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Dinosaurs of Portugal

Dinosaures du Portugal

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Abstract

A synthesis on the state of art on dinosaur knowledge in Portugal is presented. The following genera have been recognized: *Ceratosaurus*, *Torvosaurus*, *Lourinhanosaurus*, *Allosaurus*, cf. *Compsognathus*, *Stokesosaurus*, cf. *Richardoestesia*, cf. *Archaeopteryx*, *Euronychodon*, cf. *Paronychodon*, *Dinheirosaurus*, *Lourinhasaurus*, *Lusotitan*, cf. *Pleurocoelus*, *Lusitanosaurus*, *Dacentrurus*, *Dracopelta*, *Phyllodon*, *Hypsilophodon*, *Alocodon*, *Trimucrodon*, *Draconyx*, *Iguanodon*, and *Taveirosaurus*. Most are from Late Jurassic localities at the Lourinhã area and Guimarota. A new genus, *Lusotitan*, is here raised to include the Late Jurassic '*Brachiosaurus*' *atalaiensis*. Lower Cretaceous until Cenomanian material is scarce, except for dinosaur footprints. An interesting Late-Cretaceous, mostly small dinosaur association has been collected between Aveiro and Taveiro. **To cite this article:** M.T. Antunes, O. Mateus, C. R. Palevol 2 (2003) 77–95.

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Résumé

On présente une synthèse concernant l'état actuel des connaissances sur les dinosaures du Portugal. Les genres suivants ont été reconnus : *Ceratosaurus*, *Torvosaurus*, *Lourinhanosaurus*, *Allosaurus*, cf. *Compsognathus*, *Stokesosaurus*, cf. *Richardoestesia*, cf. *Archaeopteryx*, *Euronychodon*, cf. *Paronychodon*, *Dinheirosaurus*, *Lourinhasaurus*, *Lusotitan*, cf. *Pleurocoelus*, *Lusitanosaurus*, *Dacentrurus*, *Dracopelta*, *Phyllodon*, *Hypsilophodon*, *Alocodon*, *Trimucrodon*, *Draconyx*, *Iguanodon* et *Taveirosaurus*. La plupart proviennent de gisements du Jurassique supérieur des environs de Lourinhã ainsi que du gisement de Guimarota. Un genre nouveau, *Lusotitan*, est créé pour le « *Brachiosaurus* » *atalaiensis*, également du Jurassique supérieur. Le

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matériel de dinosaures, du Crétacé inférieur jusqu’au Cénomaniien, est assez pauvre, à l’exception d’empreintes de pas. Une intéressante association de Dinosaures, pour la plupart de petite taille, a été récoltée entre Aveiro et Taveiro. **Pour citer cet article : M.T. Antunes, O. Mateus, C. R. Palevol 2 (2003) 77–95.**

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Sumário

É apresentada uma síntese do conhecimento de dinossauros em Portugal, referindo os géneros *Ceratosaurus*, *Torvosaurus*, *Lourinhanosaurus*, *Allosaurus*, cf. *Compsognathus*, *Stokesosaurus*, cf. *Richardoestesia*, cf. *Archaeopteryx*, *Euronychodon*, cf. *Paronychodon*, *Dinheirosaurus*, *Lourinhasaurus*, *Lusotitan*, cf. *Pleurocoelus*, *Lusitanosaurus*, *Dacentrurus*, *Dracopelta*, *Phyllodon*, *Hypsilophodon*, *Alocodon*, *Trimucrodon*, *Draconyx*, *Iguanodon*, e *Taveirosaurus*. Na maioria, provêm do Jurássico superior da área da Lourinhã e de Guimarota. É criado o novo género *Lusotitan* que engloba o “*Brachiosaurus*” *atalaiensis* do Jurássico superior. É escasso o material do Cretácico inferior ao Cenomaniano, com excepção de pistas. Foi recolhida uma interessante associação de dinossauros, na maioria de pequeno porte, no Cretácico terminal de entre Aveiro e Taveiro.

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Keywords: Portugal; Jurassic; Cretaceous; Dinosauria; Theropoda; Sauropoda; Ornithischia; *Lusotitan*

Mots clés : Portugal ; Jurassique ; Crétacé ; Dinosauria ; Theropoda ; Sauropoda ; Ornithischia ; *Lusotitan*

Palavras chave: Portugal; Jurássico; Cretácico; Dinosauria; Theropoda; Sauropoda; Ornithischia; *Lusotitan*

1. Brief historical perspective

In Portugal, the earliest data related to dinosaurs concern the Cabo Espichel Sanctuary area. In a small chapel (Capela da Memória, built 1410), there is an 18th-century tile panel that illustrates a local, much earlier religious legend. Our Lady, the Virgin Mary (or Her image) climbed from the sea to the top of the cliff on a mule [1]. The sauropod tracks that really exist in the cliff are represented in the tiles and interpreted as mule footprints (Fig. 1). This is the earliest known illustration of dinosaur footprints [4, 5].

The Jesuit priest João de Loureiro (1717–1791) was one of the pioneers of Palaeontology. He was the first Portuguese to write a scientific note on fossils. Loureiro, who was also a medical doctor and an excellent botanist, collected fossil crabs from Vietnam (former Cochinchina), where he spent more than three decades [2, 4].

The earliest dinosaur fossils found in Portugal were two theropod teeth discovered at Porto das Barcas near Lourinhã, west central Portugal, by Carlos Ribeiro on 20 July 1863, as noted by Lapparent and Zbyszewski [21]. Later collecting was carried on by P. Choffat and described by H.E. Sauvage [43, 44]. Theropod footprints discovered near Cabo Mondego were observed

in 1884, collected and described by J.P. Gomes [18]. Collecting was carried on by H.C. Cabaço since 1942 and, following him, by G. Zbyszewski and O. da Veiga Ferreira and others.

A renewal of interest and further collecting are consequences of prospecting, exploitation for palaeontological purposes and study of Guimarota mine near Leiria since 1959 under the leadership of Walter Georg Kühne (1911–1991), with Bernard Krebs (1934–2001) and others. Several interventions elsewhere are due to amateurs and to the Museum of Natural History of the University of Lisbon.

Systematic field, most collecting and related studies have been (and are being) developed at the richest area, that of Lourinhã, by the GEAL-Museum of Lourinhã staff in collaboration with the Centro de Estudos Geológicos of the New University of Lisbon and the ‘Muséum national d’histoire naturelle’, Paris, France [25–28]. Theropod egg-laying sites with embryos skeletal parts are among GEAL’s most prominent discoveries [29–31].

Mainly through the works of Sauvage [43, 44], Zbyszewski [49], Lapparent et al. [19], Lapparent and Zbyszewski [21], Antunes [1], Thulborn [47], and Galton [14–17], the list of Portuguese dinosaurs known at the end of the 1980s is that given in Table 1.



Fig. 1. 18th-century tiles showing the footprints in the Capela da Memória (Cabo Espichel), (photo by O.M.).

Fig. 1. Tableau de carreaux du XVIII^e siècle, montrant les empreintes de pas à la Capela da Memória (bâtie en 1410), près du Cap Espichel.

The taxa with an asterisk are considered *nomina dubia* or poorly justified. *Omosaurus armatus*, *O. lennieri* and *Astrodon pusillus* are now ascribed to *Dacentrurus armatus* [16, 17]; the Portuguese *Camptosaurus* sp. was named *Draconyx loureiroi* by Mateus and Antunes [28]; the *Apatosaurus alenquerensis* was renamed *Lourinhasaurus alenquerensis* [13]; and *Brachiosaurus atalaiensis* is renamed here *Lusotitan atalaiensis* (see below).

The palaeontological work on the Guimarota coalmine has been summarized by Martin and Krebs [24]. The dinosaurs from there are mainly known from isolated teeth [35, 48, 50, 51].

2. The dinosaurs of Portugal

2.1. Lower Jurassic (Lias)

The only Lower Jurassic dinosaur so far identified is the basal thyreophoran *Lusitanosaurus liasicus* [20, 21]. It is represented by an incomplete muzzle [MH-NUL]. Age: tentatively ascribed to the Lias, Sinemurian(?). Exact locality unknown, maybe S. Pedro de Muel.

2.2. Middle Jurassic

Although scattered elements from Middle Jurassic have been found in Portugal, the ornithischian *Aloc-*

Table 1
Portuguese dinosaurs known at the end of the 1980's.
Tableau 1
Dinosaures portugais connus à la fin du XVIII^e siècle.

Theropoda	Sauropoda	Ornithischia
<i>Megalosaurus insignis</i> *	<i>Astrodon valdensis</i> *	<i>Alocodon kuehnei</i>
<i>Megalosaurus pombali</i> *	<i>Astrodon pusillus</i> *	<i>Hypsilophodon</i> sp.
<i>Megalosaurus superbus</i> *	<i>Apatosaurus alenquerensis</i>	<i>Lusitanosaurus liasicus</i>
<i>Megalosaurus pannoniensis</i> *	? <i>Bothriospondylus</i> sp.*	<i>Omosaurus armatus</i>
	<i>Brachiosaurus atalaiensis</i>	<i>Omosaurus lennieri</i>
	<i>Pelorosaurus humerocristatus</i> *	<i>Phyllodon henkeli</i>
	<i>Pleurocoelus valdensis</i>	<i>Iguanodon mantelli</i>
		<i>Pleurocoelus valdensis</i>
		<i>Camptosaurus</i> sp.
		<i>Trimucrodon cuneatus</i>

odon kuehnei from Pedrógão is the only species recognized until now [FUB].

The localities with dinosaur footprints are:

- Pedreira do Galinha (Fátima), large sauropods [39];
- Pedreira da Ribeira do Cavalo (Zambujal: Sesimbra), theropods and sauropods [23];
- Pé da Pedreira, Algar dos Potes (Santarém), theropods [40];
- Vale de Meios (Santarém), theropods [40].

2.3. Upper Jurassic

The Late Jurassic of Portugal is very rich in dinosaurs, mainly in the area of Lourinhã. The dinosaur list from Guimarota given by Martin and Krebs [24] is given in Table 2.

Mateus [25] described a new theropod species, *Lourinhanosaurus antunesi*. Mateus and Antunes [28] dealt with a new camptosaurid species, *Draconyx loureiroi*, and identified remains of the genera *Ceratosaurus* [26] and *Torvosaurus* [27]. Bonaparte and Mateus [10] described a diplodocid, *Dinheirosaurus lourinhanensis* Pérez-Moreno et al. [34] assigned theropod remains to *Allosaurus fragilis*.

Stegosaurs are common in the Late Jurassic. There are at least two species, although all stegosaur specimens (ML, MIGM, IST) have been assigned to *Dacentrurus armatus*.

Table 2
Dinosaurs from Guimarota, according to Martins and Krebs [24].
Tableau 2
Dinosaures de Guimarota, selon Martins and Krebs [24].

ORNITHOPODA	SAUROPODA	THEROPODA
<i>Phyllodon henkeli</i>	Brachiosauridae indet.	Ceratosauria indet.
Iguanodontia indet.		?Allosauroida indet.
		cf. <i>Compsognathus</i> sp.
		<i>Stokesosaurus</i> sp.
		Dromaeosaurinae indet.
		Velociraptorinae indet.
		(?)Troodontidae indet.
		cf. <i>Archaeopteryx</i> sp.
		cf. <i>Richardoestesia</i> sp.
		aff. <i>Paronychodon</i> sp

Ceratosaurus sp. (Theropoda: Ceratosauria: Ceratosauridae) [26]

Elements: femur and tibia (ML352; Fig. 2).

Locality: Rodela do Valmitão, Lourinhã.

Age: Late Jurassic, ?Upper Kimmeridgian/Tithonian, Amoreira - Porto Novo Unit.

Torvosaurus sp. (Theropoda: Tetanurae: Torvosauridae) [27]

Elements: tibia (ML430; Fig. 3).

Locality: Casal do Bicho, Alcobaça.

Age: Late Jurassic, Lower Tithonian, Bombarral Unit.

Theropoda indet. aff. *Megalosaurus*? [3]

Elements: one tooth and perhaps an indeterminate vertebra (Coll. M.T. Antunes).

Locality: Forte do Cavalo beach (Sesimbra).

Age: Late Jurassic, J³_{ES} Tithonian and Kimmeridgian, 'Calcários grés e margas de Espichel' (Mantupella et al., Carta Geológica de Portugal 1:50 000, 38-B, sheet Setúbal, 1999).

Lourinhanosaurus antunesi Mateus, 1998 (Theropoda: Tetanurae) [25, 29–31, 36]

Elements: vertebrae and hind limbs (ML 370: Fig. 4); eggs and embryonic remnants (ML 565: Fig. 5). Localities: Vale Bravo, Porto das Barcas and Paimogo near Lourinhã.

Age: Lower Tithonian, Sobral Unit.

Comments. In 1993, a nest was found at Paimogo with around one hundred theropod eggs. Some con-

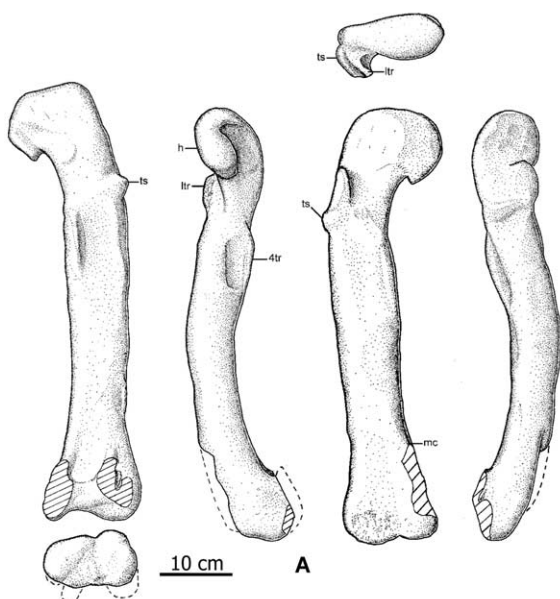


Fig. 2. *Ceratosaurus* sp. ML 352. **A**, right femur; **B**, left tibia; **4tr**, fourth trochanter, **ast**, contact with astragalus; **ca**, contact articulation; **cc**, cnemial crest; **fc**, fibular condyle; **h**, head of femur; **ic**, inner condyle; **ltr**, lesser trochanter; **mc**, medial crest; **pp**, posterior descending process; **ts**, trochanteric shelf (by O.M.).

Fig. 2. *Ceratosaurus* sp. ML 352. **A**, Fémur droit ; **B**, tibia gauche ; **4tr**, quatrième trochanter ; **ast** ; contact avec l'astragale ; **ca**, articulation/ contact ; **cc**, crête cnémiale ; **fc**, condyle du péroné ; **h**, tête du fémur ; **ic**, condyle interne ; **ltr**, trochanter mineur ; **mc**, crête médiale ; **pp**, processus descendant postérieur ; **ts**, aplatissement trochantérique.

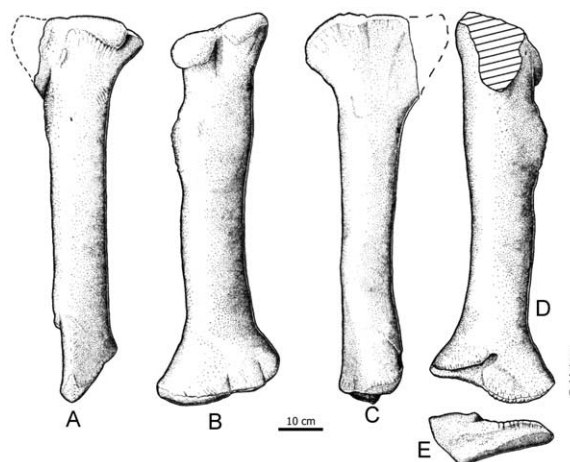


Fig. 3. *Torvosaurus* sp. Left tibia ML 430 (drawing: O.M.).

Fig. 3. *Torvosaurus* sp. Tibia gauche ML 430 (dessin : O.M.).

tain embryonic bones, which were later identified as *Lourinhanosaurus antunesi* [29]. These are the only dinosaur embryos hitherto found in Europe and some of the oldest ever found. Histological study (Fig. 6) has shown endochondral ossifications in short and long bones and calcified cartilage. The bone microstructure suggests high initial growth rates of 20 μm or more per day [36]. A subadult *Lourinhanosaurus* specimen recovered in 1982 was described in 1998 as the holotype of the genus' type species (Fig. 4). The holotype of the species, a partial skeleton (ML 370), was collected at Vale Bravo, and a femur (ML 555) at Porto das Barcas.

Allosaurus sp. (Theropoda: Tetanurae: Allosauridae) [34].

Elements: quadrate, vertebrae, pelvic girdle and hind limbs (MHNUL/AND.001). Locality: Andrés (Pombal).

Age: Late Jurassic, Camadas de Alcobça.

Comments. This specimen was identified as *A. fragilis*, but its identification at the specific level cannot be sustained and it should be regarded simply as *Allosaurus* sp.

Dinheirosaurus lourinhanensis Bonaparte and Mateus, 1999 (Sauropoda: Diplodocidae) [10, 13].

Elements: vertebrae, ribs, fragmentary limb bones, and gastroliths (ML 414 and ?ML 418; Fig. 7).

Age: Late Jurassic, Kimmeridgian to Tithonian, Amoreira-Porto Novo Unit and Bombarral Unit.

Locality: Porto Dinheiro; ?Moita dos Ferreiros.

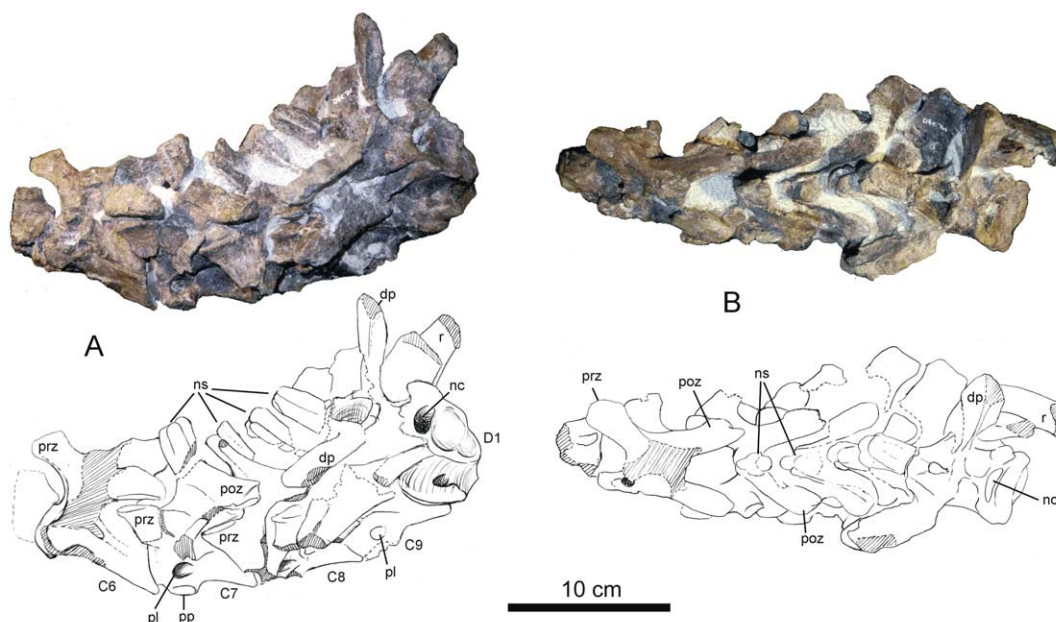


Fig. 4. *Lourinhanosaurus antunesi*, cervical vertebrae ML 370 in (A) lateral and (B) dorsal view. C6 to C9, 6th to 9th cervical vertebrae; D1, first dorsal vertebra; dp, diapophysis; nc, neural canal; ns, neural spine; pl, pleurocoel; poz, postzygapophysis; prz, prezygapophysis (drawing: Simão Mateus and O.M.).

Fig. 4. *Lourinhanosaurus antunesi*, vertèbres cervicales ML 370, vues (A) latérale et (B) dorsale. C6 à C9 : 6^e à 9^e vertèbres cervicales ; D1 : première vertèbre dorsale ; dp : dipophyse ; nc : canal neural ; ns : épine neurale ; pl : pleurocèle ; poz : postzygapophyse ; prz : prézygapophyse.

Comments. The type specimen ML 414 (Fig. 7A) was named by Bonaparte and Mateus [10] after being considered as pertaining to *Camarasaurus* and *Lourinhasaurus*. The specimen from Moita dos Ferreiros (ML 418) is a diplodocid and therefore, provisionally classified as aff. *Dinheirosaurus* according to vertebral characters, but further study needs to be done.

Lourinhasaurus alenquerensis (Lapparent and Zbyszewski, 1957) (Sauropoda) [13, 21, 33].

Elements: postcranials of several individuals (MIGM).

Localities: the major find is a partial skeleton from Moinho do Carmo, near Alenquer. Other localities are São Bernardino, Areia Branca, Porto das Barcas, Salir de Matos, Alcobaça, Praia de Santa Cruz, Chiqueda de Cima, Vale Frades, Foz do Arelho São Mamede, Torres Vedras, and Ourém (MIGM).

Age: Late Jurassic, Kimmeridgian to Tithonian.

Comments. First named by Lapparent and Zbyszewski [21] as *Apatosaurus alenquerensis*, it was

interpreted as *Camarasaurus* by McIntosh [33] and later renamed *Lourinhasaurus alenquerensis* [13]. Because a holotype was never assigned, a lectotype is here determined as *Lourinhasaurus alenquerensis*, the specimen from Moinho do Carmo (MIGM 4956-7, 4970, 4975, 4979-80, 4983-4 and 5780-1). This specimen comprises cervical, dorsal, sacral, and caudal vertebrae, cervical and dorsal ribs, scapulae, coracoids, humerus, ulna, radius, carpals, one metacarpal (?), one manus phalanx, ilium, pubis, ischium, femur, tibia, fibula, astragalus and calcaneum [21]. Despite all the different numbers, all the bones are from only one individual.

Lusotitan n. gen.

Etymology: from *Luso*, an inhabitant of Lusitania, an ancient region that partly corresponds to Portugal; and *titan*, the Greek word for a mythological giant.

Type species are given hereafter.

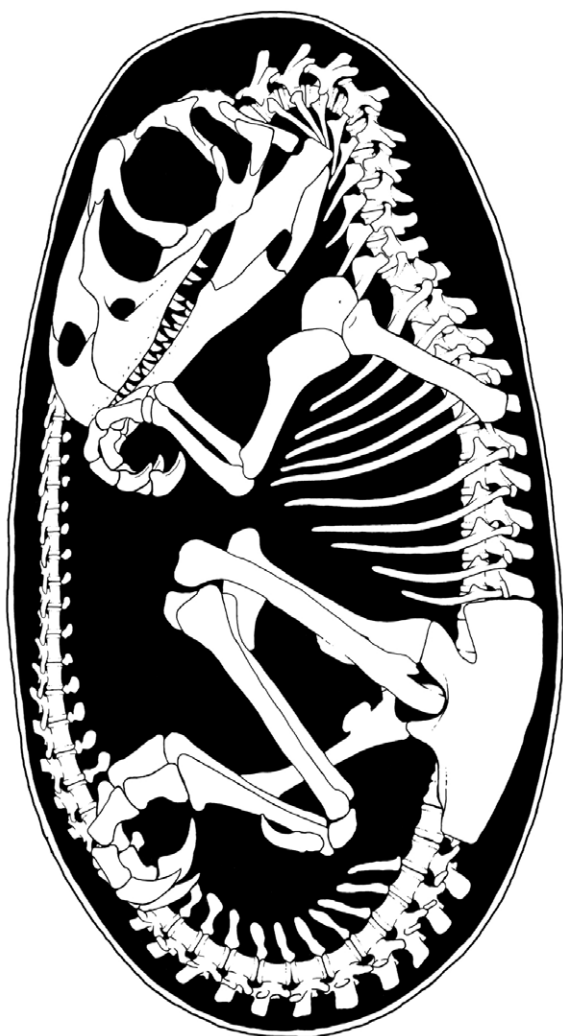


Fig. 5. Embryonic skeleton of *Lourinhanosaurus antunesi* ML 565 (drawing: S. Mateus).

Fig. 5. Squelette embryonnaire de *Lourinhanosaurus antunesi* ML 565.

Lusotitan atalaiensis (Lapparent and Zbyszewski, 1957) (Sauropoda: Brachiosauridae) [21].

Synonyms: *Brachiosaurus atalaiensis* Lapparent and Zbyszewski, 1957.

Horizon: Late Jurassic, Tithonian, Sobral Unit.

Type locality: Peralta, near Atalaia (Municipality of Lourinhã), west-central Portugal. Lectotype: *Brachiosaurus atalaiensis* was based on several specimens, but the authors never assigned the holotype specimen [21]. Hence a partial skeleton from Ata-

laia and isolated vertebrae from Areia Branca, Porto Novo (Maceira), Alcobaça, Cambelas and Praia das Almoinhas could be regarded as a syntype. Later on, we designed here as lectotype the most complete specimen (MIGM 4798, 4801-10, 4938, 4944, 4950, 4952, 4958, 4964-6, 4981-2, 4985, 8807, 8793-5; Fig. 8), which is composed of 28 vertebrae (two anterior cervicals, one mid-dorsal, two neural arches, two caudal anterior centra, one anterior caudal and an uninterrupted series of 18 caudal vertebrae), 12 chevrons, fragmented ribs, a scapula(?) distal epiphysis, two humeri, proximal left ulna, radius, partial ilium, left ischium, left pubis, left tibia, proximal end of right fibula and right astragalus [21]. The bone previously identified as a metacarpal II seems to be a sacral rib.

Diagnosis: a Brachiosaurid, according to the humerus and femur characters; mid-dorsals with very large pleurocoels; anterior caudals have well-developed transverse processes; midcaudal neural spine inclined almost vertically; posterior caudal centra has convex anterior face; mid- and posterior caudal centra are wider than high; slender pelvis; notch at the posterodorsal margin of ilium; postacetabular process of ilium bulky and without notch between this process and the ischial peduncle; obturator foramen of pubis closed; distal end of pubis anteroposteriorly expanded; tibia bowed laterally; proximal end of fibula is not rounded, but has an angular outline.

Lusotitan is regarded as a Brachiosauridae due to the low neural spines, prominent deltopectoral crest of the humerus, elongated humerus, and the longitudinal axis of the ilium is upward.

Draconyx loureiroi Mateus and Antunes, 2001 [14, 27] (Ornithopoda: Camptosauridae).

Elements: Holotype (ML 357; Fig. 9): an individual, represented by two maxillary teeth, three mid-anterior caudal centra, one chevron, the distal epiphysis of right humerus, one hand phalanx, three manus ungual phalanges, the distal epiphysis of right femur, epiphyses of right tibia and fibula, right astragalus, calcaneum, three tarsals (II-V), four metatarsals (I-IV) and foot phalanges. Two referred femora (ML 434 and MIGM).

Age: Late Jurassic, Tithonian, Bombarral Unit.

Localities: Vale Frades (Lourinhã), Praia do Caniçal and Torres Vedras.

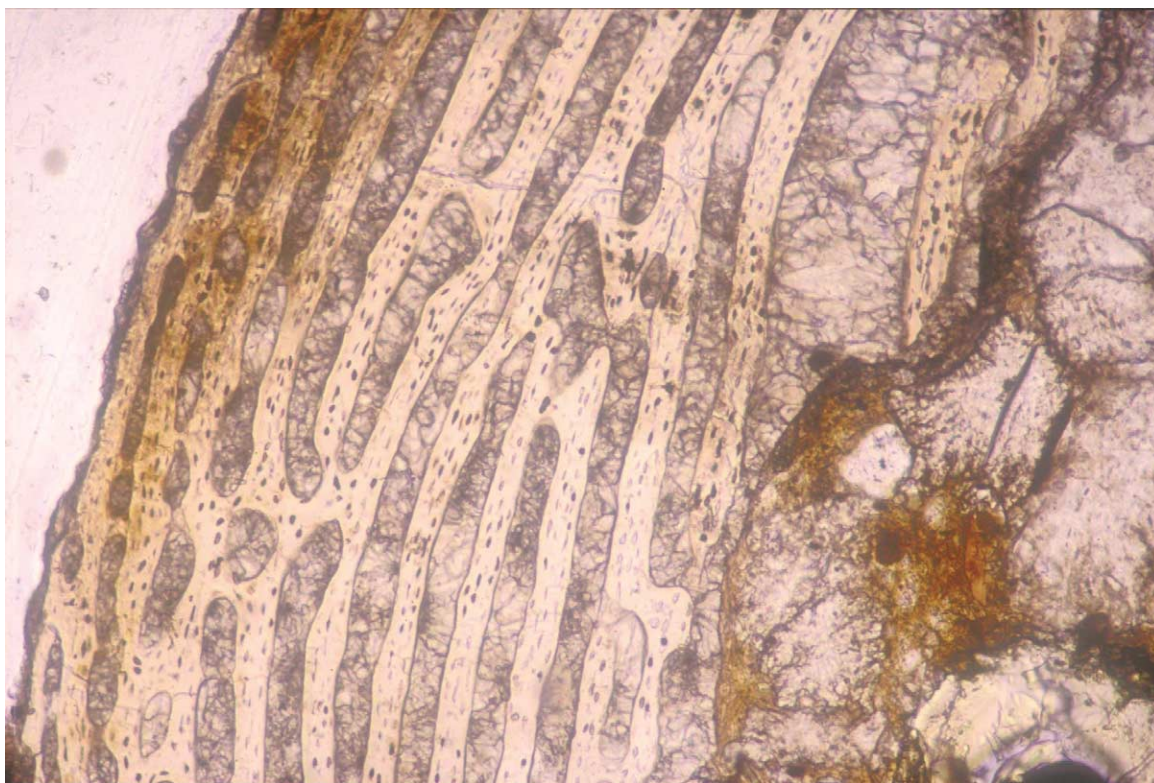


Fig. 6. Histological section of *Lourinhanosaurus* embryonic femur (photo: Armand de Ricqlès).

Fig. 6. Section histologique d'un fémur embryonnaire de *Lourinhanosaurus* (photo: Armand de Ricqlès).

Dacentrurus armatus [21].

Along the years many individuals were collected and assigned to this species.

Elements: Vertebrae, limbs, plates and caudal spines.

Locality: The specimens identified as *D. armatus* are from Alfeizerão (MIGM4877, 4971), Atalaia (Lourinhã, MIGM4953), Casal da Pedreira (Lourinhã, MIGM 4830, 4834, 4836, 4837, 4839-41, 4844-5), Lagido da Vermelha (ML436), Miragaia (Lourinhã, ML433), Moçafaneira (ECTV and ALT), Peralta (Lourinhã, ML464), Murteiras (Foz do Arelho MIGM 4860-1, 4864), Porto das Barcas (Lourinhã, ML489), Praia da Areia Branca (MIGM4862), Porto Novo (Maceira, MIGM), Praia da Malhada (Lourinhã, ML439, ML812), Pedras Muitas (Baleal, MIGM 4846-52, 4859, 4935, 8797), Porto Dinheiro (MHNUL, ML), S. Bernardino (IST), Sesimbra Beach (probably the same unit

as the above reported *Megalosaurus*?; MHNUL, collected by A.M.R. Serralheiro), Vale Pombas (Lourinhã, ML417), Valmitão (ML446).

Age: Late Jurassic; Tithonian and Kimmeridgian; Units Amoreira-Porto Novo, 'Calcários grés e margas de Espichel', Miragaia, Bombarral.

Junior synonyms: *Omosaurus armatus*, *Omosaurus lennieri*, *Astrodon pusillus* and *Dacentrurus lennieri*. *Dracopelta zbyziewskii* Galton, 1980 (Thyreophora: Nodosauridae) [14].

Elements: rib cage with thirteen dorsal vertebrae and five dermal scutes (MIGM).

Locality: Ribamar, Lourinhã municipality(?).

Comments. Galton described *Dracopelta* as a Kimmeridgian nodosaurid from Ribamar. However, at a locality named Ribamar, in the Mafra municipality, there are outcrops of Lower Cretaceous, Valanginian to Albian layers and no Jurassic beds at all. If the fossil has really been collected at this locality, it

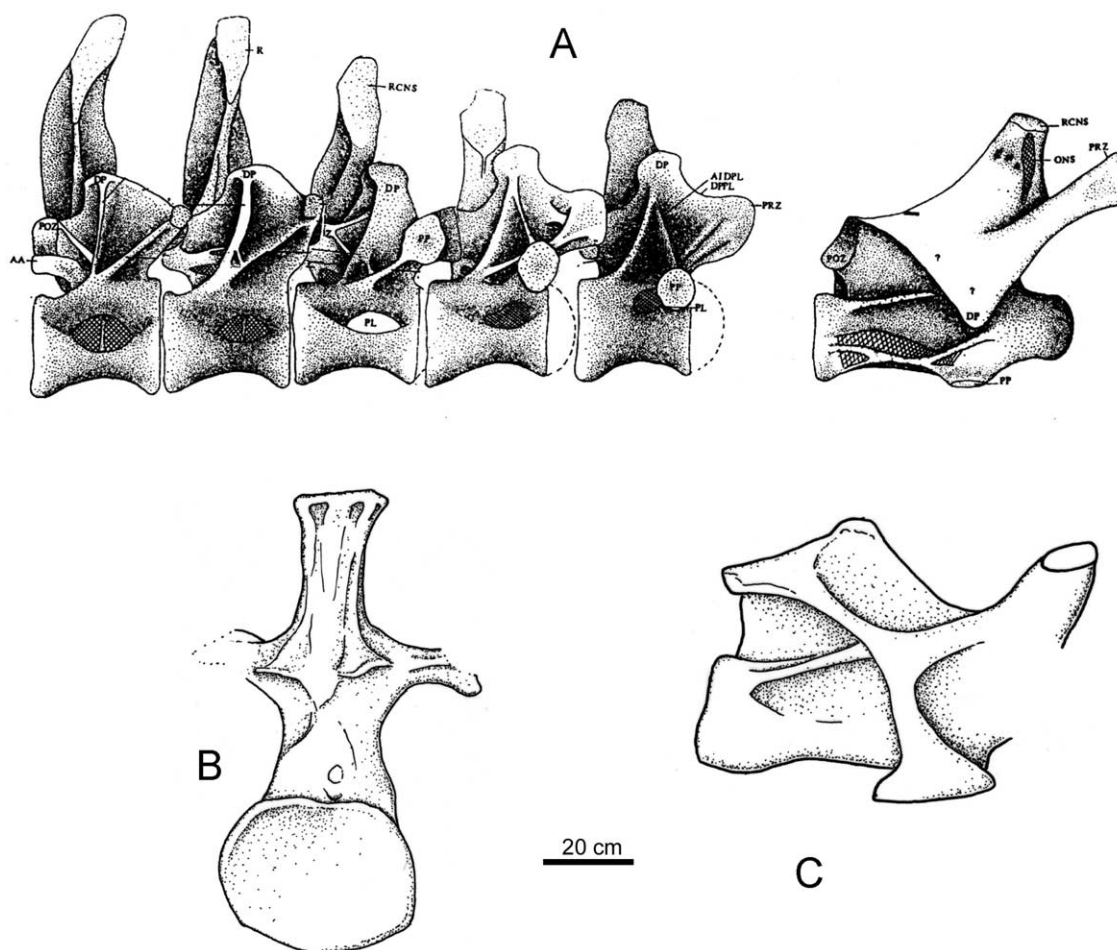


Fig. 7. *Dinheirosaurus lourinhanensis*. **A**, Holotype cervical vertebrae ML 414; **B**, cervical vertebra of specimen ML 418 aff. *Dinheirosaurus*; **C**, dorsal vertebrae of specimen ML 418.

Fig. 7. *Dinheirosaurus lourinhanensis*. **A**, Holotype, vertèbres cervicales ML 414 ; **B**, vertèbre cervicale du spécimen ML 418 ; **C**, vertèbres dorsales du spécimen ML 418.

probably would have been obtained from the Urgonian layers (Barremian to Aptian). However, another possibility for its provenience is the Kimmeridgian layers from the locality of the same name, Ribamar, near Lourinhã; the last locality is about 22.5-km far from Ribamar near Mafra. In our present status of knowledge we will consider it as Kimmeridgian in age.

In addition to these bony remains, many Late-Jurassic footprint sites have been identified in Portugal:

- Amoreira: theropod [37];
- Cabo Mondego: a large theropod [18, 19, 21];
- Cucos (Torres Vedras): stegosaurid [37];

- Escadinha (Porto das Barcas, Lourinhã): two unpublished theropod footprints (ML 454) (Fig. 10);
- Lagido do Forno (Porto das Barcas, Lourinhã): six unpublished ornithopod footprints (ML 557);
- Pedra da Mua: theropods and extensive large sauropod tracks [1, 22, 32, 38];
- Paimogo (Lourinhã): small theropod isolated footprints (P. Dantas, unpublished report);
- Pedras Negras (south of São Martinho do Porto): theropod and sauropod [37, 41];
- Porto Escada: two ornithopod footprints (ML 453) [28]; Fig. 11;

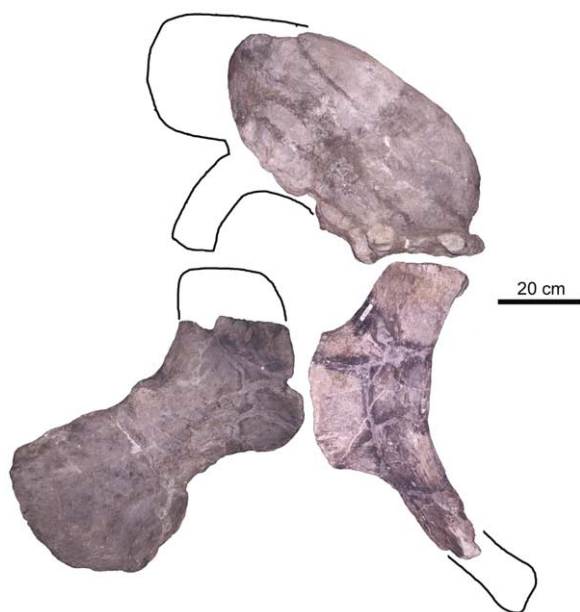


Fig. 8. *Lusotitan atalaiensis* n. gen., pelvis of the lectotype specimen.

Fig. 8. *Lusotitan atalaiensis* n. gen., pelvis du lectotype.

- Praia da Areia Branca (Lourinhã): lost by sea erosion ornithopod (?hypsilophodontid or dryosaurid) footprints, Fig. 13;
- Praia da Corva: small theropod footprints (ML 456; Fig. 12);
- Praia do Cavalo (south of Lagosteiros): a large theropod [12];
- Praia da Foia do Carro (Vila do Bispo): sauropods [42];
- Praia da Peralta (Lourinhã): unpublished small dinosaur (?) footprint;
- Praia do Salgado: sauropods [37];
- Praia de Vale Pombas: unpublished ornithopod (?);
- Praia do Valmitão (Lourinhã): Theropoda, Ornithopoda [11];
- Pedreira do Avelino (Zambujal): sauropod [3,37]; Fig. 13;
- São Martinho do Porto: theropods and ornithopods [11, 37];
- Serra da Pescaria (Nazaré): theropod and sauropod tracks; Fig. 14;
- Serra de Bouro (Foz do Arelho): theropods and sauropods [11];
- Pedreira da Ribeira do Cavalo: theropods [37].

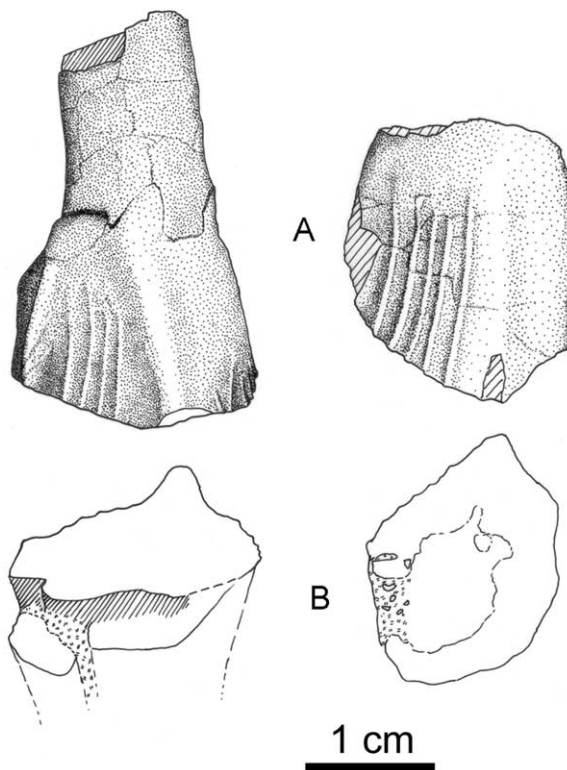


Fig. 9. *Draconyx loureiroi*, teeth in (A) labial, and (B) occlusal views (by S. Mateus).

Fig. 9. *Draconyx loureiroi*, dents en vues (A) labiale et (B) occlusale.

2.4. Lower Cretaceous

Some dinosaur teeth and bones were recovered in the Lower Cretaceous of Portugal. They are enumerated hereafter.

Theropoda indet.; cf. '*Megalosaurus superbus* Sauvage, 1882' [11, 21, 43, 44].

Elements: two isolated tooth fragments (MIGM).

Age: Lower Cretaceous, Lower Barremian, Unit: 'Formação do Papo Seco', C¹_{HB} (in part) (G. Mampupella et al., Carta Geológica de Portugal 1:50 000, 38-B sheet Setúbal, 1999).

Locality: Boca do Chapim near the coast 1 km north of Lagosteiros (Cabo Espichel).

Comments: the available material is not enough for an accurate identification. *Incerta sedis*.

Sauropoda indet.; cf. '*Astrodon* (= *Pleurocoelus*) *valdensis* Lydekker, 1889' [11, 21, 43, 44].

Elements: three isolated teeth (MIGM).

Age and locality (Boca do Chapim) as above.

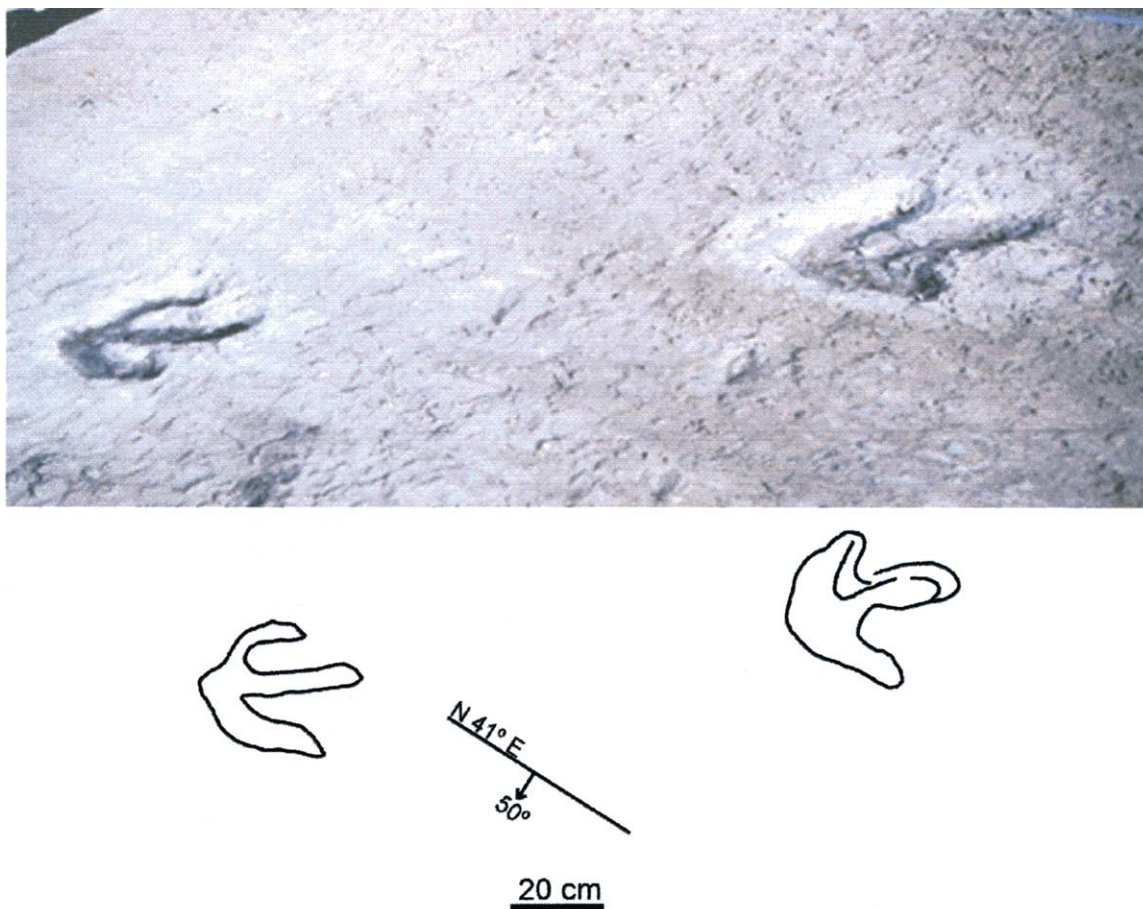


Fig. 10. Theropod footprint (ML454) from Escadinhas, Porto das Barcas (Lourinhã).
Fig. 10. Empreinte de pied à Porto Escada.

Comments: the available material is insufficient for identification. *Incerta saedis*.

Iguanodon sp. [11, 21, 43, 44].

Elements: two isolated teeth (MHNUL), two isolated teeth (MIGM), one tooth (Coll. M.T. Antunes; collected and offered by its discoverer, Jaime Martins Ferreira); three caudal vertebrae plus one fragment of caudal vertebra (MIGM); one deformed vertebral centrum (Coll. M.T. Antunes); one indeterminate bone fragment plus a distal part of femur (MIGM).

Age and locality (Boca do Chapim) as above.

Comments: the available material has been reported to *Iguanodon* cf. *atherfieldensis* Hooley [11].

The footprint localities from the Lower Cretaceous are:

Lagosteiros Bay: theropods, ornithopod and sauropods [1, 22, 32, 38]. Unit: 'Formação de Ladeiras'. Age: Hauterivian (G. Manuppella et al., Carta Geológica de Portugal 1:50 000, 38-B sheet Setúbal, 1999). A trackway produced by a very large dinosaur was reported to a sauropod. This has been contested, the same trackway being assigned to a bipedal dinosaur; we maintain our previous opinion.

Praia Grande do Rodízio (Sintra): sauropods and theropod [38].

Praia da Salema: iguanodontid [42].

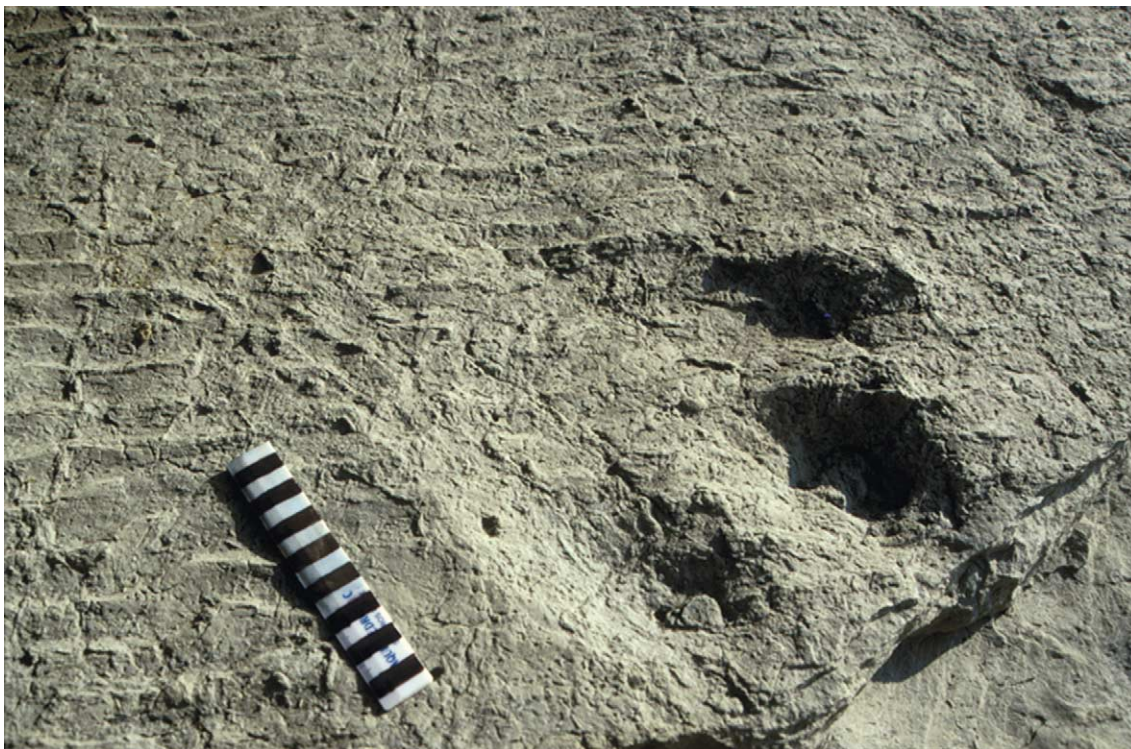


Fig. 11. Ornithischian footprint at Porto Escada.

Fig. 11. Empreintes de pied d'un Théropode à la surface d'un bloc (entre-temps détruit par la mer) à Areia Branca.

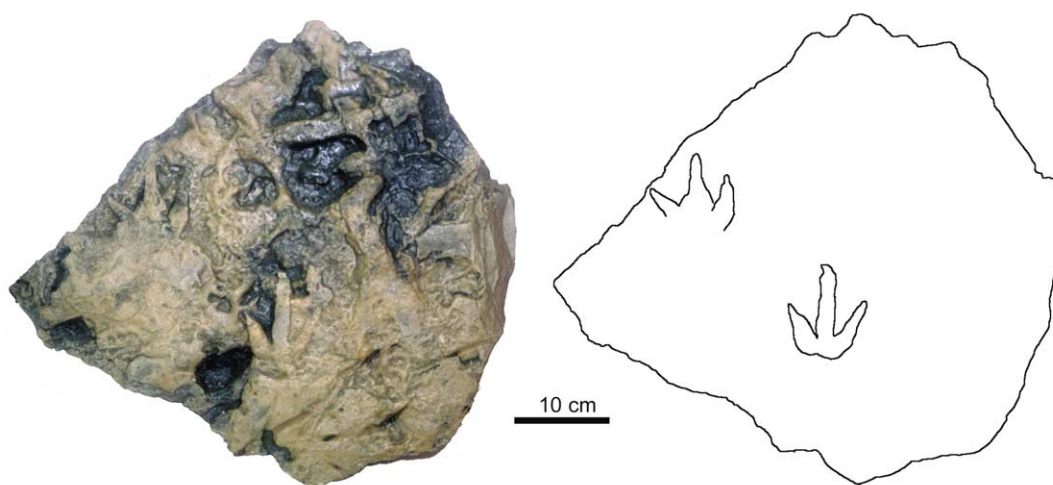


Fig. 12. Theropod footprints at Praia da Corva (ML 456).

Fig. 12. Empreintes d'un théropode récoltées à Praia da Corva (ML 456).

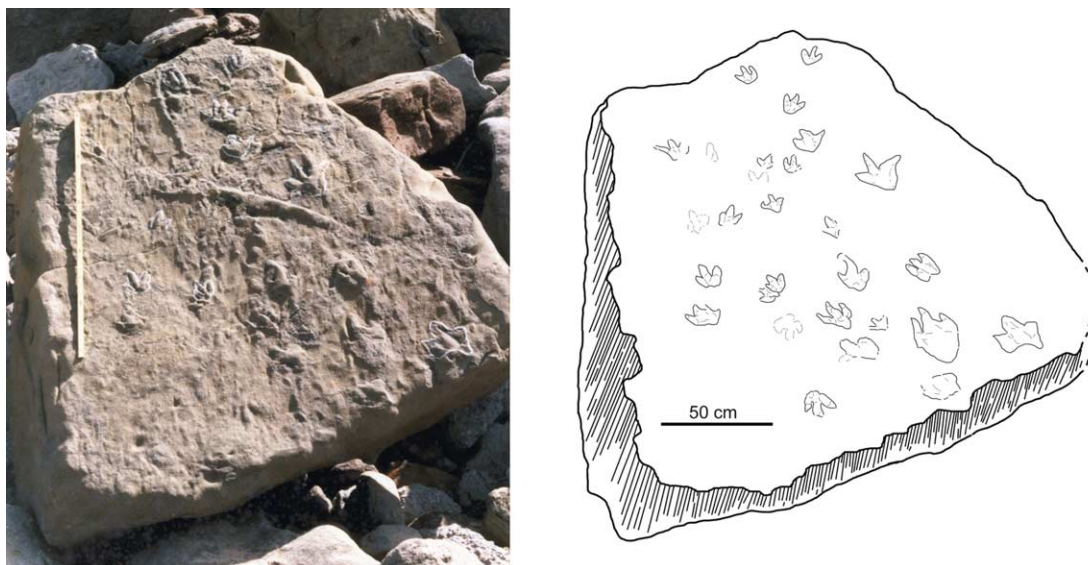


Fig. 13. Theropod footprints in a block now lost to the sea at Areia Branca.

Fig. 13. Traces de Dinosaures (en particulier des empreintes des mains et pieds de sauropode déplaçant des sédiments qui restent en relief) à Pedreira do Avelino, près de Santana (Sesimbra), peu après la découverte du site par M. Telles Antunes, en 1976 (photo et dessin : M.T. Antunes). En plus de la surface principale, alors pas encore fracturée, il y a (côté supérieur gauche) une plaque d'une couche moins épaisse, presque entièrement détruite par la suite, riche en fentes de dessiccation et en empreintes de gouttes de pluie. On y a observé quelques empreintes de dinosauriens, dont quelques-uns de très petite taille (Coll. M.T. Antunes).

Praia Santa (bay east of Praia Santa, Vila do Bispo): iguanodontid [42].

2.5. Upper Cretaceous (lower part)

A footprint locality, Pego Longo near Carenque, is known from the lower part of the Upper Cretaceous (Cenomanian), with theropod (?) and sauropod tracks [37].

2.6. Late Cretaceous

A single site, that of Viso near Arazede, had provided dinosaur remains (MIGM) that were briefly described by Sauvage [43, 44]: three tooth fragments and three ungual phalanxes (claws). Sauvage ascribed these specimens to *Megalosaurus* sp. No new material had been added until the work by Lapparent and Zbyszewski [21], who reported the same fossils to *Megalosaurus* cf. *pannoniensis* Seeley.

New collecting was carried on by Telles Antunes in the outskirts of Aveiro and, still later, at Taveiro near Coimbra in beds of approximately the same Maastrichtian age: the latest Cretaceous unit 'Argilas de Aveiro' and its lateral equivalents. Macrofossils were collected along with a rich assemblage of small vertebrate remnants obtained through washing and sieving. Antunes and Sigogneau-Russell [6–9] described an association of mostly very small dinosaurs based on teeth from Aveiro, Viso and Taveiro (Table 3).

The data suggest a very sharp decrease of the diversity of the large fauna. Most really large-sized dinosaurs were already extinct in the area. On the other hand, a varied association of small-sized, albeit highly differentiated dinosaurs still survived. Reduction of body size may be correlated with the reduction of terrestrial surface associated with insularity; that occurred in what is now the Iberian Peninsula as a consequence of the great Cenomanian transgression. No catastrophic events are needed to account for this ex-



Fig. 14. Dinosaur footprints (especially Sauropod manus and pes imprints displacing bulging sediments) at Pedreira do Avelino, near Santana (Sesimbra) shortly after the discovery of the site by M. Telles Antunes, in 1976 (photo and drawing: M.T. Antunes). Besides the main surface, then still not broken, there is (upper left side) a slab of a thinner bed (nearly destroyed later) rich in mud cracks, rain water droplet imprints and with some dinosaur footprints, including very small ones (Coll. M.T. Antunes).

Fig. 14. Empreintes de pas d'un dinosaure bipède indéterminé à Serra da Pescaria, près de Famalicão da Nazaré.

Table 3

Association of very small dinosaurs described by Antunes and Sigogneau-Russell [6–9] from data by Aveiro, Viso and Taveiro.

Tableau 3

Association de très petits dinosaures décrits par Antunes et Sigogneau-Russell [6–9] à partir des observations de Aveiro, Viso and Taveiro.

THEROPODA	SAUROPODA	ORNITHISCHIA
cf. Troodontidae		
cf.		Nodosauridae
Dromaeosauridae		
Fam. aff.	Titanosauridae	<i>Taveirosaurus costai</i>
Megalosauridae	indet.	
Cf. Coeluridae		Ornithopoda indet.

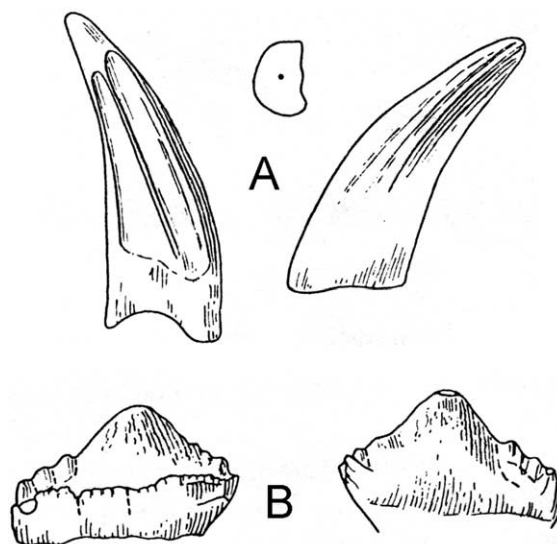


Fig. 15. Type specimens of (A) *Euronychodon portucalensis*, and (B) *Taveirosaurus costai* [6], both from Taveiro, southwest of Coimbra (after M.T.A.).

Fig. 15. Spécimens type de (A) *Euronychodon portucalensis* et (B) *Taveirosaurus costai* [6], en provenance de Taveiro, au sud-ouest de Coimbra (d'après M.T.A.).

tion, which occurred first among large animals and later among small forms.

Euronychodon portucalensis Antunes and Sigogneau-Russell, 1991 (Theropoda).

Elements: three teeth (Coll. M.T. Antunes, provisionally deposited at the CEGUNL-TV 20 (holotype), 18, and 19; Fig. 15A).

Locality: Taveiro.

Age: Maastrichtian.

Comments: this species was classified as ?Dromaeosauridae [6] and later as cf. Coeluridae and ?Troodontidae [9].

Taveirosaurus costai Antunes and Sigogneau-Russell (1991) (Ornithischia)

Elements: teeth (Coll. M.T. Antunes, provisionally deposited at the CEGUNL-TV 10 (holotype), 6–9, 11, 13–16; Fig. 15B).

Locality: Taveiro.

Age: Maastrichtian.

Comments: formerly classified as a Pachycephalosauria [5], it was reclassified as Nodosauridae [8] and Fabrosauridae. Teeth characters seem enough to define the species.

3. Final comments

The following dinosaur taxa formerly assigned to Portugal are now regarded as *nomina dubia*, because they are no longer valid names or were erroneously classified: *Megalosaurus insignis*, *M. pombali*, *M. pannoniensis* and *M. superbus*, *Erectopus superbus*, *Pleurocoelus* (= *Astrodon*) *valdensis*, *Astrodon pusillus*, *Pelorosaurus humerocristatus*, *?Bothrio-*

spondylus sp., *Morosaurus marchei*, *Omosaurus armatus*, *O. lennieri*, cf. *Craterosaurus* sp., *Camptosaurus* sp., *?Ceratopsidae* indet., cf. *Goyocephale* sp., and *Lisboasaurus estesi*.

Summing up, the list of Mesozoic dinosaurs from Portugal (Fig. 16) (for possible phylogenetic relationships, see Fig. 17; J¹ – Early Jurassic; J² – Middle Jurassic; J³ – Late Jurassic; K¹ – Early Cretaceous; K² – Late Cretaceous) is reported in Table 4.

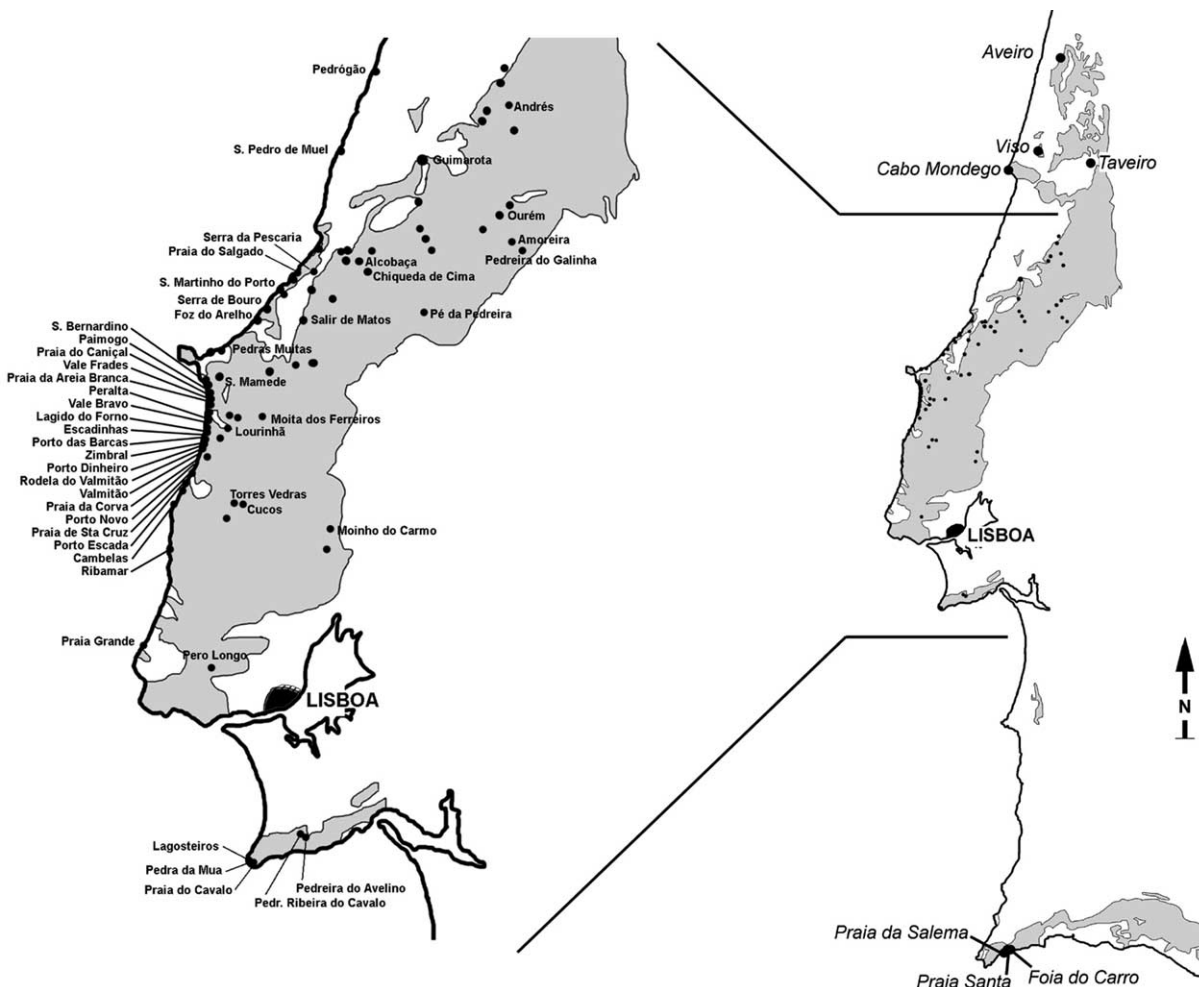


Fig. 16. Map of occurrences (cited in this paper) of dinosaurs (skeletal remains and footprints) in Portugal.
 Fig. 16. Sites à dinosaures (restes squelettiques et empreintes) du Portugal.

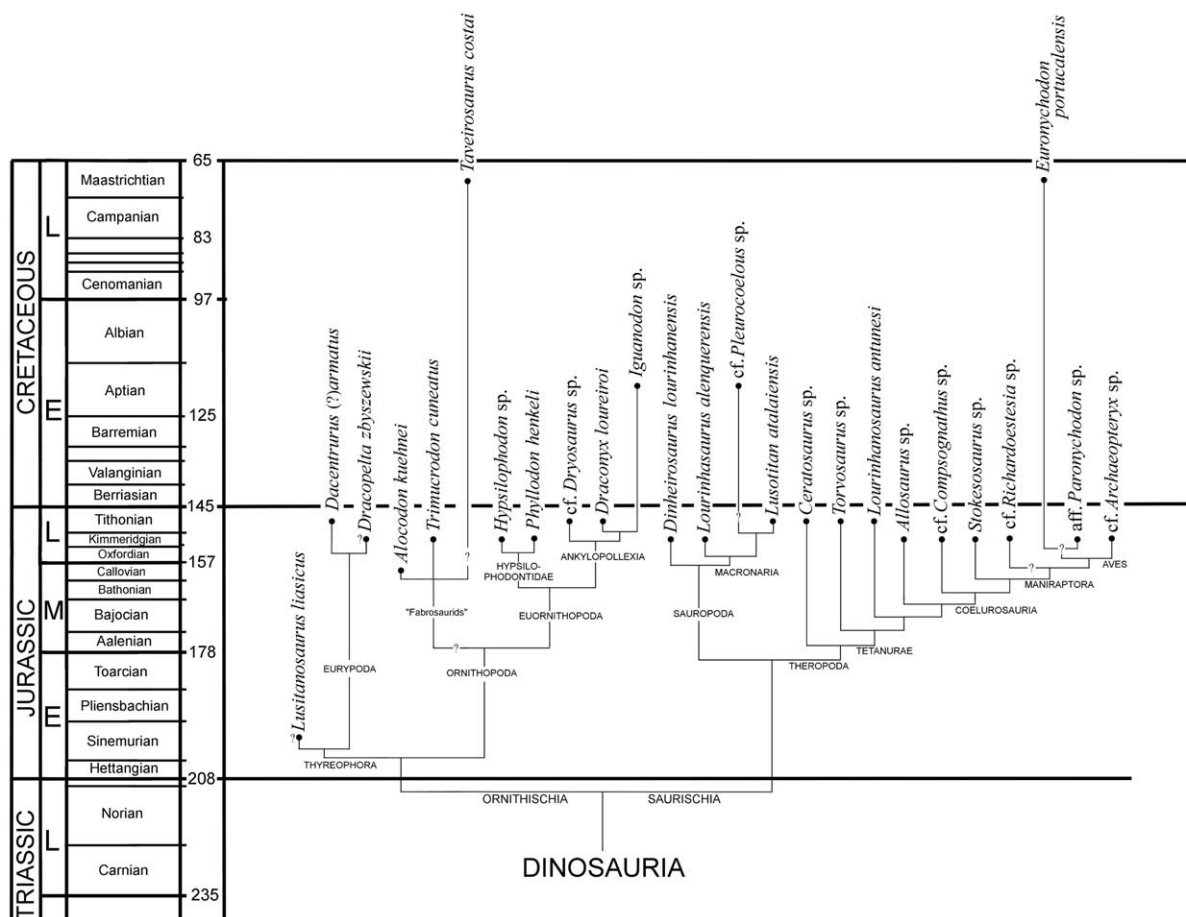


Fig. 17. Possible phylogenetic relationships of the Portuguese dinosaur genera based on our research and on Sereno [45, 46].

Fig. 17. Rapports phylogénétiques possibles des genres de dinosauriens connus au Portugal basés sur nos recherches et d'après Sereno [45, 46].

4. Institutional abbreviations

CEGUNL: Centro de Estudos Geológicos da Universidade Nova de Lisboa; FUB: Freie Universität Berlin, Germany; IST: Instituto Superior Técnico, Universidade Técnica de Lisboa; MHNUL: Museu de História Natural da Universidade de Lisboa; MIGM: Museu Geológico do Instituto Geológico e Mineiro, Portugal; ML-GEAL: Museu da Lourinhã, Portugal.

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Projecto No. 225 BO: Estudo dos ovos e embriões de dinossauro carnívoro do Jurássico da Lourinhã (Portugal)/Cooperação Científica e Tecnológica Luso-Francesa.

Table 4
Dinosaurs from Portugal.
Tableau 4
Dinosaues mésozoïques du Portugal.

THEROPODA	<i>Ceratosaurus</i> sp. (J ³)
	<i>Torvosaurus</i> sp. (J ³)
	<i>Lourinhanosaurus antunesi</i> Mateus, 1998 (J ³)
	<i>Allosaurus</i> sp. (J ³)
	Cf. <i>Compsognathus</i> sp. (J ³)
	<i>Stokesosaurus</i> sp. (J ³)
	Cf. <i>Richardoestesia</i> sp. (J ³)
	Dromaeosaurinae indet. (J ³)
	Velociraptorinae indet. (J ³)
	cf. <i>Archaeopteryx</i> sp. (J ³)
	Theropoda indet. (K ¹)
	<i>Euronychodon portucalensis</i> Antunes & Sigogneau-Russell, 1991 (K ²)
	cf. <i>Paronychodon</i> sp. (J ³)
Troodontidae indet. (J ³ ; K ²)	
SAUROPODA	<i>Dinheirosaurus lourinhanensis</i> Bonaparte & Mateus, 1999 (J ³)
	<i>Lourinhasaurus alenquerensis</i> (Lapparent & Zbyszewski, 1957) (J ³)
	<i>Lusotitan atalaiensis</i> (Lapparent & Zbyszewski, 1957) (J ³)
	Cf. <i>Pleurocoelus</i> sp. (J ³)
	Sauropoda indet. (K ¹)
ORNITHISCHIA	Titanosauridae indet. (K ²)
	<i>Lusitanosaurus liasicus</i> Lapparent & Zbyszewski, 1957 (J ¹)
	<i>Dacentrurus armatus</i> Owen, 1875 (J ³)
	<i>Dracopelta zbyszewskii</i> Galton, 1980 (J ³ or K ¹)
	<i>Phyllodon henkeli</i> Thulborn, 1973 (J ³)
	<i>Hypsilophodon</i> sp. (J ³)
	<i>Alcodon kuehnei</i> Thulborn, 1973 (J ²)
	<i>Trimicrodon cuneatus</i> Thulborn, 1973 (J ³)
	<i>Draconyx loureiroi</i> Mateus & Antunes, 2001 (J ³)
	<i>Iguanodon</i> sp. (K ¹)
<i>Taveirosaurus costai</i> Antunes & Sigogneau-Russell, 1991 (K ²)	

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