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The Hybodontiformes (Chondrichthyes: Elasmobranchii) from the Missão Velha Formation (?Lower Cretaceous) of the Araripe Basin, North-East Brazil

Les Hybodontiformes (Chondrichthyes : Elasmobranchii) de la Formation Missão Velha (?Crétacé inférieur) du Bassin d'Araripe, Nord-Est du Brésil

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ABSTRACT

The ?Early Cretaceous (pre-Aptian) Missão Velha Formation of the Araripe Basin of North-East Brazil yields remains referred to two hybodontiform shark taxa: the hybodontid *Planohybodus* and the lonchidiid *Parvodus*. Paleoenvironmental analysis of this formation suggests freshwater or perhaps brackish deposition. The specimens described here were collected from a new locality and are found in association with actinopterygian and sarcopterygian fishes and rarer turtles, crocodylomorphs and theropod dinosaurs. The chondrichthyan assemblage is represented by isolated teeth, cephalic spines, and dorsal fin spines. This is the first record of *Planohybodus* in the Araripe Basin and the first record of *Parvodus* in the Cretaceous of Gondwana.

Mots clés :
Hybodontiformes
Hybodontidae
Lonchidiidae
Formation Missão Velha
Brésil

RÉSUMÉ

La Formation Missão Velha, ?Crétacé inférieur (pré-Aptien) du Bassin d'Araripe, Nord-Est du Brésil contient des restes attribués à deux taxons d'hybodontiformes représentant deux familles distinctes : l'Hybodontidae *Planohybodus* et le Lonchidiidae *Parvodus*. Une analyse paléoenvironnementale de cette formation suggère un dépôt d'eau douce ou saumâtre. Tous les échantillons ont été collectés dans une nouvelle localité et trouvés en association avec des poissons actinoptérygiens et sarcoptérygiens, ainsi qu'avec des tortues, et des restes de crocodylomorphes et de théropodes. L'assemblage de chondrichtyens est représenté par des dents isolées, des épines céphaliques et des épines dorsales. Dans ce travail, nous présentons la première découverte de *Planohybodus* dans le Bassin d'Araripe, ainsi que de *Parvodus* dans le Crétacé du Gondwana.

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1. Introduction

Prospecting in the Araripe Basin in 1988, two of the authors (P.M.B. and D.M.M.) discovered the first fossil vertebrate bearing horizons of the Missão Velha Formation (Brito et al., 1994). Surface gleaning and screen-washing resulted in the recovery of many new vertebrate remains (Brito et al., 1994; Silva and Azevedo, 1996), some of them as yet undescribed.

Here we describe the chondrichthyans from Missão Velha Formation and consider their relevance to the palaeoenvironmental setting and their biogeographical implications. The assemblage is represented entirely by isolated teeth, cephalic spines, and dorsal fin spines of hybodontiforms. The specimens were collected from a single site (Fig. 1), and are found in association with actinopterygians (including *Lepidotes* sp. and pleuropholids) and sarcopterygians (*Mawsonia* sp., the lungfish *Ceratodus* sp.,) as well as turtles and the teeth of crocodylomorphs and theropods (Brito et al., 1994). This associated assemblage resembles others from pre-Aptian localities of the northeastern Brazilian and African Rift system (Casier, 1961, 1969; Gee, 1988; Saint-Seine, 1955; Woodward, 1888).

Hybodontiform sharks have been known from the Mesozoic of Brazil ever since the description of "*Acrodus*" *nitidus* from the Lower Cretaceous of Bahia by Woodward (1888). Brito and Ferreira (1989) described *Tribodus limae* from the Santana Formation known by numerous articulated specimens that differ from the other species of hybodonts by its distinctive crushing dentition (Brito, 1992) and hyostilic jaw suspension (Maisey and Carvalho, 1997). Other hybodontiform shark remains, such as teeth, cephalic spines, dorsal fin spines, and dermal denticles are distributed widely in the interior basins of the northeastern Brazil (e.g., Sanfranciscana, Iguatú, Rio do Peixe, Lima Campos) and have generally been referred to the form genera *Hybodus*, *Polyacrodus*, and *Planohybodus* (Brito et al., 1994; Pinheiro et al., 2011). The hybodontiforms remains here described are referred to two families: Hybodontidae Owen, 1846 and Lonchidiidae Herman, 1977.

2. Geological setting

The Missão Velha Formation is considered part of the Vale do Cariri Group (Ponte and Appi, 1990) and is the only formation in this group known to yield vertebrate fossils. The main outcrop area (Fig. 1) is located in the southern part of Ceará, northeastern Brazil, in the northeastern part of the Araripe Basin, between the towns of Brejo Santo and Missão Velha (Martill, 1993; Viana and Cavalcanti, 1991), but has correlates extending westwards, perhaps as far as Nova Olinda. It is dominated by siliciclastics comprising red and variegated mudstones with channel sandstones of variable thickness, but there have been few studies of its stratigraphy, sedimentology or palaeontology. Furthermore, precise details of its distribution within the basin, its age and relationships with other stratigraphic units remain unclear. Some authors considered it Late Jurassic (Braun, 1966; Pinto and Sanguinetti, 1958; Ponte and Appi, 1990; Silva, 1986), while others have considered Neocomian age (Beurlen, 1962, 1963; Moraes et al., 1976; Viana and Cavalcanti, 1991) or simply as Lower Cretaceous (Berthou, 1990; Pires and Guerra-Sommer, 2011). The precise age of the formation is difficult to establish, due to its lack of diagnostic fossils and lack of horizons suitable for radiometric dating. We can state that the Missão Velha Formation is older than Late Aptian as it underlies the Crato Formation, which can be reliably dated as at least Late Aptian (Batten, 2007).

A previous paleoenvironmental analysis of this formation suggested a freshwater fluviolacustrine setting (Viana and Cavalcanti, 1991). Accretionary point bars close to the fossil-bearing locality indicate a sand-dominated meandering river system at its base, becoming mud-dominated in higher parts of the sequence. In some parts of the Missão Velha Formation silicified gymnosperm logs are abundant, often of considerable diameter (they occur in fluvial sandstones interbedded within the red mudstone facies) and display prominent seasonal and traumatic growth rings (Pires and Guerra-Sommer, 2011). There are no unequivocally marine fossils in the Missão Velha Formation in the parts of the sequence we have studied. However, the absence of remains of stenohaline marine organisms does not indicate freshwater conditions (for a discussion see Laurin and Soler-Gijón, 2010; Schultze, 2009). In fact, the presence of smooth shelled cyprid ostracods in Missão Velha Formation probably indicates variable salinity, fresh to brackish water, in similar fashion to that described for the Crato and Santana formations. The cyprid ostracods of the Santana Formation also are associated to fishes and reptiles and appear to be deposited in a restricted lagoon connected to the sea, according to the most recent palaeoenvironmental models proposed for the locality (Martill et al., 2008; Smith, 2000). Actinopterygians (*Lepidotes* sp. and pleuropholids) and hybodontiform sharks from Missão Velha Formation also occur in marine deposits (Maisey, 2000; Rees and Underwood, 2008), which led us to consider the possibility of a brackish water environment.

3. Material and methods

The material collected is housed in Universidade do Estado do Rio de Janeiro (UERJ-PMB) and was prepared mechanically and/or chemically. The mechanical methods included the use of needles, small hammers, drills and tips for matrix removal and were used in most of the material. A solution of 5% formic acid diluted at buffered with tribasic calcium phosphate was used to dissolve the carbonate cement of the matrix.

3.1. Locality

The fossil locality is located adjacent to the highway BR 122, between the towns of Missão Velha and Brejo Santo (coordinates S 07° 15' 04.8"; W 39° 07' 00.3") (Fig. 1). The locality displays a series of red and green variegated clays with thin, discontinuous beds of fine sandstone and siltstone. About 5 m can be seen, overlain by up to 15 m of coarse, cross-bedded, buff-colored sandstones, sometimes with silicified wood.

Fig. 1. Map of Araripe Plateau. Asterisk indicates the fossil locality.
Fig. 1. Carte du Plateau d'Araripe. L'astérisque indique la localité fossilifère.

4. Systematic palaeontology

Order HYBODONTIFORMES Patterson, 1966
Family HYBODONTIDAE Owen, 1846
Genus *Planohybodus* Rees and Underwood, 2008
Type species: *Planohybodus peterboroughensis* Rees and Underwood, 2008.
Type locality: Callovian, Middle Jurassic of Peterborough, southern England
Planohybodus sp.
(Fig. 2A–D)

Material examined: UERJ-PMB 140 a–q (17 teeth).
Description: Teeth: the teeth are multicusped, with a prominent main cusp and a pair of small and well-developed lateral cusplets. In some specimens (Fig. 2A–D), a minute second pair of cusplets is present. The main cusp is high and wide, labio-lingually flattened. It is inclined lingually but lacks sigmoidal curvature.

Although broken, the most complete crown is 6 mm high and 7.2 mm wide. The largest isolated main cusp is 8 mm high and 6 mm wide. These cusps have an enameloid cover ornamented with short, longitudinal folds.

Most of the specimens have only the main cusp preserved, and only a few have parts of the lateral cusplets preserved. These specimens also have a lingually projecting porous root lacking differentiated foramina.

A high and wide, labio-lingually flattened main cusp as well as the ornamentation with short simple folds, and porous lingually projecting root lacking differentiated foramina are diagnostic features of the genus *Planohybodus* (Rees and Underwood, 2008).

Hybodontidae indet.
(Fig. 2K, N, O)

Material examined: UERJ-PMB 150 (cephalic spine), UERJ-PMB 152 (fin spine), UERJ-PMB 156 (fin spine).

Description: Cephalic Spine: an incomplete cephalic spine (UERJ-PMB 150) (10 mm height and 12 mm width) with a smooth basal platform slightly curved and a strongly recurved enameled crown. This specimen does not show the tip of the crown (Fig. 2N). The basal plate is somewhat T-shaped with indentations that divide it into three lobes, but one lobe (lateral or mesial) is missing. The lobes in this specimen are more elongate, narrow and recurved posteriorly than in the cephalic spine of Lonchidiidae indet (Fig. 2M). The posterior lobe has a higher angle to the crown with a substantial narrowing in its central portion, being more elongate and narrower. The crown is posteriorly recurved, with a sigmoidal profile and has some striae basally. It has a dorsal crest and two other crests (mesial and lateral) that cross the crown, until a few millimeters from the base. This specimen lacks accessory cusplets.

A T-shaped basal plate of the cephalic spines is a character of the Hybodontidae (Rees, 2008), which includes *Planohybodus*.

Fin spines: elongate, posteriorly curved fin spines (UERJ-PMB 152, UERJ-PMB 156) were collected from the Missão Velha Formation but most are incomplete (maximum height 51.1 mm; maximum width 17.3 mm) (Fig. 2K). The denticles of the posterior wall are not preserved as our material represents only the basal region of the spine below the level of the posterior closure. An ornamentation comprising 21 longitudinal ribs is clearly observed in the anterior and lateral surfaces of the mantle. The base of the trunk is unornamented.

The high number of ribs points to a taxonomic position within the Hybodontidae (Rees and Underwood, 2008), contrasting with the fin spines of Lonchidiidae, which typically bear only a few ribs (Duffin, 1985).

Family LONCHIDIIDAE Herman, 1977
Genus *Parvodus* Rees and Underwood, 2002
Type species: *Parvodus rugianus* (Ansorge, 1990).
Type locality: Early Cretaceous of Rügen, northern Germany

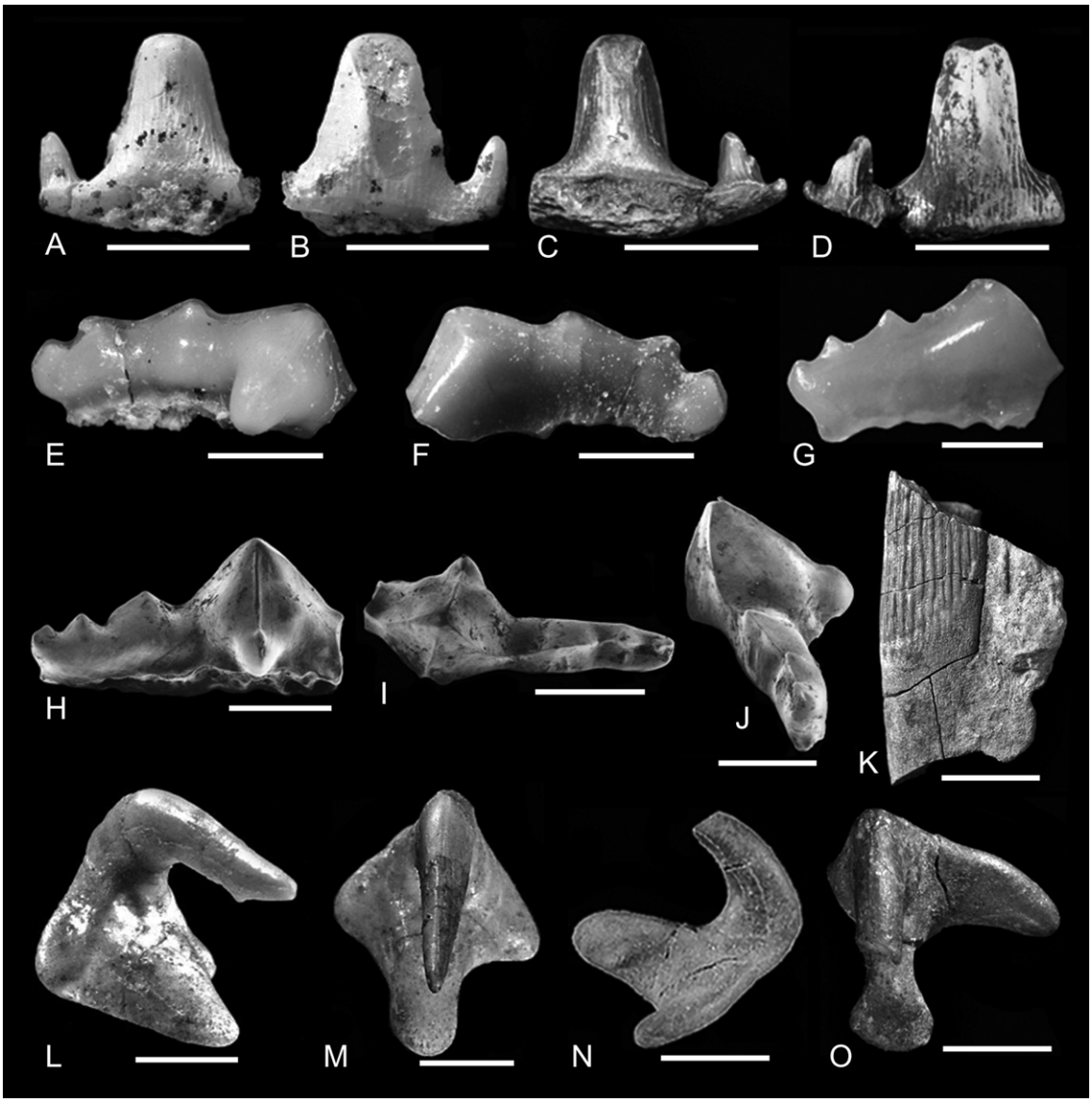

Fig. 2. A–B. *Planohybodus* tooth (UERJ-PMB 140 a) (scale bar = 5 mm) (**A**: lingual view, **B**: labial view). **C–D**. *Planohybodus* tooth (UERJ-PMB 140 b) (scale bar = 5 mm) (**C**: lingual view, **D**: labial view). **E–F**. *Parvodus* tooth (UERJ-PMB 148 a) (scale bar = 1 mm) (**E**: labial view, **F**: lingual view). **G**. *Parvodus* tooth (UERJ-PMB 148 b) (scale bar = 0.5 mm) (lingual view). **H–J**. *Parvodus* tooth (UERJ-PMB 148 c) (scale bar = 1 mm) (**H**: labial view, **I**: occlusal view; **J**: lateral view). **K**. Hybodontidae indet. fin spine (UERJ-PMB 152) (scale bar = 10 mm). **L–M**. Lonchidiidae indet. cephalic spine (UERJ-PMB 149) (scale bar = 5 mm) (**L**: lateral/mesial view, **M**: apical view). **N–O**. Hybodontidae indet. cephalic spine (UERJ-PMB 150) (scale bar = 5 mm) (**N**: lateral/mesial view, **O**: apical view).
Fig. 2. A–B. Dent de *Planohybodus* (UERJ-PMB 140 a) (échelle = 5 mm) (**A**: vue linguale, **B**: vue labiale). **C–D**. Dent de *Planohybodus* (UERJ-PMB 140 b) (échelle = 5 mm) (**C**: vue linguale, **D**: vue labiale). **E–F**. Dent de *Parvodus* (UERJ-PMB 148 a) (échelle = 1 mm) (**E**: vue labiale, **F**: vue linguale). **G**. Dent de *Parvodus* (UERJ-PMB 148 b) (échelle = 0,5 mm) (vue linguale). **H–J**. Dent de *Parvodus* (UERJ-PMB 148 c) (échelle = 1 mm) (**H**: vue labiale, **I**: vue occlusale, **J**: vue latérale). **K**. Épine de la nageoire dorsale d'Hybodontidae indet. (UERJ-PMB 152) (échelle = 10 mm). **L–M**. Épine céphalique de Lonchidiidae indet (UERJ-PMB 149) (échelle = 5 mm) (**L**: vue latérale/mésiale, **M**: vue apicale). **N–O**. Épine céphalique d'Hybodontidae indet (UERJ-PMB 150) (échelle = 5 mm) (**N**: vue latérale/mésiale, **O**: vue apicale).

Parvodus sp.
(Fig. 2E–J)

Material examined: UERJ-PMB 148 a-d (teeth).

Description: Teeth: all of the specimens assigned to *Parvodus* sp. are incomplete and minute. The largest specimen is 3 mm wide and its main cusp is 1.2 mm high (Fig. 2E, F). The smallest specimen is 1.5 mm wide and its main cusp is 0.9 mm high (Fig. 2G). Each tooth has the main cusp preserved and at least one lateral side of cusplets preserved. Well-developed and rounded labial protuberance are seen at the base of main cusp on specimens UERJ-PMB 148 a and c (Fig. 2E, H, I, J). Crowns are ornamented with few folds, which descend from the main cusp and cusplets. Nothing is preserved of the root in these specimens.

The minute size and well-developed, rounded labial protuberance are considered to be diagnostic of the genus *Parvodus* (Rees and Underwood, 2002).

Lonchidiidae indet.
(Fig. 2L, M)

Material examined: UERJ-PMB 149 (cephalic spine).

Description: Cephalic spine: specimen UERJ-PMB 149 consists of a complete cephalic spine (17.8 mm height and 13.2 mm width), with a curved and porous basal platform and a strongly recurved enameled crown (Fig. 2L, M). The basal plate is arrow-shaped (Fig. 2M) with indentations that divide it into three lobes: lateral, mesial and posterior. The mesial indentation separates the basal plate into mesial and posterior lobes, while the lateral indentation separates lateral and posterior lobes. The lobes are relatively wide and rounded. The posterior lobe has a higher angle toward the crown and is rectangular, with the posterior end rounded. The crown is posteriorly recurved, with a sigmoidal profile, and a posterior barb near the apex. This barb is connected to the tip of the crown by a posterior crest. The mesial and lateral crests leave the barb extending from the crown. A dorsal crest extends across the crown, being interrupted a few millimeters from the base. The base of the crown shows vertical striae. This exemplar lacks accessory cusplets.

The arrow-shaped basal plate described for this cephalic spine is similar to that of *Lonchidion* supporting assignment of this material to Lonchidiidae (Duffin, 1985; Rees, 2008), in which *Parvodus* is included.

5. Discussion and conclusions

Hybodontiform sharks have an almost worldwide distribution, and were common and diverse during the Mesozoic ranging through Europe, North America, Asia and Africa. Enigmatically, hybodontiforms appear scarce in South America during this time. However this may largely be due to a lack of collecting and/or documentation.

Perea et al. (2001, 2009) identified *Priohybodus arambourgi* D'Erasmo, 1960 in the Late Jurassic Tacuarembó Formation of Uruguay, while Cione et al. (2002) reported the only known record of hybodontiforms sharks in Argentina, with the description of a fin spine referred to Hybodontiformes indet.

From the Lower Cretaceous of Brazil two nominal species of hybodontiforms were described: "*Acrodus*" *nitidus* Woodward (1888) from the ?Barremian/Aptian Ilhas Formation (Bahia Group) of the Recôncavo Basin and *T. limae* Brito and Ferreira (1989), from the Albian Santana Formation of the Araripe Basin, the only hybodontiform from South America known from articulated material. This last species has now been reported from elsewhere in Gondwana and Laurasia (Vullo and Néraudeau, 2008).

The genus *Planohybodus* has a palaeogeographically restricted distribution in comparison with other hybodontiforms sharks. Previously to this study, *Planohybodus* was described from western Europe and North America (Santonian of New Mexico; Bourdon et al., 2011), with only three nominal species included in the genus: (1) *P. peterboroughensis* Rees and Underwood, 2008, from the Callovian and Oxfordian of England; (2) *P. grossiconus* (Agassiz, 1843), from the Bathonian of England, Scotland, and France, and possibly from the Toarcian of Luxembourg (Rees and Underwood, 2008); (3) *P. ensis* (Woodward, 1916) from the Berriasian-Barremian of southern England, and the Hauterivian-Barremian from northern Spain (Bermúdez-Rochas, 2009a; Rees and Underwood, 2008). There are also two undescribed species of *Planohybodus* from the Barremian of Denmark (Rees and Underwood, 2008) and the Aptian of northeastern Spain (Bermúdez-Rochas, 2009b). Recently, *Planohybodus* sp. has been reported from the Kimmeridgian of northern Spain (Bermúdez-Rochas et al., 2010). In Gondwana, *Planohybodus* had been previously described for the Cretaceous Lima Campos Basin, in North-East Brazil (Pinheiro et al., 2011).

Parvodus appears to be quite common in Laurasia, with three nominal species: *P. rugianus* (Ansorge, 1990) from the Berriasian-Valanginian of Germany, England, Denmark and Sweden (Underwood, 2002), *P. pattersoni* (Duffin, 1985) from the Bathonian of England and Scotland, and *P. curvidens* (Duffin and Thies, 1997) from the Kimmeridgian of northern Germany (Rees and Underwood, 2002).

Parvodus sp. has also been reported from the Early Cretaceous of Spain (Bermúdez-Rochas, 2009a, 2009b) and Thailand (Cuny et al., 2006). Furthermore, very similar taxa considered as *Parvodus* sp. from both the Middle Triassic and Middle Jurassic of China have been reported (Chen et al., 2007; Shang et al., 2008). There is only one previous reference to *Parvodus* from the Gondwanan record, with *Parvodus tikiensis* Prasad et al., 2008 described from the Upper Triassic of India. *P. tikiensis* (Upper Triassic of India) and *Parvodus* sp. (Early Cretaceous of Thailand) are the only species of *Parvodus* previously described from presumed continental deposits.

The material described here represents the first occurrence of *Planohybodus* in the Araripe Basin, and the first record of *Parvodus* in the Cretaceous record in Gondwana. Despite the differences in age, the Brazilian specimens show considerable similarity to the *P. tikiensis* and the teeth from the Missão Velha Formation show no diagnostic characters that would support the creation of a new taxon. On the other hand, Prasad et al. (2008) noted that *P. tikiensis* may represent a new genus distinct from *Parvodus*, but it seems probable that these two taxa could represent an evolutionary lineage of this "genus" on the Gondwana supercontinent.

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References

Agassiz, L., 1833–1843. Recherches sur les poissons fossiles, Neuchâtel et Soleure (Petitpierre) 5, 1420 p.

Ansorge, J., 1990. Fischreste (Selachii, Actinopterygii) aus der Wealdentonscholle von Lobber Ort (Mönchgut/Rügen/DDR). Paläontologische Zeitschrift 64, 133–144.

Batten, D.B., 2007. Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.). The Crato fossil beds of Brazil: Window into an ancient world. Cambridge University Press, 625 p. (pp. 566–576).

Bermúdez-Rochas, D., 2009a. New Hybodont shark assemblage from the Early Cretaceous of the Basque-Cantabrian Basin. Geobios 42, 675–686.

Bermúdez-Rochas, D., 2009b. Early Cretaceous sharks from the Cameros Basin (North of Spain). In: Hart, M. (Ed.). 8th International Symposium on the Cretaceous System, Plymouth University, 6–12 September, Abstract volume, pp. 161–162.

Bermúdez-Rochas, D., Piñuela, L., García-Ramos, J.C., Ruiz-Omeñaca, J.I., 2010. Condrictios del Jurásico Superior de Asturias (España). In: Ruiz-Omeñaca, J.I., Piñuela, L., García-Ramos, J.C. (Eds.), Comunicaciones del V Congreso del Jurásico de España. Museo del Jurásico de Asturias (MUJA), Colunga, 8-11 de septiembre de 2010. Museo del Jurásico de Asturias, Colunga, pp. 43–45.

Berthou, P.Y., 1990. Le Bassin d'Araripe et les petits bassins intracontinentaux voisins (NE du Brèsil): formation et évolution dans le cadre de l'ouverture de l'Atlantique équatorial. Comparaison avec les bassins ouest-africains situés dans le même contexte. In: Campos, D. de A, Viana, M.S., Brito, P.M., Beurlen, G. (Eds.). Atlas do Simpósio Sobre a Bacia do Araripe e Bacias Interiores do Nordeste, Crato, pp. 113–134.

Beurlen, K., 1962. A Geologia da Chapada do Araripe. An. Acad. Brasil. Ci. 34 (3), 365–370.

Beurlen, K., 1963. Geologia e estratigrafia da Chapada do Araripe. In: 17° Congresso Brasileiro de Geologia, Recife, pp. 1–47.

Bourdon, J., Wright, K., Lucas, S.G., Spielmann, J.A., Pence, R., 2011. Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone, central New Mexico. New Mexico Museum of Natural History and Science Bulletin 52, 1–54.

Braun, O.P.G., 1966. Estratigrafia dos Sedimentos da parte interior da região Nordeste do Brasil (Bacias de Tucano-Jatobá, Mirandiba e Araripe). Div. Geol. Mineral DNPM 75, 1–236.

Brito, P.M., 1992. Nouvelles données sur l'anatomie et la position systématique de *Tribodus limae* Brito and Ferreira, 1989 (Chondrichthyes, Elasmobranchii) du Crétacé Inférieur de la Chapada do Araripe (N-E-Brésil). Geobios 14, 143–150.

Brito, P.M., Ferreira, P.L.N., 1989. First Hibodont from Chapada do Araripe. An. Acad. Brasil. Ci. 61 (1), 53–57.

Brito, P.M., Bertini, R.J., Martill, D.M., Salles, L.J., 1994. Vertebrate fauna from the Missão Velha Formation (Lower Cretaceous, N.E. Brazil). In: 3° Simpósio sobre as Bacias Cretácicas Brasileiras, UNESP, Rio Claro, pp. 139–140.

Casier, E., 1961. Matériaux pour la faune ichthyologique Eocrétacique du Congo. Ann. Mus. roy. Afr. Centr., Sciences Géologiques, Série 8 (39), 1–96.

Casier, E.,1969. Addenda aux connaissances sur la faune icthyologique de la Série de Bokungu (Congo). Ann. Mus. roy. Afr. Centr., Tervuren, ser.8, Sciences Géologiques, n. 62, 1–20, est. 1–12.

Chen, L., Cuny, G., Wang, X., 2007. The chondrichthyan fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China). Hist. Biol. 19 (4), 291–300.

Cione, A.L., Acosta Hospitaleche, C., Mennucci, J.A., Cocca, S., 2002. The first shark from the Triassic-Jurassic of South America. Neues Jahrb. Geol. Palaont. 1, 9–18.

Cuny, G., Suteethorn, V., Kamha, S., Buffetaut, E., Philippe, M., 2006. A new hybodont shark assemblage from the Lower Cretaceous of Thailand. Hist. Biol. 18 (1), 21–31.

D'Erasmo, G., 1960. Nuovi avanci ittiolitici della "serie di Lugh" in Somalia conservati nel Museo Geologico di Firenze. Palaeontographia Italica 55 (n.s. 25), 1–23.

Duffin, C.J., 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935). Palaeontographica Abt A 188, 105–152.

Duffin, C.J., Thies, D., 1997. Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of Northwest Germany. Geol. Palaeont. 31, 235–256.

Gee, H., 1988. Cretaceous unity and diversity. Nature 332, 487.

Herman, J., 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphie intercontinentale. Mémoires pour servir à l'explication de Cartes Géologiques et Minières de la Belgique. Service Géologique de Belgique 15, 1–401.

Laurin, M., Soler-Gijón, R., 2010. Osmotic tolerance and habitat of early stegocephalians: indirect evidence from parsimony, taphonomy, paleobiogeography, physiology and morphology. In: Vecoli, M., Clément, G. (Eds.), The terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface. The Geological Society of London, London, pp. 151–179.

Maisey, J.G., 2000. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretaceous Research 21, 281–314.

Maisey, J.G., Carvalho, M.R., 1997. A new look at old sharks. Nature 385, 779–780.

Martill, D.M., 1993. Fossils of the Santana and Crato Formations, Brazil. Palaeontological Association, London, 159 p.

Martill, D.M., Brito, P.M., Washington-Evans, J., 2008. Mass mortality of fishes in the Santana Formation (Lower Cretaceous, ?Albian) of Northeast Brazil. Cretaceous Research 29, 649–658.

Moraes, J.F.S., Santos, J.S.A., Mascarenhas, J.C., 1976. Projeto Santana. Relatório Final da Etapa I. DNPM, Brasília, pp. 269.

Owen, R., 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. Longman, London, 308 p.

Patterson, C., 1966. British Wealden Sharks. Bull. Brit. Mus. (Nat. Hist.) 11, 283–350.

Perea, D., Ubilla, M., Rojas, A., Goso, C.A., 2001. The West Gondwana occurrence of the Hybodontid Shark *Priohybodus*, and the Late Jurassic - Early Cretaceous age of the Tacuarambó Formation, Uruguay. Palaeontology 44 (6), 1227–1235.

Perea, D., Soto, M., Veroslavsky, G., Martínez, S., Ubilla, M., 2009. A Late Jurassic fossil assemblage in Gondwana: biostratigraphy and correlations of the Tacuarembó Formation, Parana Basin, Uruguay. J. South Am. Earth Sci. 28, 168–179.

Pinheiro, F.L., Figueiredo, A.E.Q., Fortier, D.C., Viana, M.S.S., Schultz, C.L., 2011. Fauna de vertebrados Eocretácicos de um afloramento da Bacia de Lima Campos, Ceará, Brasil. Rev. Bras. Paleontol. 14 (2), 189–198.

Pinto, I.D., Sanguinetti, Y.Y., 1958. *Bisulcocypris*, a new Mesozoic genus and preliminary note about its relation with *Metacypris* and allied forms. Bol. Soc. Bras. Geo. 7, 75–90.

Pires, E.F., Guerra-Sommer, M., 2011. Growth ring analysis of fossil coniferous woods from Early Cretaceous of Araripe Basin (Brazil). An. Acad. brasil. Ci. 83 (2), 409–423.

Ponte, F.C., Appi, C.J., 1990. Proposta de revisão da coluna litoestratigráfica da Bacia do Araripe. XXXVI Congresso Brasileiro de Geologia, 1, Sociedade Brasileira de Geologia. Natal, 211–226.

Prasad, G.V.R., Singh, K., Parmar, V., Goswami, A., Sudan, C.S., 2008. Hybodont shark teeth from the continental Upper Triassic deposits of India. In: Arratia, G., Schultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 4. Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, München, Germany, pp. 413–432.

Rees, J., 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology-preliminary results. Acta Geol. Pol. 58 (2), 217–221.

Rees, J., Underwood, C.J., 2002. The status of the Shark genus *Lissodus* Brough, 1935, and the position of nominal Lissodus species within the Hybodontoidea (Selachii). J. Vert. Paleont. 22, 471–479.

Rees, J., Underwood, C.J., 2008. Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). Palaeontology 51, 117–147.

Saint-Seine, P., 1955. Poissons fossiles de l'étage de Stanleyville (Congo belge). Ann. Musée Congo Belge 14, 1–126.

Schultze, H.-P., 2009. Interpretation of marine and freshwater paleoenvironments in Permo-Carboniferous deposits. Palaeogeogr. Palaeoclimatol. Palaeoecol. 281, 126–136.

Shang, Q., Cuny, G., Chen, L., 2008. Early Middle Jurassic vertebrate microremains from the Three Gorges area, southern China. Hist. Biol. 20 (2), 87–99.

Silva, M.A.M., 1986. Lower Cretaceous sedimentary sequences in the Araripe Basin: a Revision. Rev. Brasil. Geoc. 16 (3), 311–319.

Silva, V.G., Azevedo, S.A.K., 1996. Um Dipnoi da Formação Brejo Santo, Eocretáceo da Chapada do Araripe, Ceará, Brasil. Acta Geol. Leopold., pp. 43–58.

Smith, R.J., 2000. Morphology and ontogeny of Cretaceous ostracods with preserved appendages from Brazil. Palaeontology 43 (1), 63–98.

Viana, M.S.S., Cavalcanti, V.M.M., 1991. Distribuição estratigráfica dos fósseis da Formação Missão Velha, Bacia do Araripe. Rev. Geol. 4, 81–87.
Vullo, R., Néraudeau, D., 2008. When the "primitive" shark *Tribodus* (Hybodontiformes) meets the "modern" ray *Pseudohypolophus* (Rajiformes): the unique co-occurrence of these two durophagous Cretaceous selachians in Charentes (SW France). Acta Geol. Polonica 58 (2), 249–255.
Woodward, A.S., 1888. Notes on some vertebrate fossils from the Province of Bahia, Brazil, collected by Joseph Mawson. Ann. Mag. Nat. Hist. 2, 132–136.
Woodward, A.S., 1916. The Fossil Fishes of the English Wealden and Purbeck Formations. Palaeontol. Soc. Monographs. Part I, London, pp. 1–48.