

New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal

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Received: 26 August 2006 / Revised: 23 November 2006 / Accepted: 24 November 2006 / Published online: 23 December 2006
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Abstract More than one century after its original description by Marsh in 1877, we report in this paper the first uncontroversial evidence of a member of the genus *Stegosaurus* out of North America. The specimen consists of a partial skeleton from the Upper Jurassic of Portugal, herein considered as *Stegosaurus* cf. *ungulatus*. The presence of this plated dinosaur in the upper Kimmeridgian–lower Tithonian Portuguese record and synchronic levels of

the Morrison Formation of North America reinforces previous hypothesis of a close relationship between these two areas during the Late Jurassic. This relationship is also supported by geotectonic evidences indicating high probability of an episodic corridor between the Newfoundland and Iberian landmasses. Together, Portuguese *Stegosaurus* discovery and geotectonic inferences could provide a scenario with episodic faunal contact among North Atlantic landmasses during the uppermost Kimmeridgian–lowermost Tithonian (ca. 148–153 Ma ago).

Electronic supplementary material Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s00114-006-0209-8> and is accessible for authorized users.

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Keywords Upper Jurassic · Portugal · Stegosauria · Phylogeny · Paleogeography

Abbreviations

LHNB	Laboratório de História Natural da Batalha, Batalha, Portugal
DMNH	Denver Museum of Natural History, Denver, CO, USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, CT, USA

Introduction

The described dinosaur fauna from the Lourinhã Group (sensu Yagüe et al. 2006) of the Upper Jurassic Lusitanian Basin currently consists of almost 20 genera (Lapparent and Zbyszewski 1957; Dantas 1990; Antunes and Mateus 2003). Portuguese Upper Jurassic ornithischians are represented by the ankylosaur *Dracopelta* (Galton 1980a; Pereda Suberbiola et al. 2005), the stegosaur *Dacentrurus* (Galton 1991), the ornithomimid *Draconyx* (Mateus and Antunes 2001), as well as some ornithomimid remains still under study (Dantas et al. 2000). Theropods consist of *Lourinhanosaurus* (Mateus 1998), *Allosaurus* (Pérez-Moreno et al. 1999; Dantas et al. 1999; Rauhut and Fechner 2005), *Ceratosaurus* (Mateus and Antunes 2000a), *Torvosaurus* (Mateus and Antunes 2000b), and *Aviatyrannis* (Rauhut 2003). Described sauropods are the basal neosauropod *Lourinhasaurus alenquerensis* (Dantas et al. 1998), the diplodocoid *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus 1999), and the brachiosaur *Lusotitan atalaiensis* (Antunes and Mateus 2003).

Relationships between the Upper Jurassic Portuguese and North American Morrison Formation dinosaur faunas have been largely discussed. A strange combination of shared taxa and endemism has been used as an argument to justify processes of dispersion or vicariance (Galton 1980c; Pérez-Moreno et al. 1999; Antunes and Mateus 2003). At present, only one dinosaur species, *Allosaurus fragilis*, is shared between these two regions (Pérez-Moreno et al. 1999). Other putative shared forms such as the theropods *Ceratosaurus* and *Torvosaurus* (Antunes and Mateus 2003) are based on such a scarce Portuguese evidence that it does not allow a specific assignment. Other referred genera, such as the ornithomimid *Camptosaurus* (Galton 1980c) or the sauropods *Apatosaurus*, *Camarasaurus*, and *Brachiosaurus* (Lapparent and Zbyszewski 1957; McIntosh 1990), were successively reinterpreted as endemic taxa (Antunes and Mateus 2003).

The plated dinosaur *Stegosaurus* was named by O.C. Marsh in 1877 from material coming from the Upper Jurassic Morrison Formation of North America. Since then, abundant remains from the Kimmeridgian–Tithonian of the US, mostly from Colorado, Wyoming, and Utah, were assigned to *Stegosaurus* (Gilmore 1914; Galton and Upchurch 2004). However, the genus was never confidently recorded out of North America. In Europe, some scarcely informative stegosaurian specimens were also referred to this genus but were rejected later. Among these cases, *Stegosaurus priscus* from the Middle Jurassic of England (Nopcsa 1911) was later referred to as a juvenile individual of *Lexovisaurus* (Hoffstetter 1957). The type specimen of *Omosaurus armatus* Owen 1875, from the Upper Jurassic of England was also referred to as *Stegosaurus armatus* (Lydekker 1890) but was later reinterpreted as *Dacentrurus armatus* (Lucas 1902). At present, stegosaurian record from Europe is exclusively composed of the Stegosaurinae *Lexovisaurus* (Middle Jurassic of England and France), the basal Stegosauridae *Dacentrurus* (Upper Jurassic of England, France, Portugal, and Spain), and the scarcely known *Craterosaurus* (Early Cretaceous of England; Galton and Upchurch 2004).

Despite the fact that several authors had traditionally suggested the close relationship between North American and Portuguese Kimmeridgian–Tithonian dinosaur fauna, it seems that the most recent literature tends to minimize the number of shared forms. However, the discovery of a new partial stegosaurian individual at the Casal Novo locality (Batalha, Central Portugal) belonging to the Upper Jurassic Alcobaça Formation (Lourinhã Group, sensu Yagüe et al. 2006) allows us to reinforce the hypothesis of a close relationship between the faunas of the eastern and western Proto-North Atlantic coasts. The character combination interpreted on the available material justifies the assignment of this specimen to one of the North American species of the genus *Stegosaurus*, *Stegosaurus unguiculatus*. That is the first indisputable discovery of *Stegosaurus* outside North America.

Materials and methods

The new stegosaurian specimen herein described is the only dinosaur found in the Casal Novo locality (Batalha, Portugal; see Fig. 1a). The remains were collected in sediments, mainly fluvial in origin, attributed to the upper Kimmeridgian–lower Tithonian (Fig. 1b). The fossiliferous layer is intercalated between grayish clays with abundant vegetal remains, tubular bioturbation, and carbonate concretions, representing abandoned alluvial plains, with subaerial exposure, vegetal colonization, and pedogenesis. The vertebrate remains occur in a coarse sandy layer (0.8 m

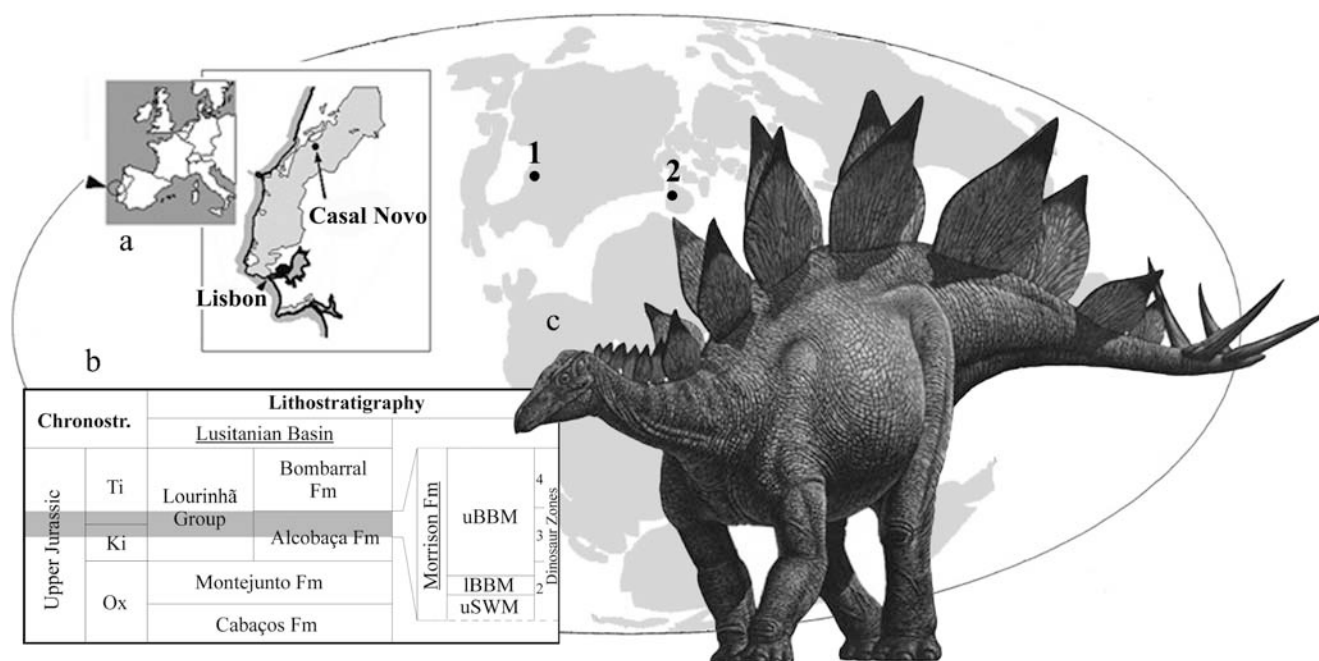


Fig. 1 Late Jurassic (Kimmeridgian, ca. 153 Ma) palaeogeography and principal *Stegosaurus ungulatus* fossiliferous exposures (black circles). Number 1 corresponds to Bolla's Quarry (Colorado), Carnegie Quarry (Utah), Reed's Quarry 11, 12, 13 and AMNH Sheep Creek Quarry D (Wyoming) in the Morrison Formation (Turner and Peterson 1999), and number 2 corresponds to Casal Novo (Alcobaça Formation). **a** Maps showing Portugal and the location of the fossiliferous site. **b** Chronostratigraphic context of the Casal Novo

fossil site. Gray band marks the age range of the fossil site. Contemporaneous levels and stratigraphic ranges of dinosaurs in the Morrison Formation are shown (adapted from Turner and Peterson 1999). **c** Life restoration of *S. ungulatus*. **Chronostr** Chronostratigraphy, *Fm* Formation, *Ki* Kimmeridgian, *IBBM* lower part Brushy Basin Member, *Ox* Oxfordian, *Ti* Tithonian, *uBBM* upper part Brushy Basin Member, *uSWM* upper part Salt Wash Member

thick) with abundant intraclasts, bones, and large trunk debris at the base, representing a high-energy channel with a coarser lag deposit.

The specimen LHN(CN)1 is a partial skeleton composed of one tooth, five cervical vertebrae (including the axis), five dorsal vertebrae, cervical and dorsal ribs, three caudal vertebrae, chevrons, preacetabular process of the left ilium, right tibia, fibula, astragalus and calcaneus, a cervical plate, and several fragments of plates. The specimen LHN(CN)1 is housed at the Laboratório de História Natural da Batalha (Portugal).

Results

The only recovered cranial remain is an isolated tooth (Fig. 2o–p). It is extremely small and displays a large lingual wear facet. The cingulum is prominent and both sides of the crown present numerous secondary ridges. In the postcranial skeleton, the prezygapophyses of the axis (Fig. 2a) are prominent and extend well forward of the anterior centrum face. The neural spine begins posteriorly than in *Stegosaurus stenops* and has a strongly concave cranial outline in lateral view. This axis morphology is distinct from that in *Stegosaurus*, in which the prezygapophyses are

much smaller and do not extend beyond the centrum, but a great variability of the character exists in the available specimens (Gilmore 1914; Ostrom and McIntosh 1966). Unfortunately, no axis has been assigned to *S. ungulatus*, and so it is not possible to make a comparison. There is a second platycoelous (flat–concave) cervical centrum (Fig. 2b), which probably belongs to the third cervical vertebra. The remaining cervical vertebrae (probably, the fourth, fifth, and sixth) are amphicoelous with the posterior articular surface more concave than the anterior one. In these vertebrae, the diapophyses are dorsoventrally flattened. The most complete vertebrae (Fig. 2c–d) are similar to the fourth or fifth cervical of the holotype of *S. ungulatus*, although, in the case of Casal Novo, the neural arches are lightly less bowed backwardly (Ostrom and McIntosh 1966; Carpenter et al. 2001). The postzygapophyses extend well backward of the posterior centrum face and the neural spines are small and slightly developed, similar to *S. ungulatus* (Gilmore 1914; Ostrom and McIntosh 1966). Five dorsal vertebrae and an isolated dorsal neural arch were recovered. The only preserved anterior dorsal vertebra has a large and rounded neural canal (Fig. 2e). There is an almost complete, exceptionally preserved midposterior dorsal vertebra (Fig. 2f–h) that has the anterior articular surface higher than the posterior one. The centrum of this vertebra is

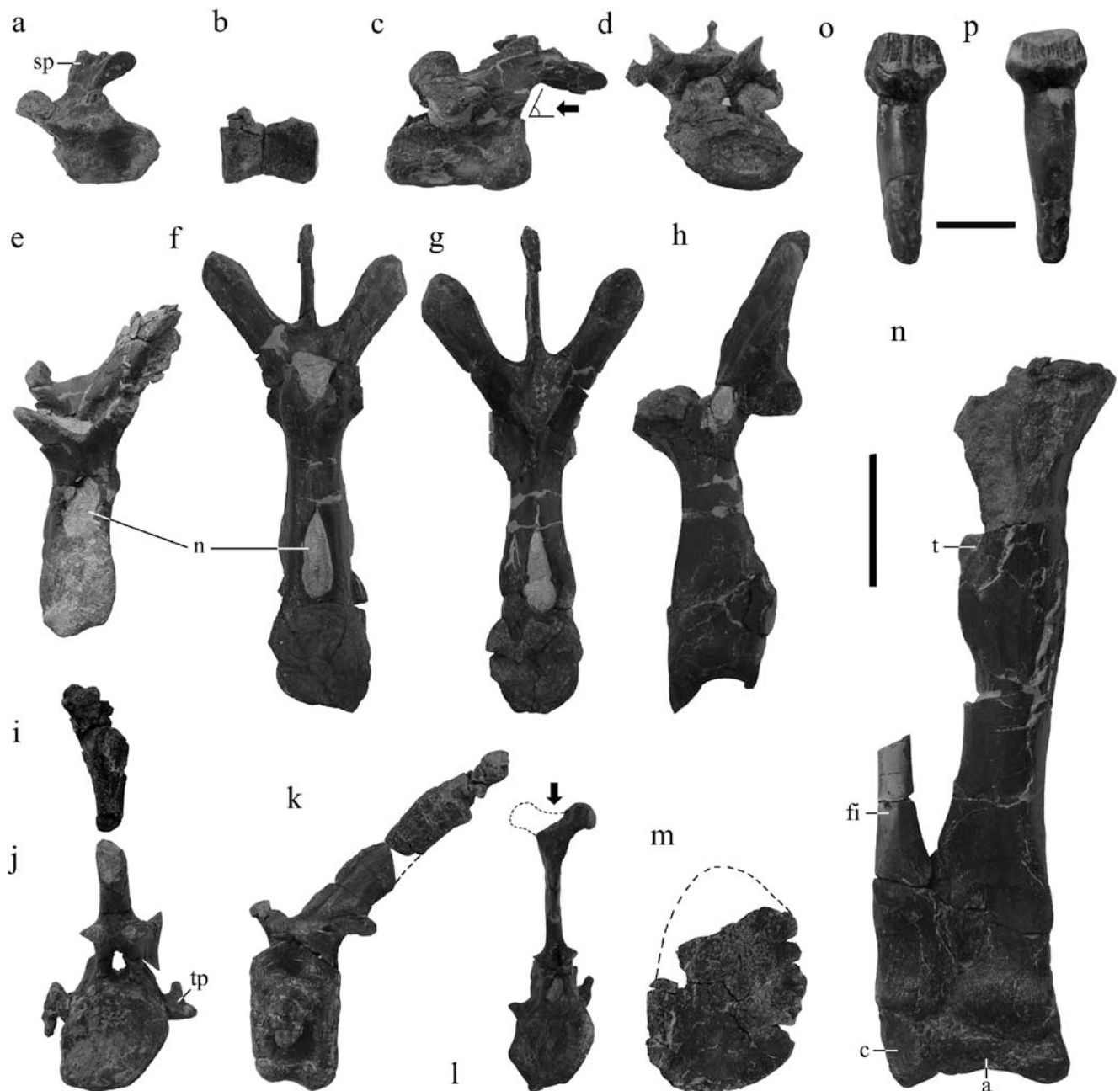


Fig. 2 Select elements of the stegosaurian specimen LHNB(CN) 1. **a** LHNB(CN)-1-17; axis in left lateral view. **b** LHNB(CN)-1-13; centrum of the third cervical vertebra in left lateral view. **c**, **d** LHNB(CN)-1-16; fourth or fifth cervical vertebra **c** in left lateral view and **d** in anterior view. **e** LHNB(CN)-1-06; anterior dorsal vertebra (probably the third) in anterior view. **f–h** LHNB(CN)-1-10; midposterior dorsal vertebra **f** in anterior view, **g** in posterior view, **h** in right lateral view. **i** LHNB(CN)-1-04; distal part of an anterior caudal vertebra neural spine in posterior view (probably belonging to LHNB(CN)-1-03). **j** LHNB(CN)-1-03; anterior caudal vertebra in posterior view. **k** Reconstruction of an

anterior caudal vertebra in left lateral view based on LHNB(CN)-1-03 and LHNB(CN)-1-04. **l** LHNB(CN)-1-02; midcaudal vertebra in anterior view. **m** LHNB(CN)-1-07; cervical plate in lateral view. **n** LHNB(CN)-1-05; right tibia, fibula, astragalus and calcaneum in anterior view. **o**, **p** LHNB(CN)-1-01; isolated tooth **o** in labial view, **p** in buccal (or lingual) view. **a** Astragalus, **c** calcaneum, **fi** fibula, **n** neural canal, **sp** neural spine, **t** tibia, **tp** transverse process. Black arrows indicate posterior slope in **c**, and medial groove in **l**. Scale bars: **a–n** 100 mm; **o–p** 1 mm

amphicoelous, spool-shaped, with its articular faces oval in outline and deeper than broad. Its neural arch is high and the neural canal is taller than broad. Its prezygapophyses and the wedge-shaped postzygapophyses are ventromedially

fused. From the posterior face of the pedicel arises a prominent ridge extending from the base of the postzygapophyses to the neural canal. The triangular diapophyses are dorsolaterally oriented above 60° from the horizontal.

Dorsal vertebrae have a tall pedicel region similar to that of *Stegosaurus* (Gilmore 1914), *Kentrosaurus* (Galton 1982), and *Wuerhosaurus* (Dong 1973, 1993). The only anterior caudal vertebra (Fig. 2j,k) has an amphicoelous centrum that is axially short. The transverse processes have a tall dorsal projection (Fig. 2j), which is common in *Stegosaurus* (Gilmore 1914; Galton and Upchurch 2004) and *Hesperosaurus* (Carpenter et al. 2001; Galton and Upchurch 2004). The neural spine is tall, slightly more than twice the height of the centrum. The top of the neural spine is transversally expanded and it is partially preserved a sagittal groove, similar to those of the condition that exhibits *Stegosaurus* (Fig. 2i; Gilmore 1914; Carpenter and Galton 2001; Galton and Upchurch 2004). Centra of the middle caudal vertebrae (Fig. 2l) have a hexagonal cross-section and, when preserved, the top of the neural spine is expanded and grooved, like in *Stegosaurus*.

The pelvic girdle is just represented by a long and slender preacetabular process of the left ilium similar to that of *Hesperosaurus* (Carpenter et al. 2001), *Wuerhosaurus* (Dong 1973, 1993), *Lexovisaurus* (Galton 1985), and *Stegosaurus* (Gilmore 1914; Ostrom and McIntosh 1966). The recovered portion of the hindlimbs consists of a nearly complete right tibia, lacking its cnemial crest and the region of the fibular condyle. In the dorsal view, the outline of the rugose proximal end is rounded. Only the most distal part of the fibula is preserved and fused to the tibia. The fibula is slender, having a straight shaft that is slightly expanded at the distal end. The astragalus and calcaneum are preserved strongly fused to the tibia and fibula. This complex (Fig. 2n) is similar to that of *S. unguatus* (Ostrom and McIntosh 1966).

The only preserved cervical plate (Fig. 2m) is small and thin, with a rough basal end. This plate is taller than long, and similar to the cervical plates of *Stegosaurus* (Gilmore 1914).

Discussion

The genus *Stegosaurus* is composed of three species: *S. stenops*, *S. armatus* (including *S. unguatus*), and *Stegosaurus longispinus* (Galton and Upchurch 2004). The status of *S. unguatus* is provisional; it is probably a junior synonym of *S. armatus* (for a detailed discussion, see Carpenter and Galton 2001; Galton and Upchurch 2004). Here, the phylogenetic analysis and discussion are based on the available information of *S. stenops* and *S. unguatus*.

Results of the phylogenetic analysis (Fig. 3; see [Electronic Supplementary Information](#)) strongly support the referral of the specimen LHNH(CN)1 to the genus *Stegosaurus*. A derived feature shared by the Portuguese

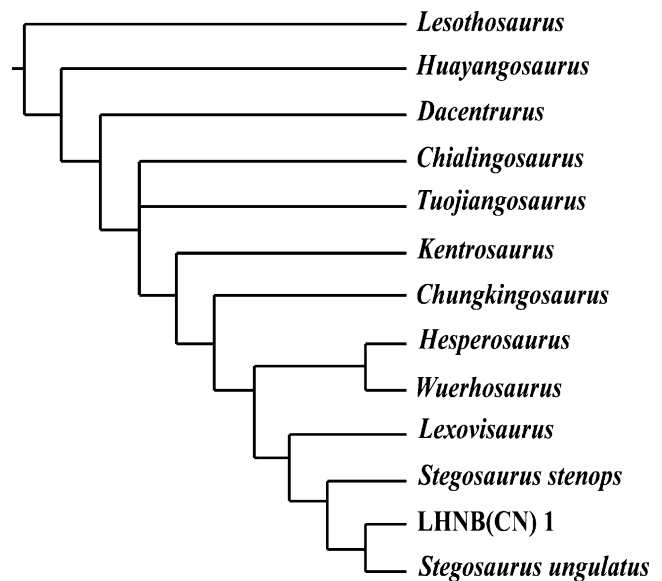


Fig. 3 Phylogenetic relationship of LHNH(CN) 1 among the Stegosauria. Strict consensus of three trees with the following statistics: tree length 76; consistency index 0.829, homoplasy index 0.171, retention index 0.812, rescaled consistency index 0.673

specimen with *Stegosaurus* is that the neural spines of the anterior caudal vertebrae are greatly expanded transversely and have grooved tops (Fig. 2i). This character is largely considered as a synapomorphy of the genus *Stegosaurus* (Galton 1985; Carpenter and Galton 2001; Galton and Upchurch 2004). Moreover, the Portuguese specimen and *Stegosaurus* are united on the basis of several features that include a dorsal prominence on the transverse process of the anterior caudal vertebrae (Fig. 2j), axially short anterior caudal centra (Fig. 2k), teeth with numerous secondary ridges on both sides of the crown (Fig. 2o,p), and thin and large dermal plates. LHNH(CN)1 is more closely related to *S. unguatus* material than to *S. stenops* as evidenced by its extremely high neural canals (Fig. 2i,l; Gilmore 1914). The Portuguese specimen also shares some additional features with *S. unguatus* such as the caudal edge of the neural arches of *S. unguatus* slopes posteriorly on the anterior cervical vertebrae (Carpenter et al. 2001). However, this condition has also been observed in the specimen DMNH 1483, attributed to *S. stenops* (Carpenter, personal communication; Fig. 2c). Besides that, the anterior cervical vertebrae present vertical neural arches and the postzygapophyses extended backward the posterior centra face as in *S. unguatus* and less than in the *S. stenops* specimen YPM 1856 (Ostrom and McIntosh 1966). The similarity of LHNH(CN)1 with *S. unguatus* and the absence of autapomorphies preclude the erection of a new species. Therefore, the Portuguese stegosaur is herein considered as *Stegosaurus* cf. *unguatus*.

Conclusion

The evolution of the Lusitanian Basin and other Mesozoic sedimentary basins bordering the incipient North Atlantic Ocean is related to initial episodes of continental crustal extension and consequent failed rifting. Thus, comparing the characteristics displayed by all the West Iberian and Newfoundland marginal basins, including the Lusitanian Basin, a common tectonic history and a very similar stratigraphic record is recognizable (Hiscott et al. 1990; Wallrabe-Adams et al. 2005).

Since the first phase of rifting, which occurred at Upper Triassic times, until the complete regional continental breakup that took place during the Cretaceous period, at least three rifting episodes were registered (Driscoll 1995; Kullberg 2000). The breakup occurred at different times, running from South to North along sectors tectonically framed by main transform faults. The southernmost is the Azores–Gibraltar Shear Zone separating Iberia from Africa, and the northernmost is the North Pyrenean Fault separating Iberia from Eurasia (Fig. 4). The latter was formed between magnetic polarity chrons M25 (154.3 Ma, upper-

most Oxfordian) and M21 (147.7 Ma, Middle Tithonian; Schettino and Scotese 2002)

The second rifting episode developed in the Lusitanian Basin during the Late Jurassic, with a maximum registered in the early Kimmeridgian (Rasmussen et al. 1998; Alves et al. 2003) that resulted in surrounding emergent areas due to the formation of important marginal reliefs by rift shouldering. The exhumation of these marginal reliefs favored the income of large quantities of clastics that led to an almost complete infill of the basin in the uppermost Kimmeridgian/lowermost Tithonian (Kullberg 2000). Consequently, conditions for restricted circulation in the nearby seas and enlargement of emerged areas were set. To the North, the rifting migration to the offshore Galicia basins favors, since early Kimmeridgian, the deposition of continental clastics interbedded with shales, representing alluvial and delta environments. In the Lusitanian Basin, those deposits correspond to the Alcobaça, Sobral, and Bombarral formations (Lourinhã region) in the central basin sector, and to the north, it corresponds to the Alcobaça and Bombarral formations (Batalha region; Fig. 1b) or only to the Bombarral Formation (Coimbra region).

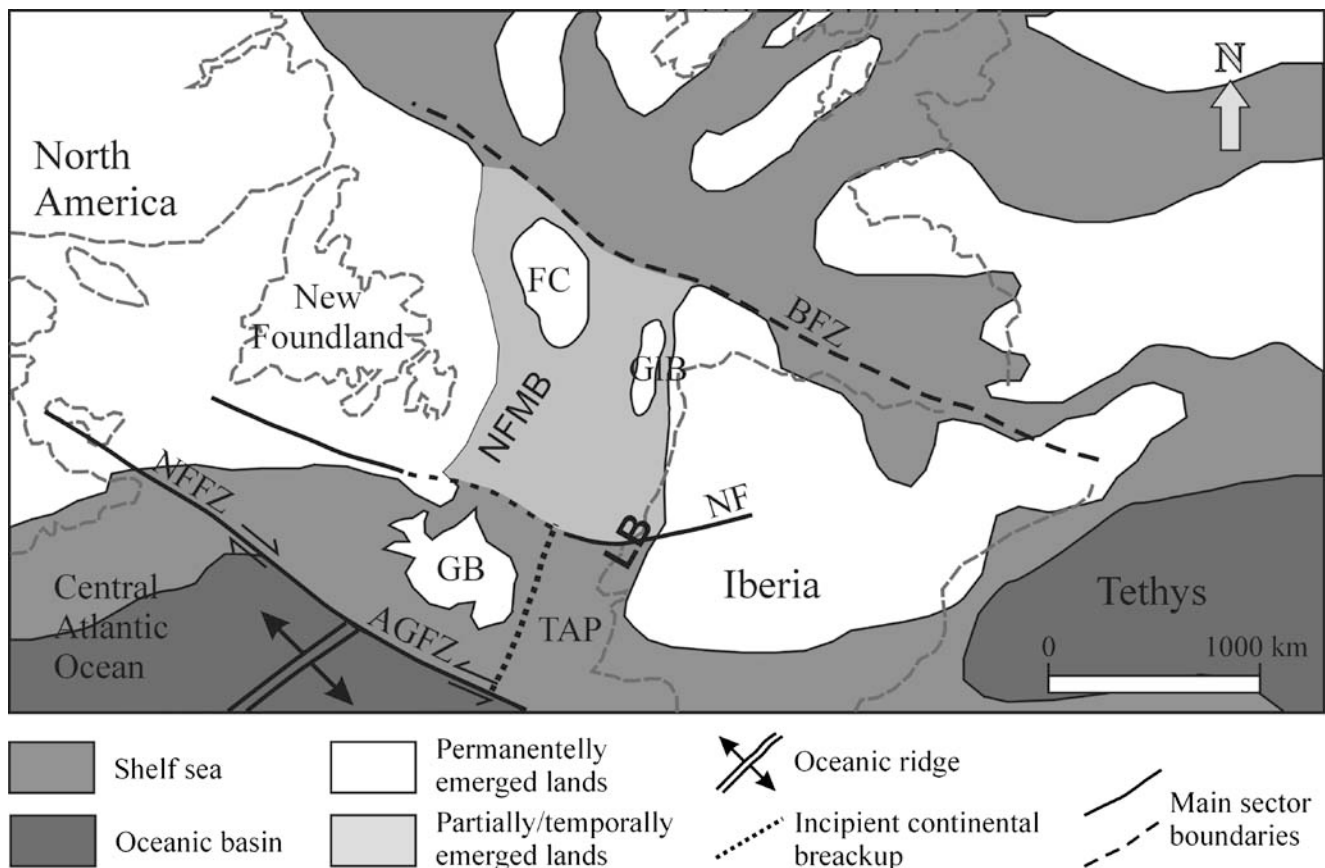


Fig. 4 Palaeogeographic and palaeotectonic map of the North Atlantic during the upper Kimmeridgian. AGFZ Azores–Gibraltar Fault Zone, BFZ Biscay Fault Zone, FC Flemish Cap, GB Grand Banks, GIB Galicia Bank, LB Lusitanian Basin, NFFZ Newfoundland

Fault Zone, NF Nazaré Fault, NFMB Newfoundland Marginal Basins (e.g., Jeanne d'Arc, Carson and Orphan basins), TAP Tagus Abyssal Plain. Adapted from Ziegler (1988), Kullberg (2000), Dercourt et al. (2000), and Schettino and Scotese (2002)

A contact between the dinosaur faunas of North America and Europe during the Late Jurassic has previously been hypothesized based on other dinosaurs groups (Galton 1980b,c; Galton and Powell 1980; Pérez-Moreno et al. 1999; Rauhut 2003). Here we propose a model based on an episodic “Newfoundland–Iberia” corridor as the better scenario to explain the faunal similarity during the uppermost Kimmeridgian–lowermost Tithonian (ca. 148–153 Ma). This corridor is supported by geological evidence, mainly from rock facies, showing a general synchronic regressive tendency during that interval in the Proto-North Atlantic Basins (Hiscott et al. 1990), although the global eustatic transgression was registered worldwide between the upper Kimmeridgian–lower Tithonian. This regressive tendency continues until the Berriasian, when a new rifting episode is registered between Iberia and Newfoundland (R4, Alves et al. 2006; Kullberg et al. 2006). After Montenat et al. (1988), the evolution of the sedimentary sequence from Kimmeridgian to “Portlandian” resulted in almost total emersion of the Lusitanian Basin. In the external basins of the Iberian margin (e.g., the Peniche and Porto Basins), the J3 megasequence (from Alves et al. 2006) that ended at the Berriasian (above Lourinhã Group) is composed of sands, red marls, and carbonates deposited in shallow-marine to fluvial-deltaic environments. The same interbedded sandstones and shales sequences deposited in alluvial plain environments that span from the Late Jurassic until the Early Cretaceous (below the Avalon unconformity) are also described for the Grand Banks region (Grant and McAlpine 1990; Wade and MacLean 1990; Enachescu 1992). This regressive tendency favors the enlargement of the emerged areas and the reduction of marine barriers between both Atlantic marginal continental landmasses (Iberia and Newfoundland; Ziegler 1990; Dercourt et al. 1993, 2000). This is also registered by the isolation of marine faunal forms such as ammonoids (Terrinha et al. 2002). Since the upper Kimmeridgian, even in the southernmost regions of the Lusitanian Basin with open marine facies, the Boreal ammonite faunas disappeared while species typical of the Tethyan realms persisted (Terrinha et al. 2002). This is a clear evidence for the interruption of broad and deep marine communication between southwest Iberia and the northern proto-Atlantic areas (Fig. 4).

Acknowledgements We thank Mr. Rui de Sousa Pinheiro and his son, who found the fossil site, and their family for their hospitality during the fieldwork. We also thank the volunteers that collaborated in the excavation and the preparation of the material, for their help particularly Ms. Graça Ramalheiro; P.M. Galton, K. Carpenter, and two anonymous referees for their useful comments; and R. Martín for drawings. This research was supported by the project POCTI/1999/PAL/36550—“Dinosaur Osteological and Ichnological studies of the Mesozoic of Portugal (Dinos)” —from the Fundação para a Ciência e a Tecnologia (Portugal), Câmara Municipal da Batalha, and the Agreement of Collaboration JCCM-UAM.

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