Mastro are the first occurrences of goniopholid from the Lower Cretaceous fossil record in Portugal. Among pterosaurs, ornithocheirids have long been known from the Early Cretaceous of Europe, whereas stenochasmatoids were formerly seen as mainly Asiatic in distribution. Now, however, both clades are reported from southern England and from the Galve fauna of Spain (Sánchez-Hernández et al., 2007).

Among the dinosaurs, baryonychid theropods, pelorosaurid sauropods, the occurrence of three teeth of sauropod (*Astrodon valdensis*) at the Papo-Seco Formation (Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Figueiredo, 2005, 2010; Mateus et al., 2011) should be noted, and iguanodontians are typical Early Cretaceous forms, known throughout Europe (Weishampel et al., 2004; Sánchez-Hernández et al., 2007; Norman, 2011a). With larger collections, other dinosaur groups expected from this site might be spinosaurid theropods, hylsiplodontid-like ornithopods, and armour plates of stegosaurs or ankylosaurs. The iguanodonts appear in several formations of Lower Cretaceous of Western Europe, such as Sainte-Barbarbe Clays, Vectis Fm., Camarillas Fm. Pinila de los Moros Fm. Castrillo de la Reina Fm. and Wessex Fm. In these formations there are referred the genera *Iguanodon*, *Mantellisaurus*, *Delapparentia* and *Proplani- coxa* (junior synonym of *Mantellisaurus* by Norman, 2011b) (Sanz et al., 1984, 1987; Buscalioni and Sanz, 1987; Ortega et al., 2006, Torcida Fernández-Baldor, 2006; Paul, 2008, 2012; Carpenter and Ishida, 2010; Llandres Serrano et al., 2013, Gasca et al., 2014). The remains of
iguanodonts presented in this study display a better fit with the first two (Iguanodon and Mantellisaurus).

7. Conclusions

The palaeontological site of Areias do Mastro has yielded an important set of remains, including fossils of vertebrates. These include several fossils of fishes and reptiles (crocodiles, pterosaurs and dinosaurs). The presence of some taxa in the site is recognized here for the first time, including the three teeth of pterosaurs (two teeth of Ctenochasmatoidae, and a tooth of Ornithocheiridae), are the only taxon known in the Early Cretaceous of Portugal, excluding a vertebra referred by Galton (1994).

In addition, dinosaur remains (sauropod, iguanodonts and Baryonyx) which may have derived from several inland environments, likely transported to the present location where the sediments indicate marine and continental environments.

Most of the remains were collected in a single stratum, which gives us an idea of the fossiliferous association, consisting of crocodiles and turtle remains identified in other studies (Figueiredo, 2002, 2004, 2005), dinosaurs, pterosaurs, and fishes. The sediments of the studied layer indicate a continental shelf deposition zone, in calm lagoon waters frequented by marine fauna, and mixed with transported remains of land animals that lived nearby and on the shores of this lagoon. The faunal remains confirm the sedimentological analysis, mainly because pterosaurs (Baryonyx and Goniotholidids) frequented coastal and estuarine areas and fish Lepidotes are characteristic of lagoon habitats.

The reference to Cretaceous dinosaurs ornithischians in Portuguese territory is rare (Figueiredo, 2014). The Iguanodon referenced by Lapparent and Zbyszewiski, 1957 is among the few specimens referenced. The identification of the three remains of Iguanodonts increases the registration and diversity of these dinosaurs from the Portuguese Lower Cretaceous.

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