Mesozoic marine reptile palaeobiogeography in response to drifting plates

N. Bardet, J. Falconnet, V. Fischer, A. Houssaye, S. Jouve, X. Pereda Suberbiola, A. Pérez-García, J.-C. Rage, P. Vincent

PII: S1342-937X(14)00183-X
DOI: doi: 10.1016/j.gr.2014.05.005
Reference: GR 1267

To appear in: *Gondwana Research*

Received date: 19 November 2013
Revised date: 6 May 2014
Accepted date: 14 May 2014

Please cite this article as: Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda Suberbiola, X., Pérez-García, A., Rage, J.-C., Vincent, P., Mesozoic marine reptile palaeobiogeography in response to drifting plates, *Gondwana Research* (2014), doi: 10.1016/j.gr.2014.05.005

Mesozoic marine reptile palaeobiogeography in response to drifting plates

To Alfred Wegener (1880-1930)

Bardet N.[a*], Falconnet J. [a], Fischer V.[b], Houssaye A.[c], Jouve S.[d], Pereda Suberbiola X.[e],
Pérez-García A.[f], Rage J.-C.[a] and Vincent P.[a,g]

[a] Sorbonne Universités CR2P, CNRS-MNHN-UPMC, Département Histoire de la Terre,
Muséum National d'Histoire Naturelle, CP 38, 57 rue Cuvier, 75005 Paris, France;
bardet@mnhn.fr, falconnet@mnhn.fr, jcrage@mnhn.fr, pvincent@mnhn.fr

[b] Département de Géologie, Université de Liège / Département de Paléontologie, Institut
Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; v.fischer@ulg.ac.be

[c] Steinmann Institut für Geologie, Paläontologie und Mineralogie, Universität Bonn,
Nussallee 8, 53115 Bonn, Germany; houssaye@uni-bonn.de

[d] Muséum d'Histoire Naturelle, Marseille, France; jouvestephane@yahoo.fr

[e] Departamento Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad
del País Vasco / EHU, Apdo 644, Bilbao, Spain; xabier.pereda@ehu.es

[f] Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense
de Madrid, José Antonio Novais 2, 28040 Ciudad Universitaria, Madrid, Spain
; paleontologo@gmail.com

[g] Staatliches Museum für Naturkunde, Rosenstein 1, D-70191, Stuttgart, Germany,
pvincent@mnhn.fr

* corresponding author: E-mail: bardet@mnhn.fr, Tel: (33) 1 40793455, Fax: (33) 1
40793580

Abstract

During the Mesozoic, various groups of reptiles underwent a spectacular return to an aquatic life, colonizing most marine environments. They were highly diversified both systematically and ecologically, and most were the largest top-predators of the marine ecosystems of their time. The main groups were Ichthyosauria, Sauropterygia, Thalattosauria, and several lineages of Testudinata, Crocodyliformes, Rhynchocephalia and Squamata. Here we show that the palaeobiogeographical distribution of these marine reptiles closely followed the break-up of the supercontinent Pangaea and that they globally used the main marine corridors created by this break-up to disperse. Most Mesozoic marine reptile clades exhibit a cosmopolitan, or at least pandemic, distribution very early in their evolutionary history. The acquisition of morphological adaptations to a fully aquatic life, combined to special thermophysiological characteristics, are probably responsible for these animals to become efficient long-distance open-marine cruisers. Generally, Early Triassic taxa were near-shore animals mainly linked to the Tethys or Panthalassa coastlines. By the end of the Triassic and during the Jurassic, the break-up of Pangaea resulted in the formation of large marine corridors connecting the Tethys to the North Atlantic and Pacific realms, a trend increasing on during the Cretaceous with the expansion of the Atlantic Ocean and the break-up of the southern Gondwana, allowing open-sea marine reptiles to spread out over large distances. However, if large faunal interchanges were possible at a global scale following a dispersal model, some provinces, such as the Mediterranean Tethys, were characterized by a peculiar faunal identity, illustrating an absence of migration with time despite the apparent lack of barriers. So, if Continental Drift enabled global circulations and faunal interchanges via dispersals among Mesozoic marine reptiles, others parameters, such as ecological and biological constraints, probably also played a role in the local endemic distribution of some of these marine groups, as they do today.

Keywords - Marine reptiles, Mesozoic, Pangaea break-up, dispersal, endemism.

1. Introduction

Mesosaurus, known from Early Permian strata, is one of the first marine reptiles known in the fossil record (Fig. 1). Its co-occurrence in both Africa (South Africa, Namibia) and South America (Brazil, Uruguay, Paraguay) also made it one of the key-fossils used by the German meteorologist Alfred Wegener (1880-1930) to support his theory of Continental Drift, first briefly published in 1912, then extensively in 1915 and in later editions (Wegener, 1912; 1915).

But *Mesosaurus* was only the 'tip of the iceberg'. Indeed, during the Mesozoic Era, numerous clades of reptiles invaded the aquatic realm, colonizing all marine environments (e.g. Mazin, 2001; Houssaye, 2009). Like the Cenozoic marine mammals, they exemplify convergent evolution and a wide range of adaptations to the marine realm, including both morphological, physiological and ecological characteristics. These reptile clades were highly diversified, both systematically and ecologically, and most became the largest top-predators of the marine ecosystems of their time. Some were exclusively marine and only known during the Mesozoic, such as ichthyosaurs, sauropterygians and thalattosaurs, whereas others included marine representatives at some periods only of their evolutionary history, like chelonians, crocodyliforms, rhynchocephalians and squamates. Adaptations to a marine life are also found in minor diapsid offshoots, such as Late Carboniferous araeoscelidians (deBraga and Reisz, 1995), several Triassic taxa that are nanchungosaurids (Carroll and Dong, 1991), omphalosaurids (Maisch, 2010), *Helveticosaurus* (Rieppel, 1989), poposauroids (e.g., Li et al., 2012), protorosaurs (e.g., Rieppel et al., 2008) and the phytosaur *Mystriosuchus planirostris* (e.g., Gozzi and Renesto, 2003), as well as in the Late Cretaceous hesperornithiforms and ichthyornithiforms marine birds (e.g. Chinsamy et al., 1998; Rees and Lindgren, 2005). Some marine reptile lineages survived the Cretaceous-Palaeogene (K/Pg) boundary, being known in the Cenozoic up to the present time. Nowadays however, compared to this Mesozoic radiation, marine reptiles are only minor components of the marine biotas, being represented essentially by turtles and snakes.

In parallel to these biological radiations, at the dawn of the Mesozoic Era, large-scale geological phenomena driven by mantle convection strongly affected the face of Planet Earth: at the beginning of the Triassic, the tectonic forces moving the plates one relative to another resulted in the break-up of the huge and unique Palaeozoic continental mass known as Pangaea into two major continental landmasses: the Laurasia in the North and the Gondwana in the South, both notched East by the Tethys Ocean. The break-up of Pangaea carried on during the Jurassic and later, progressively forming the continents known today: North America and Eurasia inherited from the Laurasia; South America, Africa, Antarctica, Australia and India from the Gondwana. The break-up of the Pangaea prompted at the same time the progressive opening of several new oceanic ways and realms (Atlantic and Pacific oceans), as well as the closure of some others (Tethys Ocean). As opposed to the vicariant evolution suffered by continental faunas as a result of isolation, these marine ways permitted nektonic faunas to disperse, roughly according to the classical Wallace'model.

This break-up of the Pangaea was first evidenced and demonstrated by the German meteorologist Alfred Wegener (Wegener, 1912; 1915 and later editions). Wegener's original concept of Continental Drift (*Kontinentalverschiebung*), definitively accepted by the scientific community only in the 1960s, has been completed, improved – and in a sense renewed – by the important geological discoveries made after WWII with the development of Deep Sea Drilling Programs, mainly in the geomagnetism and geophysics fields. This concept, although not strictly synonymous to Wegener's Continental Drift, is nowadays known as the Plate Tectonic Theory. A major weakness in Wegener' theory was its incapacity to explain the mechanisms responsible for the Earth crust movements. Nevertheless, if mantle 'plumes' are nowadays suspected to be responsible for them, the exact mechanisms remain rather poorly known (Torsvik and Cocks, 2012). Like Darwin's Theory of Evolution for Biology, Wegener's one represented a new paradigm in Geology, and probably corresponds to one of the most important discoveries ever made in this field, whose consequences extend well beyond the scope of Earth Sciences, as it also has important biological, biogeographical and even economical implications. Tribute must thus be paid to Wegener, whose main quality was probably to have been able to accumulate and combine scientific facts issued from several research fields far beyond his own discipline, in order to elaborate a solid theory. This very modern multidisciplinary and integrative approach, proposed by an ‘outsider’ in Geology, has to be pointed out and this is the reason why this work is dedicated to Alfred Wegener.

In this paper, we compile an exhaustive database of palaeobiogeographical and stratigraphical occurrences of marine reptiles at the generic and suprageneric levels and record their hosting palaeoenvironments. Then, we analyse the dispersal patterns, or lack thereof, assuming monophyly of the genera in our database and their phylogenetic relationships. The aim of this paper is to demonstrate that the palaeobiogeographical distributions of Mesozoic marine reptiles closely followed as a whole the break-up of the Pangaea induced by plate tectonic movements.

2. Material and Methods

2.1. Material

In the present study, the term ‘reptiles’ is restricted to amniotes that are called reptiles in common language, and thus excludes birds, that would have obscured the analysis. We consider as ‘marine’ reptiles those that basically lived and fed in the marine environment. This is not often straightforward to determine based on the fossil record, as it is sometimes difficult for living species. For example, if there is no doubt concerning extant marine turtles (Chelonioidea), the ‘marine’ iguana *Amblyrhynchus cristatus*, which feeds exclusively on algae, is also considered a marine reptile, although it spends most of its time on land. For the aim of this work, a series of data indicative of a marine lifestyle have been considered for each taxon, such as anatomical and histological adaptations, sedimentological context in which the fossils have been unearthed, supposed dietary preferences, etc.

As it is the case in Cenozoic marine mammals, Mesozoic marine reptiles do not correspond to a monophyletic assemblage but to a polyphyletic one, composed of various reptilian clades that repeatedly invaded the marine realm mostly during this Era, which is considered as their ‘golden age’. These clades convergently adapted to an aquatic life and exhibit diverse morphologies (see Houssaye, 2009; Fig. 1). Each clade within this polyphyletic assemblage is nevertheless monophyletic. All are considered diapsids, at the possible exception of turtles and ichthyosaurs, whose relationships among reptiles are still strongly debated (e.g. Lee, 1997; Li et al., 2011; Lyson et al., 2013; Maisch, 2010; Rieppel and Reisz, 1999). Even within diapsids, their phylogenetical relationships remain debated (e.g. compare Li et al., 2011 and Neenan et al., 2013). This large-scale problem is however out of the scope of this paper.

Seven clades of Mesozoic marine reptiles, the most diversified ones and those potentially bearing a palaeobiogeographical signal (that is, de facto excluding the one-time taxa), have been considered. This includes fully marine taxa, such as ichthyosaurians (earliest Triassic – early Late Cretaceous), thalattosaurians (? earliest to latest Triassic) and sauropterygians (Early Triassic – latest Cretaceous), but also clades comprising marine lineages along their evolutionary history, such as testudinatans (Late Triassic; Late Jurassic – earliest Cretaceous; Early Cretaceous – recent), crocodyliforms (Early Jurassic – Early Cretaceous; Late Cretaceous – Palaeogene), rhynchocephalians (Early to latest Jurassic; Albian) and finally squamates (Late Cretaceous; Palaeogene – recent) (Fig. 1).

For the aim of this work, these groups are briefly introduced below and details are provided concerning their general morphological characteristics, systematics, phylogenetical position, main ecological adaptations, as well as patterns of global evolution (diversity) and distribution (palaeobiogeography and chronostratigraphy). For each clade, we built a global database including all occurrences for each stage of the Mesozoic Era, at the generic level.

The database is provided as summary Tables in Appendix 1. In total, more than 320 genera and 520 species, and much more palaeobiogeography-relevant occurrences of marine reptiles have been recorded for the Mesozoic, as summarized below.

CLADE	**GENERA**	**SPECIES**
Ichthyosauria	55	91
Thalattosauria	14	18
Sauropterygia	>110	>170
Testudinata	67	>85
Rhynchocephalia	3	4
Crocodyliformes	20	56
Squamata	>55	>100
TOTAL	**>324**	**>524**

2.2. Methods

The relation between distributional changes and geological processes is crucial in every palaeobiogeographical study (Cecca, 2002). The two ‘classical’ aims of palaeobiogeography, as originally described by Wallace (1876, 1880) and summarized by Patterson (1983) are: 1) to use the distributions of fossil organisms as a guide to Earth History (= to identify patterns) and, 2) to explain these distributions through application of Earth History and Evolution theories (= to find processes responsible for the patterns) (see Cecca, 2002). In this classical view, the main processes used to explain the distributions are dispersal, vicariance and ecological/biological factors.

This classical view has been brought up to date by Rosen (1988) who distinguished: 1) ‘pure’ palaeobiogeography (historical biogeography), whose aims are to combine patterns and processes by studying both the factors responsible for the organism geographical distributions over time and the explanations for these distributions, with respect to evolutionary and geological processes; 2) ‘applied’ biogeography aiming to use the organism distributions to infer ecological roles of factors such as temperature, water depth, primary productivity, etc., or to infer past tectonic events and palaeogeographical configurations. The best example of ‘applied’ palaeobiogeography is present in Wegener’s work. Rosen (1988) identifies and distinguishes the main patterns (distributional area, endemism, disjunctive and cosmopolitan distribution) from the main processes (maintenance, dispersal, origination). For historical and explanatory details of all these concepts, we refer to Cecca (2002).

Whether we consider the aims of Palaeobiogeography in their classical or synthetic assertion, the main goals of our work have been to characterize the patterns of distributions of each clade of interest and to hypothesize the processes that could explain these distributions. Special attention has been paid to: 1) Vicariance, which applies when two populations are isolated by a geographical barrier. At a global scale, plate tectonics is the major geological factor responsible for vicariance. In the marine realm however, these mechanisms are relatively poorly known, at least for nektonic organisms with a high capacity to disperse along marine ways. Concerning Mesozoic marine reptiles this is particularly true as some were adapted to cruise over long distances. 2) Dispersal, which refers to species movements away from an existing population or away from the center of origin (but see below). The dispersal basic mechanism is movement from one place to another and can be passive, depending on the capacities of the organisms to use the natural environmental kinetic energy (wind, currents, gravity), or active, depending mainly on both the locomotor capabilites of the organisms and on the pressure for resources in an ecosystem. The dispersal of the taxa can be partial, almost global (pandemic taxa) or global (cosmopolitan taxa). 3) Endemism, which refers to organisms that are solely found in a restricted area. This specific distribution can be linked to diverse environmental and/or biological factors but also to preservation biases.

Concretely, we have first mapped the distribution of the taxa (genera or palaeobiogeography-relevant suprageneric occurrences) on Mesozoic palaeogeographical maps at selected key periods (Early, Middle and Late Triassic; Early, Middle and Late

Jurassic; Early, mid and Late Cretaceous). The maps used were those of Blakey (available at http://www2.nau.edu/rcb7/, updated page: March 2011, Copyright Ron Blakey). We have then hypothesized the possible scenarios that could have been responsible for these distributions, by analysing the taxa distribution patterns in regard to the main marine corridors and routes resulting from the break-up of the Pangaea during the Mesozoic (see Blakey, 2008) as disclosed by Hallam (1994). We have also investigated on some ecological and biological factors that could have been responsible for the specific distribution of some taxa.

2.3. Potential biases

The major biases that affected organism palaeobiogeographical distribution rely on the incompleteness of both the fossil and stratigraphical records, as well as historical and taphonomical biases of discovery. As such, the interpretation of the observed patterns as truthful always needs to be taken with caution. For example, the origination centre of organisms cannot be objectively identified, as it is highly susceptible to be affected by these biases; however, the recognition of the oldest record areas has been considered useful to describe historical patterns of distributional change (Cecca, 2002). Also, the choice of the taxonomical rank used can impact on the distributional patterns inferred and thus can imply conceptual differences for process explanations (Rosen 1988). This applies to most fossil groups, but more especially to large vertebrates, such as Mesozoic marine reptiles, mostly top-predators, which represented only a small proportion of the original biocoenosis. As such, their remains are exceedingly rare as compared to other groups, such as invertebrates, and thus more prone to discovery biases. As far as the biostratigraphical record and taphonomical biases are concerned, it should be noted that some Lagerstätten outcrops artificially increase the diversity at some time intervals (e.g. Toarcian of Western Europe), whereas some stratigraphical intervals characterized by few deposits of marine sediments have yielded rare marine reptile remains (e.g. earliest Cretaceous of Europe). Finally, the potentially fossil-rich stratigraphical successions have received different attention depending on the geographically variable interest in Vertebrate Palaeontology and on the degree of development of industrial quarrying activities. As a result a large part of Mesozoic marine reptile specimens come historically from Europe and North America.

However, to cope with these issues, we designed this study by considering a large number of specimens from a wide range of clades, likely possessing distinct physiological and ethological features. As such, the broad and general trends we discuss hereafter are evidenced by the record of several lineages and likely represent genuine biosphere – geosphere interactions.

3. Overview of the biogeographic history of Mesozoic marine reptiles

3.1. Ichthyosauria (Fig. 2, Table 1 in Appendix)

Ichthyosauria is a successful clade of marine reptiles, currently known by 55 genera and 91 species, that spanned most of the Mesozoic Era, from the Olenekian (Early Triassic) to the end of the Cenomanian (early Late Cretaceous), and that possesses the most extreme adaptations to life in the open aquatic realm (Motani, 1999b, 2005). They are best known for their peculiar and unique Bauplan resembling that of cetaceans or fishes and that includes a fusiform body shape, an elongated snout, limbs modified into compact hydrofoils (Motani, 1999a), as well as dorsal and caudal fins essentially composed of soft-tissue (McGowan, 1992). Though this body plan is present in derived forms only and was acquired progressively (Lingham-Soliar and Reif, 1998), ichthyosaurs already display numerous adaptations to a fully aquatic lifestyle at the very beginning of their evolutionary history. No terrestrial or semi-aquatic form is known, although the earliest forms retained a plesiomorphic pelvic girdle still connected to the axial skeleton and limbs with elongated elements, as in terrestrial amniotes (Motani, 1998, 1999a).

Ichthyosauria is the first major clade of amniote to colonize the marine realm (Motani, 2005). The earliest ichthyosaurs are already diversified and geographically dispersed, probably because of their early acquisition of several adaptations for an active swimming. Indeed, seven genera occur in numerous Early Triassic localities along the northern coast of the Pangaea that are British Columbia, Svalbard, Japan, China and Thailand (Brinkman et al., 1992; Maisch, 2010; Maxwell and Kear, 2013; Motani, 1998), suggesting a radiation very early in the Triassic or even deeper in time. By the Middle Triassic, ichthyosaurs dispersed within the northern hemisphere, reaching Europe, Nevada, and California (Fröbisch et al., 2006; Jiang et al., 2007; Sander, 1989). During the Late Triassic, the whale-sized shastasaurids colonized the Tethys and Pantalassa oceans, with remains found in California, British Columbia, China and Tibet (Ji et al., 2013; Sander et al., 2011). At the same time (Carnian), the parvipelvians, derived ichthyosaurs with a peculiar thunniform body shape, appeared on the northwestern coast of the Pangaea (British Columbia) (McGowan, 1995, 1997). The Late Triassic is often regarded as the 'golden age' of ichthyosaurs, with the presence of numerous taxa exhibiting a wide variety of body plans and feeding ecologies (Sander et al., 2011; Thorne et al., 2011), as well as extreme disparities in adult body sizes, from the <1 m long *Hudsonelpidia brevirostris* (McGowan, 1995) to the >20 m long *Shonisaurus sikkaniensis* (Nicholls and Manabe, 2004).

A significant part of this diversity vanished during or at the end of the Late Triassic (Thorne et al., 2011) and only parvipelvians survived this event, forming a post-Triassic stable monophyletic clade named Neoichthyosauria that rapidly radiated during the latest Triassic (Fischer et al., 2013). However, neoichthyosaurians never re-achieved the disparity of their Late Triassic cousins, even if they colonized numerous feeding guilds within the Early Jurassic ecosystems of the European archipelago (Fischer et al., 2011; Martin et al., 2012).

The rapid neoichthyosaurian radiation also gave rise to the thunnosaurians, a clade of highly modified forms adapted for rapid sustained swimming that contains the iconic genera

Ichthyosaurus and *Stenopterygius* (Lingham-Soliar and Plodowski, 2007). Despite an outstanding number of specimens in western Europe (McGowan, 1974), the worldwide record of Early Jurassic ichthyosaurs is poor as only a few specimens are known outside of Europe, namely in British Columbia, Argentina and New Zealand (McGowan and Motani, 2003). Toarcian ichthyosaurs appear rather geographically widespread within the European archipelago (Fischer et al., 2011).

History repeated during the middle Toarcian–Bajocian interval, when all ichthyosaurs except thunnosaurians went extinct, greatly reducing the diversity and disparity of the group. This diversity drop appears protracted in time and is not linked to the Early Toarcian mass extinction (Maxwell et al., 2012; Vincent et al., 2013a). Two thunnosaurian clades persisted and produced forms that survived up to the Cretaceous: the poorly known lineage of *Malawania* (Fischer et al., 2013) and baracromians that gave rise to Ophthalmosauridae, whose first record occurrs at the Aalenian –Bajocian boundary in South America (Fernández, 2003). Ophthalmosauridae epitomizes the trend towards improved pelagic life initiated and developed in the successive clades Parvipelvia and Thunnosauria: compared to more basal ichthyosaurs, they have larger eyes, a more regionalized vertebral column, a shorter tail, a higher aspect-ratio caudal fluke, broader and more compact fore paddles, and a reduced pelvic girdle (Motani et al., 1998). Ophthalmosaurids then rapidly radiated and dispersed, reaching a global distribution and a high taxonomic diversity by the Late Jurassic (Druckenmiller et al., 2012).

Up to recently, Cretaceous ichthyosaurs were considered poorly diversified after a supposed third major extinction event at the end of the Jurassic (Bakker, 1993; Bardet, 1995; Benson et al., 2010) up to their final extinction at the Cenomanian–Turonian boundary (Bardet, 1992). However, recent data indicate an extensive survival of ichthyosaurs across the Jurassic–Cretaceous boundary and a high diversity during the Early Cretaceous (Fischer et al., 2012, in press; Zammit, 2012). This new data suggest that ichthyosaurs remained taxonomically and ecologically diverse and geographically widespread up to their final extinction.

3.2. Thalattosauria (Fig. 3, Table 2 in Appendix)

Thalattosauria is one of the short-lived clades of marine diapsids that flourished during the Triassic, for a total of 14 genera and 18 species recognized (Benton et al., 2013; Liu, 2013; Müller, 2005; Müller et al., 2005; Nicholls and Brinkman, 1993; Nicholls, 1999; Rieppel, 1987; Zhao et al., 2013). They were medium- to large-sized animals, ranging from 1 to 4.4 m in length and characterized by a triangular skull (Müller et al., 2005; Zhao et al., 2010). With a slender elongated body, a compressed tail, and short limbs also suitable for terrestrial locomotion, the Bauplan of thalattosaurs is typical of anguilliform ambush predators: propulsion was ensured by body and tail undulations while limbs were either used to maneuver or maintained along the body to reduce drag (Massare, 1997; Müller et al., 2005). They were probably near-shore inhabitants (Benson and Butler, 2011). Thalattosaurs include two main lineages, with distinct ecological adaptations: the Askeptosauroidea were near-surface generalist predators whereas Thalattosauroidea adapted toward a pelagic life and showed an increasing heterodonty to occupy a larger number of palaeoecological guilds (e.g., Benton et al., 2013; Massare, 1997; Müller, 2005).

The oldest known thalattosaurs are from the Lower-Middle Triassic of North America (British Columbia, Nevada) (Nicholls and Brinkman, 1993; Sander et al., 1994). The Middle Triassic global transgression then favored the diversification of thalattosaurs in facilitating their dispersal from the Eastern Panthalassa to the Tethys (Benson and Butler, 2011). They are indeed known in Europe (Swiss, Spain) as early as at the Anisian-Ladinian boundary and during the Ladinian (Rieppel, 1987; Rieppel and Hagdorn, 1998; Müller, 2005), as well as in the Ladinian of China (Sun et al., 2005). During the Early Carnian, both their systematics and palaeoecological diversity greatly increases (7 species known in China) (Benton et al., 2013; Liu, 2013; Zhao et al., 2013), probably following the demise of plesiopedal eosauropterygians (Benton et al., 2013). During the Late Triassic however, thalattosaurs began to vanish, probably in relation to a global regression that reduced the habitat of these near-shore mostly durophagous animals (Benton et al., 2013). They disappeared at the end of the Carnian in China, but were still present in the Carnian-Norian of the eastern coast of North America (Nevada, California, British Columbia, Alaska) (Storrs, 1991; Nicholls, 1999; Adams, 2009), as well as in the Norian of Europe (Italy) (Dalla Vecchia, 1994; Müller et al., 2005). The last thalattosaur known is an unnamed thalattosauroid from the Rhaetian of Austria (Müller, 2007).

3.3. Sauropterygia (Fig. 4, Table 3 in Appendix)

Sauropterygia is by far the most successful marine reptilian clade with the longest fossil record, spanning around 180 million years, from the late Early Triassic to the end of the Cretaceous (Benson et al., 2010). It is also the largest clade of marine reptiles (Motani, 2009), being known by more than 110 genera and 170 species. They include two major lineages with drastically different morphologies and exploiting a wide range of habitats and ecological niches: the placodonts and the eosauropterygians (Rieppel, 2000).

Placodontia represents the sister-group of eosauropterygians and includes the unarmored or partially armored Placodontoidea and the strongly armored Cyamodontoidea (Fabbria et al., 2013; Rieppel, 2000). They were short-necked animals with robust skulls bearing a characteristics low crushing dentition, traditionally regarded as durophagous bottom dwellers (Rieppel, 2002). Indeed, both placodontoids and cyamodontoids were well adapted to ‘walk’ on the shallow seafloor thanks to their peculiar morphologies, coupled to a pachyostotic skeleton, which increased their body weight and procured them a thick skeleton used as ballast (Scheyer et al., 2012). Known by ten genera when they first appeared at the beginning of the Middle Triassic (Early Anisian), they then radiated during the Middle Triassic to become extinct at the end of the Late Triassic (Rhaetian) (Scheyer, 2007). Whereas cyamodontoids were a very diverse group being known by about 8 genera, placodontoids are known by only two (Jiang et al., 2008). They were found in both the Western and Eastern Tethys, being mainly known in Europe, but also in North Africa and the Middle East, as well as in China (Li and Rieppel, 2002; Jiang et al., 2008; Scheyer et al., 2012). The palaeobiogeography of placodonts shows they were mainly linked to coastal environments of the Tethys Ocean margins and, up to now, they have not been found outside from this Tethyan Realm.

Eosauropterygians, with a total of 106 genera currently known, represent a very diversified clade of gracile animals with an elongated neck that first appeared in the Induan (Early Triassic) and encompass pachypleurosaurs, nothosaurs, and pistosaurs – including plesiosaurs (Rieppel, 2000). Eosauropterygians are restricted to the Triassic with the exception of the Plesiosauria that thrived until the end of the Cretaceous. The fossil record shows that eosauropterygians were very diverse and widespread geographically.

Most Triassic eosauropterygians (in total 22 genera) are recorded from the Middle Triassic, very few having been found in Lower Triassic strata (Rieppel, 2000). Pachypleurosaurs were relatively small animals that diversified in the Tethyan Ocean during the Middle Triassic (Rieppel, 2000). Nothosaurs and pistosaurs were medium-sized to large animals that fed on invertebrates, fishes, and even probably on small marine reptiles (Rieppel, 2002). Most Triassic eosauropterygians were probably amphibious forms, using an axial undulatory locomotion but retaining terrestrially-proportioned limbs allowing some degree of terrestrial locomotion. However, some nothosaurs and pistosaurs could have been fully marine inhabitants using paraxial locomotion. Triassic eosauropterygians are well known thanks to numerous specimens found mainly in Europe but also in China. Only one taxon, *Corosaurus*, was found out of this Tethys Realm, namely in North America. Like placodonts, the bulk of Triassic eosauropterygians were restricted to coastal environments of the Tethyan Realm.

Plesiosauria (84 genera) appear to be obligatory aquatic animals (Rieppel, 2000). They possess an unusual body plan with a relatively short and stiff trunk, expanded ventral elements of the pectoral and pelvic girdles as well as a reinforced gastral ribcage (Storrs, 1993). Among Sauropterygia, plesiosaurs show the most advanced adaptations to a marine lifestyle, being unique for displaying four enlarged hydrofoil-shaped propulsive flippers for swimming (Carpenter et al., 2010; Massare, 1994; Rieppel et al., 2002). These peculiar features make them unique among both extinct and extant marine reptiles (Massare, 1994; Carpenter et al., 2010), being the only ones with sea-turtles to swim without using an axial undulatory locomotion, relying completely on paraxial propulsion (Storrs 1993). Plesiosauria present a large range of body morphologies characterized by variation in the proportions between head size and neck length, resulting in two general morphotypes (O'Keefe, 2001, 2002): 'plesiosauromorphes' with a long neck and a small head carried to the extreme in some Late Cretaceous elasmosaurids, whose neck, representing 2/3 of their total body length, reached up to 72 cervical vertebrae; 'pliosauromorphes' with a short neck and a large head, with emblematic taxa such as *Liopleurodon* or *Kronosaurus*, whose skull is about 1/3 of their total length. Their diverse morphologies suggest the colonization of numerous feeding guilds. A recent study (Bernard et al., 2010) has shown that they were most likely 'warm-blooded'. The combination of unusual body plans, various morphologies and a peculiar palaeobiology certainly explains the evolutionary success of Plesiosauria in the open marine realm and their survival during three quarters of the Mesozoic. Though *Alexyisaurus* and *Thalassiodracon*, the earliest taxa known, come from the Norian and Rhaetian / Hettangian (Sennikov and Arkhangelsky, 2010; Benson et al., 2012), undetermined material from the Middle Triassic (Benton, 1993) as well as the recent reinterpretation of the Carnian *Bobosaurus* as the oldest plesiosaur (Fabbria et al., 2013), extend their fossil record back to at least the Carnian or even the Middle Triassic.

Plesiosaurs highly diversified during the Jurassic and achieved a cosmopolitan distribution as early as the Early Jurassic, being known mainly in the Tethys Realm (Europe, China) but also by isolated remains from Canada, Australia and Chile. Except the genera *Leptocleidus*, *Libonectes*, *Aristonectes*, *Tuarangisaurus* and *Mauisaurus*, which had a cross-oceanic distribution (see Table 3), most plesiosaur genera appear to have been rather endemic, their known occurrences being restricted to some basins (e.g. *Dolichorhynchops*; see Table 2). The numerous Mesozoic extinction events (Bakker, 1993) did not seem to strongly affect them as they remained taxonomically and ecologically diverse and geographically widespread up to their final extinction at the end of the Cretaceous (Vincent et al., 2011, 2013b).

3.4. Testudinata (Fig. 5, Table 4 in Appendix)

Turtles (crown Testudinata) are one of the most successful clade of reptiles, with a long evolutionary history originating into the Triassic and carrying on today. They are known by hundreds of fossil and living taxa, distributed in most environments except those corresponding to the coldest areas of the Earth. Turtles are characterized by an exclusive Bauplan incorporating the development of a shell, so that the girdle elements are located inside the ribcage. They are the only marine reptiles with plesiosaurs (see above) to use ‘underwater flight’ as a mode of swimming. Both the phylogenetical relationships of turtles among sauropsids (anapsids versus derived diapsids, e.g. Lee, 1997; Rieppel and Reisz, 1999) as well as their ecological origin (see below) gave rise to numerous hypotheses. Some authors indeed proposed that the first turtles evolved in aquatic environments (e.g. Rieppel and Reisz, 1999) whereas others indicated that this clade originated in terrestrial ones (e.g. Lee, 1996). One of the most recent parsimonious hypothesis considers a terrestrial origin for them, rooted in the Permian (Anquetin, 2009; Lyson et al., 2013). Despite this possible terrestrial origin, several lineages of turtles evolved, early and independently in their history, aquatic abilities, the basal *Odontochelys* from the Early Carnian of China representing the earliest known marine turtle (Li et al., 2008; Reisz and Head, 2008). Within the crown group Testudines, several lineages of both Pan-Cryptodira and Pan-Pleurodira were also adapted to live in marine environments.

Among Pan-Cryptodira, three basal groups of Eucryptodira are exclusively known in Late Jurassic coastal marine environments of Europe: Eurysternidae, Plesiochelyidae and Thalassemydidae (Lapparent de Broin et al., 1996). The record of Plesiochelyidae and Eurysternidae is very abundant, illustrating a wide systematical diversity (Joyce, 2000; Lapparent de Broin, 2001; Pérez-García, in press). Eurysternids probably lived in brackish waters whereas plesiochelyids have been recognized as truly marine organisms based on a series of taphonomical, geochemical and anatomical arguments (see Broin, 1994; Billon-Bruyat et al., 2005). The limbs of Plesiochelyidae which are not totally modified into paddles indicate that these turtles were not adapted to a pelagic life (Lapparent de Broin et al., 1996, Billon-Bruyat et al., 2005). These three groups disappeared during the Jurassic-Cretaceous transition, probably as a result of the regression restricted to the European shallow sea-shelf, which drastically reduced their habitats (Bardet, 1994; Pérez-García, 2012; Pérez-García et al., 2013). Another Eucryptodira incertae sedis, *Neusticemys*, corresponding to a probable inhabitant of protected marine environments, was found in the Pacific Realm, namely in the Tithonian of Argentina (de la Fuente and Fernández, 2010).

The most sucessful clade of marine turtles corresponds to a monophyletic group of the crown Cryptodira, the Pan-Chelonioidea, identified in the fossil record as early as in the Early Cretaceous (Aptian) (Nicholls, 1997; Parham and Pyenson, 2010). It rapidly radiated during the Cretaceous, being one of the rare groups of marine reptiles that survived the K-Pg extinction event. It is still represented today by five genera and six species of Cheloniidae, and by one of Dermochelyidae (Meylan, 2006a). It is noteworthy that Pan-Chelonioidea shows a much higher morphological, systematical and presumed ecological diversity during the Cretaceous than during the Cenozoic and today (Hirayama, 1997). Pan-Chelonioidea includes two probably basal clades of bottom-dwelling turtles, inhabitants of near-shore marine environments: the Sandownidae (Tong and Meylan, 2013), known from the Aptian to the Palaeocene along the North American, European and African Atlantic coasts, and whose evolutionary history has been suggested as connected to the development of the Atlantic

Ocean; and the clade *Toxochelys-Ctenochelys* (Brinkman et al., 2006; Parham and Pyenson, 2010), exclusively known from the Late Cretaceous of North America.

Chelonioidea is defined by the elongation and modification of the forelimbs into large paddles, used as propulsive organs for 'underwater flight'. This and other morphological (e.g. reduction of the shell ossification) and physiological (e.g. development of a broad interorbital opening accommodating a large salt gland) adaptations allowed this clade to be the only one with a pelagic lifestyle, being identified as 'true' sea-turtles (Hirayama, 1997; Nicholls, 1997; Anquetin, 2009). Chelonioids are divided into two major clades, the Dermochelyoidea (Protostegidae and Dermochelyidae) and the Pan-Cheloniidae (whose crown group is Cheloniidae). Protostegidae are known from at least the Aptian, being the most dominant group of Pan-Chelonioidea until the Turonian, with a worldwide record except in Antarctica (Hirayama, 1997). This group includes most of the known largest turtles (e.g. *Protostega* and *Archelon*), whose carapace length exceeded two meters. Protostegidae drastically declined during the Late Cretaceous, probably becoming extinct shortly before the end of the Cretaceous (Meylan, 2006a). Some members of the Protostegidae were probably cosmopolitan (e.g. *Desmatochelys* and *Protostega*). In contrast, despite the wide Cenozoic and current geographical distribution of both Cheloniidae and Dermochelyidae, most of them had a limited distribution area during the Cretaceous (Hirayama, 1997). The wide diversity of these two groups, much higher than that recognized in the Cenozoic, may be a result of this endemism, contrasting with the cosmopolitan distribution of the extant taxa (Hirayama, 1997; Meylan, 2006b).

Pan-Pleurodira also developed marine representative along their evolutionary history, though none of them reached the high degree of marine adaptation and the diversity exemplified by pan-chelonioids. During the Late Jurassic-Early Cretaceous interval, a basal monophyletic clade of shallow-marine turtles with a wide palaeobiogeographical distribution is known, including taxa in Europe, Cuba, Argentina and Colombia (Lapparent de Broin et al., 2007; Cadena et al., 2013).

All living representatives of the crown Pleurodira inhabit freshwater environments. However, during the Late Cretaceous-Early Palaeogene interval, some members of the Bothremydidae invaded the sea, occupying coastal and shallow marine niches on both sides of the opening Atlantic, and in the Mediterranean Tethys (Nicholls, 1997; Moody, 1997; Lapparent de Broin and Werner, 1998). Some genera, such as *Bothremys* and *Taphrosphys*, have a relatively abundant record and wide distribution, being known in North America, Africa, the Middle East and Europe (Broin, 1977; Bardet et al., 2000; Gaffney et al., 2006).

3.5. Crocodyliformes (Fig. 6, Table 5 in Appendix)

Crocodyliforms is a large clade of reptiles known since the Triassic (Norian). Of this flourishing past diversity, only one group survives today, that is the crocodylians represented by crocodiles, alligators and gavials, i.e., at least 23 species in total. Crocodiles represent the largest extant reptilian predators, ranging in size from less than 2 m to more than 8 m. They are characterized by a broad body with short legs, a long muscular tail and the possession of a thick skin-bearing osteoderms. All living crocodiles are semi-aquatic animals restricted to tropical belts and only one, *Crocodylus porosus*, spends time in the marine realm.

During the Mesozoic, crocodyliforms diversified in nearly all environments, whether terrestrial, freshwater or marine. Four clades of fossil crocodyliforms (Pholidosauridae, Crocodylia, Dyrosauridae, Thalattosuchia) were found in marine sediments and dyrosaurids and thalattosuchians are almost exclusively marine forms. Thalattosuchians are the most interesting for palaeobiogeographical purposes (see Discussion). They are often considered as closely related to other longirostrine crocodyliformes, Pholidosauridae and Dyrosauridae, but these phylogenetical relationships remain debated (Jouve, 2009; Pol and Gasparini, 2009; Wilberg, 2012).

Thalattosuchians are traditionally divided into two groups (e.g. Kälin, 1955), a view confirmed by recent phylogenetical analyses: the teleosauroids and metriorhynchoids (e.g. Young and Andrade, 2009). All teleosauroids have a long and slender snout suggesting a mainly piscivorous diet, even if the diet of some of them was probably more varied. Their aquatic habits were probably close to those of living species, with limbs, though shorter than in extant species, still allowing them to walk on land. Teleosaurids were particularly diversified during Callovian and Oxfordian times. It is interesting to note that their diversity decreases from the Kimmeridgian while that of metriorhynchoids on the contrary increases and reaches its maximum during the Lower Tithonian (Young et al., 2010). The marine morphology of Metriorhynchoidea was acquired progressively and includes mainly limbs transformed into paddles (Wilberg, 2012), a hypocercal tail in some cases (Young and Andrade, 2009) and the loss of osteoderms. Metriorhynchoid diversity appears high and stable from the Oxfordian to the Kimmeridgian, with a peak during the Early Tithonian (11 species known). This diversity declines sharply at the beginning of the Late Tithonian and continues throughout the Berriasian (Young et al., 2010). The thalattosuchians seem to vanish during the Valanginian. The causes of their extinction remain unknown and could be linked to the Late Tithonian - Early Cretaceous global regression as well as to Early Cretaceous climatic changes, though a bias in the fossil record cannot be discarded.

The palaeobiogeographical distribution of thalattosuchians through time is poorly known and difficult to understand. If most of the Early Jurassic thalattosuchians come from Europe, the oldest remains have been unearthed in the Sinemurian and Pliensbachian of Chile, Argentina, and India (Vignaud, 1995), meaning that thalattosuchians were already widespread at the first stages of their history. The thalattosuchians are mainly present in Europe during the Toarcian-Early Cretaceous interval (see Vignaud, 1995 for an overview), but have been sporadically described from the same interval in Asia, Africa and Oregon (Vignaud, 1995). They are also well known in the Middle-Late Jurassic of the Mexican Gulf (Gasparini, 1992; Gasparini and Iturralde-Vinent, 2006; Young et al., 2010) and the Middle Jurassic-Early Cretaceous of South America (Gasparini et al., 2005, 2008; Young et al., 2010; Herrera et al., 2013; Vignaud, 1995), and more especially in the Late Jurassic-Lower Cretaceous of Argentina (Gasparini et al., 2005) were several taxa were described. The South

American thalattosuchians are particularly significant because they contribute to the knowledge of the history of the passage between the East Pacific and Central Atlantic oceans (see Discussion).

3.6. Rhynchocephalia (Fig. 7, Table 6 in Appendix)

Rhynchocephalia is a long-lived clade of small to medium-sized lepidosauromorphs that was successful during the early Mesozoic. They appear in the fossil record in the Ladinian before diversifying and spreading during the Late Triassic-Jurassic interval; they become much scarcer afterwards and are represented today by only a single species of *Sphenodon* (Jones et al., 2009, 2013). Most of their representatives retained the usual terrestrial reptilian morphology but specializations toward a marine mode of life occurred at least two times during their history: in the Pleurosauridae (Jurassic) and in the Opisthodontia *Ankylosphenodon* (Albian). It has been alleged that Sapheosauridae were also marine forms (Reynoso, 2000), but there is currently little evidence supporting this claim.

The Pleurosauridae represent a small clade of marine reptiles restricted to the Jurassic of the European Archipelago. Compared to terrestrial rhynchocephalians, pleurosaurids are characterized by a triangular skull with posteriorly located external nares and orbits, and a very elongated streamlined body ending in a deep, laterally compressed tail typical of undulatory axial swimmers (Carroll and Wild, 1994; Carroll, 1985; Fabre, 1981). The reduction of the limbs and the weak ossification of the skeleton (Carroll and Wild, 1994; Fabre, 1981) show that they spent more time in water (Jones, 2009). These adaptations, already present in the earliest pleurosaurid *Palaeopleurosaurus* from the Toarcian of Germany (Carroll and Wild, 1994; Carroll, 1985), appear more pronounced in *Pleurosaurus*, a genus typically found in French and German lagoonal Plattenkalke of Kimmeridgian-Tithonian age (Carroll and Wild, 1994; Fabre, 1981). The last marine rhynchocephalian is *Ankylosphenodon*, from the Albian of Mexico (Reynoso, 2000). The presence of *Ankylosphenodon* and of a distant terrestrial relative in the same region of Mexico indicates that what was an island during the Early Cretaceous acted as a refuge area for relictual rhynchocephalians taxa (Reynoso, 2000).

3.7. Squamata (Fig. 8, Table 7 in Appendix)

Squamata, whose earliest confirmed forms were recovered from the Middle Jurassic (Bathonian) (Rage, 2013) are currently the most diversified group of reptiles, being known by more than 9400 species of lizards, snakes and amphisbaens, and represent the second-largest order of vertebrates after perciform teleostean fishes. They are mainly characterised by their scaly skin and mobile quadrate bone that provides movements of the upper jaw relatively to the braincase, permitting to accommodate for large preys. Currently, they are also the most variably sized order of reptiles, ranging from less than 20 mm to over 9 m long and they included in the past much larger fossil taxa (e.g. mosasaurids, see below).

Squamata were the last clade of Mesozoic marine reptiles to invade the marine realm during the Late Cretaceous, from the Early Cenomanian to the latest Maastrichtian. Though restricted in time, as compared to previously mentioned clades, this squamate radiation is probably the most spectacular one in terms of the diversity reached as well as of the ecological niches invaded in this small time interval (about ‘only’ 30 Ma). These Late Cretaceous marine squamates are all part of the Pythonomorpha clade, as originally defined by Cope (1869) and recognized by recent phylogenies (e.g. Lee, 2009; Palci and Caldwell, 2010), that includes Mosasauroidea and Ophidiomorpha.

Mosasauroidea include all taxa previously assigned to the families Aigialosauridae and Mosasauridae. They are mainly characterised by an elongated ‘varanoid’ anguilliform body and large and elongated skull. They display a large range of ecological adaptations illustrated by their body and tooth sizes and morphologies, from small gracile piscivorous to large opportunist top-predators, passing via robust durophagous forms. Along their evolutionary history, they displayed three morphotypes illustrating steps in their gradual adaptation to increasingly open-sea habitats (Bell and Polcyn, 2005; Caldwell and Palci, 2007). Plesiopedal and plesiopelvic mosasauroids (with terrestrial-like limbs and a sacrum) were small (1-2 m long) essentially, if not exclusively, shallow water poorly active swimmers (Houssaye, 2013b). They lived from the Early Cenomanian to the Early Turonian in both margins of the Mediterranean Tethys (Europe, Israel), except *Vallecillosaurus* fom Mexico (see Bardet et al., 2008). Plesiopedal and hydropelvic mosasauroids (with terrestrial-like limbs but no sacrum), are medium sized forms (1.5-3 m long), known only in the Middle Turonian of Morocco and Texas (Bardet et al., 2003; Bell and Polcyn, 2005). They are considered as more active swimmers than the plesiopelvic forms but still not efficient pelagic swimmers (Houssaye, 2008; Houssaye et al., 2013a). Finally, hydropedal and hydropelvic mosasauroids (with flippers and no sacrum), the ‘true mosasaurids’, were large (3-15 m long) open-sea active swimmers able to cross large oceanic realms (Houssaye et al., 2013a). They exhibited large powerful flippers and often a hypocercal tail increasing swimming performances, from an anguilliform to a thunniform locomotion (Lindgren et al., 2011, 2013). They underwent a spectacular radiation during the Late Turonian-Maastrichtian interval, being known by 28 genera and more than 67 species, to reach a cosmopolitan distribution favoured by marine routes largely opened at this time, before to disappear during the K-Pg extinction event (e.g. Jouve et al., 2008).

Late Cretaceous marine Ophidiomorpha include stem-ophidians (e.g. ‘dolichosaurs’, *Pontosaurus*, adriosaurs) and a few Ophidia (Pachyophiidae, Nigerophiidae and Palaeophiidae) (Palci and Caldwell, 2007). The stem-ophidians, long-bodied lizards no more than 1 m long, were all found in near-shore environments, except *Dolichosaurus* and *Coniasaurus,* considered to have also lived in open marine environments. These two taxa (that could be synonymous) lack bone mass increase and are interpreted as surface (or subsurface) swimmers (Houssaye, 2013b), whereas pachyosteosclerotic stem-ophidians are conversely considered shallow water poorly active divers (Houssaye, 2013b). It is noteworthy that all these taxa were restricted geographically to the Mediterranean Tethys Realm (Europe and Middle-East) and stratigraphically to the Lower Cenomanian-Lower Turonian interval, except *Coniasaurus*, also found in the Western Interior Seaway of North America up to the Middle Santonian (see Bardet et al., 2008). Late Cretaceous marine Ophidia include Pachyophiidae (hind-limbed snakes), Nigerophiidae and Palaeophiidae and are all considered as poorly active shallow divers (Houssaye, 2013b). Pachyophiidae were very restricted in both time and space as they all come from the Early to Late Cenomanian of the Mediterranean Tethys (Europe, North Africa, Middle-East). Palaeophiidae, although essentially occurring in the Cenozoic (Houssaye et al., 2013b), are represented by one specimen of *Palaeophis* in the Maastrichtian of Morocco (Rage and Wouters, 1979). These aquatic snakes likely lived in marine or marginal marine waters (Parmley and DeVore, 2005). During the Mesozoic, the marine Nigerophiidae included *Kelyophis* from the Maastrichtian of Madagascar and *Indophis* from the Maastrichtian of India (LaDuke et al., 2010; Prasad and Rage, 1995).

4. Discussion

At the beginning of the Mesozoic Erea, Pangaea was surrounded by two main oceans, Panthalassa and Tethys. As this time, the main marine routes accessible for marine faunas to disperse were *de facto* peri-Pangaean, Tethyan and trans-Panthalassan. The beginning of the break-up of the Pangaea by Triassic time has permitted the individualization of the continents we are nowadays familiar with, progressively separated through time by increasingly wide marine ways (see Blakey, 2008). All these marine ways were established across Pangaea as a result of its fragmentation due to sea-floor spreading but also to sea-level rises. They represented suitable dispersal routes for nektonic faunas and have probably played an important role in the distribution patterns of Mesozoic marine reptiles, as will be discussed below. During the Jurassic, several marine corridors (trans-Pangaean) and routes (peri-Pangaean) have been reconstructed on the basis of distribution patterns of marine invertebrates (mainly cephalopods and bivalves) (Hallam, 1994; see Cecca, 2002 for details). Peri-Pangaean routes include the Boreal Route, bordering the northern Pangaea coasts and the Austral Route, bordering the shelves of the southern Pangaea. The main trans-Pangaean corridors are: 1) the Viking Corridor (Westermann, 1993), an epicontinental seaway roughly superimposed to the future North Atlantic rift, which acted as a marine dispersal way by the late Early Jurassic (Pliensbachian or Toarcian); 2) the Mozambique Channel (Enay et al., 1993), linking eastern Africa to the southern Andes via Antarctica, though being probably opened since the Callovian, becomes fully effective by the Tithonian; 3) the Hispanic Corridor (Smith, 1983) stretching roughly along the Central Atlantic rift in the Caribbean region, exists since at least the Bathonian (Bartolini and Larson, 2001; Gasparini and Iturralde-Vinent, 2006), but became an effective dispersal route by the Oxfordian (Westermann, 1993). By the dawn of the Early Cretaceous, the Central Atlantic was becoming a mature ocean, the Tethys connected with the Atlantic, and continental rifting leading to the formation of the South Atlantic was initiated between South America and southern Africa (see Blakey, 2008). During the 'middle' Cretaceous, the break-up of the Gondwana was nearly complete with the separation of India from Madagascar, followed by that of Antarctica and Australia; at that time, one of the most extensive and rapid episodes of sea floor spreading produced rapid dispersal of continents and an extensive epicontinental flooding (see Blakey, 2008), thus creating large seaways.

The early acquisition of aquatic adaptations toward a pelagic lifestyle permitted ichthyosaurs to rapidly conquer a wide biogeographic range (Fig. 2). During the Early Triassic, in the absence of intracontinental seaways, ichthyosaurs were seemingly restricted to the northern Pangaean coasts. Their presence in Middle Triassic strata of Europe suggests that they reached the Western Tethys probably via the Tethyan shores. Shastasaurid ichthyosaurs are the first clade to colonize the entire oceans of the Late Triassic, possibly because of their gigantic, baleen whale-like body plan rather than the existence of dispersal routes. By at least the Early Jurassic, the intra-Pangaean seaways probably allowed repeated faunal exchanges, especially between western Pangaean coasts and the European archipelago. Phylogenetic analyses imply at least two major dispersal events during which parvipelvian lineages reached western Pangaea, evolved new forms there and then replaced ancestral Tethyan faunas: early parvipelvians by the Late Triassic (Motani, 1999b) and early ophthalmosaurids by the early Middle Jurassic (Fernández, 2003). Ophthalmosaurid ichthyosaurs then maintained a global distribution for the last 70 million years of their reign, probably because of the conjunction of three factors: their swimming-efficient body plan, the elevated sea levels, and the dispersed landmasses. Indeed, the newly opened seaways issued from the Pangaea fragmentation, like the Viking and Hispanic corridors during the Jurassic, as well as the South Atlantic and other southern ways derived from the break-up of the southern Gondwana during the early Cretaceous permitted dispersal across nearly all latitudes. Yet, the recent discovery of a long-lived lineage of non-ophthalmosaurid ichthyosaurs whose only record after the Early Jurassic is the Early Cretaceous of Iraq (Fischer et al., 2013), indicate that the palaeobiogeographic history of parvipelvian ichthyosaurs is probably more complex than long imagined.

Thalattosaurs are first known in the Early Triassic of the western coast of the Pangaea. Then, the Middle Triassic global transgression favoured the diversification of Middle and Late Triassic askeptosauroids and thalattosauroids (Fig. 3) in facilitating their dispersal from the Eastern Panthalassa to the Tethys Realm. While they were probably near-shore inhabitants not fully adapted for a pelagic life, both groups had a remarkable transoceanic disjunctive distribution, which implies that the relationships of the East Pacific, European, and Southern China provinces were more complex during the Triassic than previously thought.

Remains of the Early Triassic sauropterygians (Fig. 4) were found only in low paleolatitudes: eastern Panthalassa, as well as western and eastern parts of the Tethys. This pan-oceanic distribution indicates that they already conquered oceans with distant connections very early in their evolution. Although trans-oceanic crossing on drifting plant logs cannot be excluded, it seems highly unlikely that this pan-oceanic dispersal was reached by ocean-cruising animals. Indeed, early sauropterygians were probably near-shore ocean-dwellers relatively poorly adapted to open oceanic conditions (Scheyer, 2007). As a result, they probably dispersed along coastal areas and shallow marine platforms, mainly of the Tethys Ocean where their remains essentially come from. Given the absence of low latitude marine connections between the Pantalassa and Tethys oceans at this time, such dispersal possibly took place through the high-latitude Arctic area, via the Boreal route (see Hallam, 1994). Evidence for exceptionally warm conditions in this area during the Early Triassic (Brayard et al., 2007) gives support to this hypothesis. Special attention is paid here to placodonts, typical inhabitants of coastal environments of the Tethys Ocean, especially its western part where most of their remains were found (Europe, North Africa, Middle-East). It is probable that the combination of both biological characteristics (they were pachyostotic durophagous bottom-dwellers) and favourable palaeoenvironmental conditions (the Western Tethys was a warm and shallow marine region at this time) could explain that they only slightly dispersed and remained restricted to the Tethys Ocean shores, from China to Europe. Upper Triassic plesiosaur occurrences are only known in the Northern hemisphere and are very scarce, possibly in relation to the rarity of Norian and Rhaetian open-marine strata, due to the low sea level during this time interval (Haq et al., 1987). It is thus difficult to trace back the possible origin of this clade. Geographically, the oldest plesiosaurs (*Alexyisaurus*) come from the Norian of Arctic Russia but their origin could be older if *Bobosaurus* (Carnian of Italy) is considered as belonging to this clade (Sennikov and Arkhangelsky, 2010; Fabbria et al. 2013). Other plesiosaurian remains from the Triassic are non-diagnostic (Storrs, 1994; Benton, 1993). As soon as the Early Jurassic, plesiosaurs reached a noteworthy cosmopolitan distribution, being particularly numerous in Europe but also present at high latitude, such as in Australia, Chile and Canada (Kear, 2012; Nicholls, 1976; Gasparini, 1992). This cosmopolitan distribution coincides with a global sea-level rise (Haq et al., 1987), as well as with the global fragmentation of the Pangaea and the opening of new marine corridors and ways, like the Hispanic and Viking Corridors, and later the South Atlantic. Like ichthyosaurs, plesiosaurs were both morphologically and physiologically (Bernard et al., 2010) adapted to long distance cruising and these biological characteristics, coupled with the geological constraints previously mentioned, are probably responsible for their high capacity of dispersal resulting in their cosmopolitan distribution as soon as the early stages of their evolution. On the contrary, it is interesting to note that the latest Cretaceous plesiosaurs, despite being highly diversified and distributed worldwide, as shown by their occurrence in shallow marine environments of both hemispheres, from polar to equatorial palaeolatitudes, were characterized by a quite high degree of endemism (see details in Vincent et al., 2011).

Thalattosuchian crocodyliforms are of particular interest to understand the chronological sequences of the opening of the Hispanic Corridor, which has been debated for a long time. Indeed, while the geological record does not support the existence of this corridor before the Bathonian (Bartolini and Larson, 2001) and its effectiveness from the Oxfordian onward (Westermann, 1983), biogeographical arguments based on the distributions and affinities of the Early Jurassic Western Tethys and the Eastern Panthalassa invertebrate faunas (ammonites and bivalves) suggest that this corridor was possibly effective, at least sporadically, as early as in the Pliensbachian (Smith, 1983) (see Cecca, 2002 for a detailed review). In this context, marine crocodyliforms provide evidence consistent with an early activitation of this corridor as a marine dispersal way for pelagic marine faunas. Indeed, some thalattosuchian remains unidentified at the familial level found in both the Sinemurian of Chile and Argentina, suggest at least a sporadic opening of the Hispanic Corridor during the Lower Jurassic, and thus earlier as previously thought (Fig. 5). However, the identification of these remains either as teleosauroids or as metriorhynchoids could be of palaeobiogeographic importance, as the former were probably more terrestrial animals than the later. Thus, if a continental passage between the Central Atlantic and the eastern Pacific could be envisaged for teleosauroids, using ‘jumping’ between flooded areas, this dispersal pattern is less probable for fully aquatic metriorhynchoids for which it would imply the existence of a seaway. The presence of confirmed metriorhynchoids in the Bajocian and Bathonian of Argentina (Gasparini et al., 2005, 2008) suggests an effective passage from this interval onward.

Although some early representatives of the stem group of Testudines were adapted to life in water (Reisz and Head, 2008), they lacked the morphological adaptations required for an open-sea global distribution. The first important radiation of ‘marine turtles’ occurred in the Late Jurassic (Fig. 6). At that time, several European basal members of Eucryptodira (e.g. the abundant and diverse members of Plesiochelyidae) were apparently restricted to near-shore environments of the western part of the Tethys (Europe), being not morphologically adapted for large-scale dispersal in the marine realm (Lapparent de Broin et al., 1996). The South American *Neusticemys* cannot be recognized as a form related to these European taxa or to the so far known representatives of that clade. Another contemporaneous clade, composed of basal member of the Pan-Pleurodira, is recognized in Europe, the Caribbean and South America. This large distribution implies that during the Oxfordian, a marine seaway (i.e. the Hispanic Corridor) may have occurred in the Caribbean, connecting the Western Tethys with the Pacific Ocean (de la Fuente and Iturralde-Vinent, 2001; Cadena and Gaffney, 2005). Several lineages of Pan-Chelonioidea (the ‘true’sea turtles) are identified from the Early Cretaceous; as soon as they appear in the fossil record, they exhibit a large distribution pattern, being known in the Tethys Ocean, the Western Interior Seaway of North America and on both sides of the proto-South Atlantic Ocean. This clade was very abundant and diverse during the Late Cretaceous and still occurs nowadays. Many lineages of Late Cretaceous Pan-Chelonioidea fully adapted to life in open-marine environments and exhibit wide distributions pattern, being often cosmopolitan (Hirayama, 2007). They probably used the marine routes widely opened during the Late Cretaceous to disperse. However, if we consider these Cretaceous-Palaeocene Pan-Chelonioidea in details, their palaeobiogeographical distribution appears rather limited, most genera being endemic, unlike their modern relatives that have a cosmopolitan distribution (Hirayama, 1997; Hirayama and

Tong, 2003). This suggests that their dispersal was probably limited by biological or ecological constraints (Bardet, 2012).

In spite of their advanced adaptations for an aquatic life, pleurosaurid rhynchocephalians were restricted to a narrow peri-Alpine area of the European Archipelago (Fig. 7). This is even more striking during the Late Jurassic, with *Pleurosaurus* being limited to tropical shallow lagoonal deposits. The dispersal of pleurosaurids inside and outside the Western Tethys was likely limited because of strong ecological constraints such as environmental preferences or dietary specializations. It was once suggested that pleurosaurids fed on dead animals that would have not tolerated the high salinity of they lagoons they lived in (Fabre, 1981), but their dentition indicates a rather omnivorous diet (Jones, 2009). In any case, it seems that pleurosaurids strongly depended on their environment as their extinction at the end of the Jurassic coincides with the disappearance of French and German peri-Alpine tropical lagoons.

An important diversity of squamate taxa occurs in marine environments at the early Late Cretaceous (Fig. 8). This radiation is sudden and probably associated with the transgression event that created many fairly warm shallow carbonate plateform environments (Bardet et al., 2008; Jacobs et al., 2005; Rage, 2013). Most of the Cenomanian pythonomorphs are restricted to the Mediterranean part of the Tethys, essentially to its Northern margin, apart from *Coniasaurus* that dispersed and reached the Western Interior Seaway of North America, where it survived up to the Santonian. This endemism is surprising as no physical barrier prevented these taxa from dispersing. However, most of them, notably because of bone mass increase, are considered poorly active swimmers and could thus probably not become widespread beyond the carbonate plateforms they were living in. It is interesting to note that bone mass increase did not affect *Coniasaurus* for which a mode of life similar to that of the pelagic snake *Pelamis*, only extant marine snake with a broad distribution, was suggested (Houssaye, 2013b). Most marine pythonomorphs disappeared at the Cenomanian-Turonian boundary, which is probably related to the reduction of their habitat (Bardet et al., 2008). Conversely, one group underwent a spectacular radiation at that time: the hydropedal mosasauroids. On both thermophysiological and histological evidences (Bernard et al., 2010; Houssaye and Bardet, 2012; Houssaye et al., 2013a), these taxa are interpreted as efficient pelagic swimmers and were thus probably able to disperse along long distances. Indeed, from Turonian to Maastrichtian times, 'true' mosasauroids disperse globally. It seems that they initially dispersed in the Mediterranean Tethys westward, probably using palaeocurrents active at that time (see Bardet et al., 2008). From the Turonian their distribution can be considered as pandemic, as they were found in Africa, South America, Europe and North America and they Santonian to Maastrichtian interval they ecame cosmopolitan, their remains having being unearthed from all continents, including Antarctica. Contrary to Pan-chelonioid turtles and plesiosaurs that, though having a global distribution at high taxonomical level show a rather high degree of endemism at the generic one, most mosasaurid genera exhibit a very large distribution pattern (e.g. *Mosasaurus*, *Tylosaurus*, *Prognathodon*, etc.). However, in some specific cases, it appears that their distribution could have been influenced by latitudinal gradients, as demonstrated for the faunas from the Western Interior Seaway of North America (Nicholls and Russell, 1990), the Northern and Southern margins of the Mediterranean Tethys (Bardet, 2012) and the Weddelian Province (Martin and Fernández, 2007); this suggests that their biological characteristics could be responsible for and have influenced their ecological preferences.

5. Conclusion

From all the data outlined above, the following conclusions can be drawn. Firstly, it is noteworthy that most Mesozoic marine reptile clades exhibit a cosmopolitan, or at least pandemic, distribution very early in their evolutionary history. The acquisition of morphological adaptations to a fully aquatic life (see Houssaye, 2009), combined with special thermophysiological characteristics (Bernard et al., 2010; Houssaye, 2013a), are probably responsible for these animals to become efficient open-marine cruisers. Secondly, most of these groups switched from a peri-Pangaean shelf distribution (Panthalassa and Tethys near-shore environments) to a global one, probably thanks to the marine ways opening from the break-up of Pangaea, as attested for other nektonic marine faunas. They probably firstly used peri-Pangaean routes like the *Boreal Route* during the Triassic, as exemplified by ichthyosaurs, thalattosaurs and sauropterygians, then the trans-Pangaean marine corridors like the *Hispanic Corridor* during the Jurassic (see Gasparini and Fernández, 2005 for details), and finally the largely opened ‘true’ oceanic ways (Atlantic Ocean) during the Late Cretaceous, as exhibited by mosasaurs, plesiosaurs and chelonians. However, despite this global distribution, some taxa exhibit a certain degree of endemism when a lower taxonomical rank is used. This is for example the case for Cretaceous ichthyosaurs, plesiosaurs and chelonians (Vincent et al., 2011; Hirayama and Tong, 2003; Fischer et al., in press). Others, like mosasaurs (see Bardet, 2012), though exhibiting a remarkably global distribution, show at specific level parceling patterns likely linked to palaeolatitudinal gradients, for example in the Western Interior Seaway (Nicholls and Russell, 1990) and in the Mediterranean Tethys (Bardet, 2012), where the faunas differ from North to South. Finally, some groups, such as placodonts during the Triassic, pleurosaurid rhynchocephalians and basal Testudines during the Late Jurassic, as well as ophidiomorph squamates during the early Late Cretaceous, appear endemic to the Western Tethys. Specific biological characteristics like bone mass increase and ecological/ethological preferences or constraints (e.g. palaeotemperatures, food resources) could be responsible for these distributional patterns. To sum up, the break-up of the Pangaea during the Mesozoic Era has played a key role in the distribution patterns observed in marine reptiles, which process here is assumed to mainly be dispersal. A certain endemism is however recorded for some groups, depending on the taxonomical rank used.

Acknowledgments

This paper was written following an invitation from M. Santosh, Editor-in-Chief of Gondwana Research. We warmly thank him for his interest in our work. We are also thankful to the Editorial Board of Gondwana research, more especially to T.J. Horscroft, for providing useful informations and quick answers to all our questions. This work was originally presented as a tribute to Alfred Wegener in the 4th International Geologica Belgica Meeting (Brussels, september 2012), organized under the general theme '**Moving plates and melting icecaps - Processes and forcing factors in geology'** to celebrate the centenary of Alfred Wegener's first paper on the concept of Continental Drift (Wegener, 1912). N.B. especially thanks R. Blakey (Northern Arizona University, Flagstaff, USA) for the interchange of useful informations concerning his palaeogeographical maps as well as for his courtesy and kindness. A. Houssaye and P. Vincent acknowledge financial support from the Alexander von Humboldt Foundation and X. Pereda Suberbiola from the Ministerio de Economía y Competitividad of Spain (project CGL2010-18851/BTE) and the Gobierno Vasco/Eusko Jaurlaritza (group IT834-13). Finally, we thank the referees Z. Gasparini (La Plata, Argentina) and Anne Schulp (Leiden, The Netherlands) for their constructive reviews that permitted to improve the manuscript.

References

Adams, T.L., 2009. Deposition and taphonomy of the Hound Island Late Triassic vertebrate fauna: fossil preservation within subaqueous gravity flows. Palaios 24, 603–615.

Anquetin, J., 2009. A new stem turtle from the Middle Jurassic of the Isle of Skye, Scotland, and a reassessment of basal turtle relationships. University College London and The Natural History Museum. Phd dissertation. 287 pp.

Bakker, R.T., 1993. Plesiosaur Extinction Cycles-Events that Mark the Beginning, Middle and End of the Cretaceous, In: Caldwell, W.G.E., Kauffman, E.G. (Eds.), Evolution of the Western Interior Basin: Geological Association of Canada, Special Paper, Stittsville, Ontario, Canada, pp. 641–664.

Bardet, N., 1992. Stratigraphic evidence for the extinction of the ichthyosaurs. Terra Nova 4, 649–656.

Bardet, N., 1994. Extinction events among Mesozoic marine reptiles. Historical Biology 7, 313–324.

Bardet, N., 1995. Evolution et extinction des reptiles marins au cours du Mésozoïque. Palaeovertebrata 24, 177–283.

Bardet, N., Cappetta, H., Pereda Suberbiola, X., Mouty, M., Al Maleh, A.K., Ahmad, A.M., Khrata, O., Gannoum, N., 2000. The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. Geological Magazine 137, 269–290.

Bardet, N., Pereda Suberbiola, X., Jalil, N.-E., 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. C. R. Palevol 2, 607-616.

Bardet, N., Houssaye, A., Pereda Suberbiola, X., Rage, J.C., 2008. The Cenomanian-Turonian (Late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. Bulletin de la Société Géologique de France 179, 605-622.

Bardet, N., 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: a palaeobiogeographical approach. Bull. Soc. Geol. France 183, 6, 573-596.

Bartolini, A., Larson, R., 2001. Pacific microplates and the Pangea supercontinent in the Early-Middle Jurassic. Geology 29, 735-738.

Bell, G.L.J., Polcyn, M.J., 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84, 177-194.

Benson, R.B.J., Butler, R.J., 2011. Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases, in: McGowan, A.J., Smith (Eds.), Comparing the Geological and Fossil Records: Implications for Biodiversity Studies, Geological Society, London, Special Publications, pp. 191–208.

Benson, R.B., Butler, R.J., Lindgren, J., Smith, A.S., 2010. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting the vertebrates. Proc. R. Soc. B. 277, 829–834.

Benson R.B.J., Evans M. & Druckenmiller P.S. 2012. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. PLoS ONE 7: e31838.

Benton, M.J. 1993. Reptiles. 681-715. In: Benton, M.J. (Ed.). The Fossil Record 2. Chapman and Hall, London, 845 pp.

Benton, M.J., Zhang, Q., Hu, S., Chen, Z.-Q., Wen, W., Liu, J., Huang, J., Zhou, C., Xie, T., Tong, J., Choo, B., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Science Reviews 125, 199–243.

Bernard A., Lécuyer C., Vincent P., Amiot R., Bardet N., Buffetaut E., Cuny G., Fourel F., Martineau F., Mazin J.-M. & Prieur A. 2010: Regulation of body temperature by some Mesozoic marine reptiles. Science 328, 1379–1382.

Billon-Bruyat, J.-C., Lécuyer, C., Martineau, F., Mazin, J.M., 2005. Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles, and crocodilians. Palaeogeography, Palaeoclimatology, Palaeoecology 216, 359–375.

Blakey, R., 2008. Gondwana paleogeography from assembly to breakup—A 500 m.y. odyssey. In: Fielding, C.R., Frank, T.D., and Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space, 1–28, Geological Society of America Special Paper 441.

Brayard, A., Escarguel, G., Bucher, H., 2007. The biogeography of Early Triassic ammonoid faunas: clusters, gradients, and networks. Geobios 40, 6, 749–765.

Brinkman, D.D., Xijin, Z., Nicholls, E.L., 1992. A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada. Palaeontology 35, 465–474.

Brinkman, D., Hart, M., Jamniczky, H., Colbert, M., 2006. *Nichollsemys baieri* gen. et sp. nov, a primitive chelonioid turtle from the late Campanian of North America. Paludicola 5, 111–124.

Broin, F. de, 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle C38, 1–366.

Broin, F. de, 1994. Données préliminaires sur les chéloniens du Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France). Géobios, Mém. Spéc. 16, 167–175.

Buffetaut, E., Lauverjat, J., 1978. Un crocodilien d'un type particulier dans le Cénomanien de Nazaré (Portugal). Comptes Rendus sommaires des Séances de la Société Géologique de France 1976, 78–82.

Cadena, E.A., Gaffney, E.S., 2005. *Notoemys zapatocaensis*, a new side-necked turtle (Pleurodira: Platychelyidae) from the Early Cretaceous of Colombia. American Museum Novitates 3470, 1–19.

Cadena, E.A., Jaramillo, C.A., Bloch, J.I., 2013. New material of the platychelyid turtle *Notoemys zapatocaensis* from the Early Cretaceous of Colombia; implications for understanding Pleurodira evolution, In: Brinkman, D. Holroyd, P., Gardner J. (Eds.), Morphology and Evolution of Turtles: Vertebrate Paleobiology and Paleoanthropology, Springer, pp. 105–120.

Caldwell, M.W., Palci, A., 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. Journal of Vertebrate Paleontology 27, 863–-880.

Carpenter, K., Sanders, F., Reed, B., Reed, J., Larson, P.,2010. Plesiosaur swimming as interpreted from skeletal analysis and experimental results. Transactions of the Kansas Academy of Science 113, 1–2, 1–34.

Carroll, R.L., 1985. A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeontographica Abteilung A 189, 1–28.

Carroll, R.L., Dong, Z.-M., 1991. *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. Philosophical Transactions of the Royal Society B: Biological Sciences 331, 131–153.

Carroll, R.L., Wild, R., 1994. Marine members of the Sphenodontia, in: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge & New York, pp. 70–83.

Cecca F., 2002. Palaeobiogeography of marine fossil invertebrates – concepts and methods. Taylor & Francis, London, 273 pp.

Chinsamy, A., Martin, L.D., Dobson P., 1998. Bone microstructure of the diving *Hesperornis* and the volant *Ichthyornis* from the Niobrara Chalk of western Kansas. Cretaceous Research 19, 2, 225–233.

Clark, J.A., 2004. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: ornithurae). Bulletin of the American Museum of Natural History Number 286, 1-179.

Cope, E.D., 1869. On the reptilian orders Pythonomorpha and Streptosauria. Proc. Boston Soc. Nat. Hist., 12, 250–266.

Dalla Vecchia, F.M., 1994. Reptile remains from the Middle-Upper Triassic of the Carnic and Julian Alps (Friuli-Venezia Giulia, northeastern Italy). Gortania, Atti del Museo Friulano di Storia Naturale 15, 49–66.

DeBraga, M., Reisz, R.R., 1995. A new diapsid reptile from the uppermost Carboniferous (Stephanian) of Kansas. Palaeontology 38, 199–212.

De la Fuente, M.S., Fernández, M.S., 2010. An unusual pattern of limb morphology in the Tithonian marine turtle *Neusticemys neuquina* from the Vaca Muerta Formation, Neuquén Basin, Argentina. Lethaia 44, 15–25.

De la Fuente, M. S., Iturralde-Vinent, M., 2001. A new pleurodiran turtle from the Jagua Formation (Oxfordian) of Western Cuba. Journal of Paleontology 75, 860–869.

Druckenmiller, P.S., Hurum, J., Knutsen, E.M., Nakrem, H.A., 2012. Two new ophthalmosaurids (Reptilia: Ichthyosauria) from the Agardhfjellet Formation (Upper Jurassic: Volgian/Tithonian), Svalbard, Norway. Norwegian Journal of Geology 92, 311–339.

Enay, R., Bellion, Y., Cariou, E., Guiraud, R., Mangold, C., Ricou L.E., Thierry, J., 1993. Callovian. In: Dercourt, J. Ricou, L.E., Vrielynck, B. (Eds.), Atlas Tethys Palaeoenvironmental Maps. BEICIP-FRANLAB, Rueil-Malmaison.

Fabbria M., Dalla Vecchia F.M. & Cau A. 2013. New information on Bobosaurus forojuliensis (Reptilia: Sauropterygia): implications for plesiosaurian evolution. Historical Biology.

Fabre, J., 1981. Les rhynchocéphales et les ptérosauriens à crête pariétale du Kiméridgien supérieur-Berriasien d'Europe occidentale: le gisement de Canjuers (Var-France) et ses abords. Fondation Singer-Polignac, Paris.

Fernández, M., 2003. Ophthalmosauria (Ichthyosauria) forefin from the Aalenian-Bajocian boundary of Mendozo Province, Argentina. J. Vertebr. Paleontol. 23, 691–694.

Fischer, V., Guiomar, M., Godefroit, P., 2011. New data on the palaeobiogeography of Early Jurassic marine reptiles: the Toarcian ichthyosaur fauna of the Vocontian Basin (SE France). Neues Jahrbuch für Geologie und Paläontologie 261, 111–127.

Fischer, V., Maisch, M.W., Naish, D., Liston, J., Kosma, R., Joger, U., Krüger, F.J., Pardo-Pérez, J., Tainsh, J., Appleby, R.M., 2012. New ophthalmosaurids from the Early Cretaceous of Europe demonstrate extensive ichthyosaur survival across the Jurassic–Cretaceous boundary. PLoS ONE 7, e29234.

Fischer, V., Appleby, R.M., Naish, D., Liston, J., Riding, J.B., Brindley, S., Godefroit, P., 2013. A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. Biology Letters 9, 20130021.

Fischer, V., Bardet, N., Guiomar, M., Godefroit, P., 2014. High Diversity in Cretaceous Ichthyosaurs from Europe Prior to Their Extinction. PLoS ONE 9, e84709.

Fröbisch, N.B., Sander, P.M., Rieppel, O., 2006. A new species of *Cymbospondylus* (Diapsida, Ichthyosauria) from the Middle Triassic of Nevada and a re-evaluation of the skull osteology of the genus. Zool. J. Linn. Soc. 147, 515–538.

Gaffney, E.S., Tong, H., Meylan, P.A., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300, 1–700.

Gasparini, Z.B., 1992. Marine reptiles from the circum-Pacific region. In: Westermann, G.E.G. (Ed.), The Jurassic of the Circum Pacific. Cambridge University Press. Cambridge University Press, Cambridge, pp. 361–364.

Gasparini, Z., Fernández, M., 2005. Jurassic marine reptiles of the Neuquén Basin: records, faunas and their palaeobiogeographic significance. In: Veiga, G. D., Spalletti, L. A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society, London, Special Publications, 252, 279–94.

Gasparini , Z., Iturralde-Vinent, M. 2006 The Cuban Oxfordian herpetofauna in the Caribbean Seaway. Neues Jahrbuch für Mineralogie und Paläontologie Abhandlungen, 240(3), 343-371.

Gasparini, Z.B., Cichowolski, M., Lazo, D.G., 2005. First record of *Metriorhynchus* (Reptilia: Crocodyliformes) in the Bathonian (Middle Jurassic) of the eastern Pacific. Journal of Paleontology 79, 801–805.

Gasparini, Z., Paulina-Carabajal, A., Chong, G., 2008. Un nuevo espécimen de cocodrilo marino del Jurásico Medio del norte de Chile: revalidación de *Metriorhynchus westermanni* (Crocodyliformes: Metriorhynchidae). Revista geológica de Chile 35, 335–346.

Gozzi, E., Renesto, S., 2003. A complete specimen of *Mystriosuchus* (Reptilia, Phytosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). Rivista Italiana di Paleontologia e Stratigrafia 109, 475–498.

Hallam, A., 1994. An outline of Phanerozoic Biogeography. Oxford University Press.

Haq, B.U., Hardenbol, J., Vail, P.R. 1987. Chronology of fluctuating sea levels 826 since the Triassic. Science 235, 1156–1167.

Herrera, Y., Gasparini, Z., Fernández, M.S., 2013. A new Patagonian species of *Cricosaurus* (Crocodyliformes, Thalattosuchia): first evidence of *Cricosaurus* in Middle–Upper Tithonian lithographic limestone from Gondwana. Palaeontology 56, 663–678.

Hirayama, R., 1997. Distribution and diversity of Cretaceous chelonioids, In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient marine reptiles: Academic Press, San Diego, pp. 225-241.

Hirayama, R., Tong, H., 2003. *Osteopygis* (Testudines: Cheloniidae) from the Lower Tertiary of the Ouled Abdoun phosphate basin, Morocco. Palaeontology, 46, 845-856.

Houssaye, A., 2008. A preliminary report on the evolution of the vertebral microanatomy within mosasauroids (Reptilia, Squamata), In: MJ, E. (Ed.), Proceedings of the Second Mosasaur Meeting. Fort Hays State University, Hays, pp. 81-89.

Houssaye, A., 2009. "Pachyostosis" in aquatic amniotes: a review. Integrative Zoology 4:325-340.

Houssaye, A., 2013a. Bone histology of aquatic reptiles: what does it tell us about secondary adaptation to an aquatic life? Biological Journal of the Linnean Society 108, 1, 3-21

Houssaye, A., 2013b. Paleoecological and morphofunctional interpretation of bone mass increase: an example in Late Cretaceous shallow marine squamates. Biological Reviews 88, 117-139.

Houssaye, A., Bardet, N., 2012. Ribs and vertebrae microanatomical characteristics in hydropelvic mosasauroids. Lethaia 45, 200-209.

Houssaye, A., Rage, J.-C., Bardet, N., Vincent, P., Amaghzaz, M., Meslouh, S., 2013. New highlights about the enigmatic marine snake Palaeophis maghrebianus (Palaeophiidae; Palaeophiinae) from the Ypresian Phosphates (Middle Eocene) of Morocco. Palaeontology, 56, 3, 647–661.

Houssaye, A., Lindgren, J., Pellegrini, R., Lee, A.H., Germain, D., Polcyn, M.J., 2013. Microanatomical and Histological Features in the Long Bones of Mosasaurine Mosasaurs (Reptilia, Squamata) – Implications for Aquatic Adaptation and Growth Rates. PLoS One. 2013; 8(10): e76741.

Hua, S., Buffetaut, É., 1997. Part VI. Crocodylia. Introduction, in: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, San Diego, pp. 357–374.

Jacobs, L.L., Polcyn, M.J., Taylor, L.H., Ferguson K., 2005b. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. Neth. J. Geosci., 84, 3, 269–281.

Ji, C., Jiang, D.-Y., Motani, R., Hao, W.-C., Sun, Z.-Y., Cai, T., 2013. A new juvenile specimen of *Guanlingsaurus* (Ichthyosauria, Shastasauridae) from the Upper Triassic of southwestern China. J. Vertebr. Paleontol. 33, 340–348.

Jiang, D.-Y., Schmitz, L., Motani, R., Hao, W.-C., Sun, Y.-L., 2007. The mixosaurid ichthyosaur *Phalarodon* cf. *P. fraasi* from the Middle Triassic of Guizhou Province, China. J. Paleontol. 81, 602-605.

Jiang, D-Y., Motani, R., Hao, W-C., Rieppel, O., Sun, Y-L., Schmitz, L., Sun, Z-Y., 2008. First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the Eastern Tethys. J Vertebr Paleontol. 28, 3, 904–908.

Jones, M.E.H., 2009. Dentary tooth shape in *Sphenodon* and its fossil relatives (Diapsida: Lepidosauria: Rhynchocephalia), in: Koppe, T., Meyer, G., Alt (Eds.), Comparative Dental Morphology, Frontiers of Oral Biology 13. Karger, Basel, pp. 9–15.

Jones, M.E.H., Tennyson, A.J.D., Worthy, J.P., Evans, S.E., Worthy, T.H., 2009. A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). Proceedings of the Royal Society of London. Series B, Biological Sciences 276, 1385–1390.

Jones, M.E., Anderson, C.L., Hipsley, C.A., Müller, J., Evans, S.E., Schoch, R.R., 2013. Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). BMC evolutionary biology 13, 1–21.

Jouve, S., 2009. The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and phylogenetic analysis of Thalattosuchia. Journal of Vertebrate Paleontology 29, 88–102.

Jouve, S., Bardet, N., Jalil, N.-E., Suberbiola, X.P., Bouya, B., Amaghzaz, M., 2008. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. Journal of Vertebrate Paleontology 28, 409–421.

Joyce, W.G., 2000. The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurystemidae) from the Upper Jurassic of Germany and its taxonomic implications. Journal of Paleontology 74, 684–700.

Kälin, J.A., 1955. Zur Stammesgeschichte der Crocodilia. Revue Suisse de zoologie 2, 347–356.

Kear B. P. 2012. A revision of Australia's Jurassic plesiosaurs. Palaeontology 55, 5, 1125-1138

LaDuke, T.C., Krause, D.W., Scanlon, J.D., Kley, N.J., 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga Basin, Madagascar. Journal of Vertebrate Paleontology 30, 109-138.

Lapparent de Broin, F. de, 2001. The European turtle fauna from the Triassic to the Present. Dumerilia 4, 155–216.

Lapparent de Broin, F. de, Werner, C., 1998. New late Cretaceous turtles from the Western Desert, Egypt. Annales de Paléontologie 84, 131–214.

Lapparent de Broin, F. de, Lange-Badré, B., Dutrieux, M., 1996. Nouvelles découvertes de tortues dans le Jurassique Supérieur du Lot (France) et examen du taxon Plesiochelyidae. Revue de Paléobiologie 15, 533–570.

Lapparent de Broin, F. de, de La Fuente, M., Fernandez, M., 2007. *Notoemys laticentralis* (Chelonii, Pleurodira), Late Jurassic of Argentina: New examination of the anatomical structures and comparisons. Revue de Paléobiologie 26, 99–136.

Lee, M.S.Y., 1996. Correlated progression and the origin of turtles. Nature 379, 811–815.

Lee, M. Y. S., 1997. Reptile relationships turn turtle. Nature 389, 245–246.

Lee, M.S.Y., 2009. Hidden support from unpromising data sets strongly unites snakes with anguimorph 'lizards'. J. Evol. Biol. 22, 1308-1316.

Li, C., Rieppel, O., 2002. A new cyamodontoid placodont from Triassic of Guizhou, China [in Chinese]. Chinese Sci Bull. 47, 2, 156–159.

Li, C., Wu, X.-C., Rieppel, O., Wang, L.-T., Zhao, L.-J., 2008. An ancestral turtle from the Late Triassic of southwestern China. Nature 456, 497–501.

Li, C., Rieppel, O., Wu, X.-C., Zhao, L.-J., Wang, L.-T., 2011. A new Triassic marine reptile from southwestern China. Journal of Vertebrate Paleontology 31, 303–312.

Li, C., Wu, X.-C., Zhao, L.-J., Sato, T., Wang, L.-T., 2012. A new archosaur (Diapsida, Archosauriformes) from the marine Triassic of China. Journal of Vertebrate Paleontology 32, 1064–1081.

Lindgren, J., Caldwell, M.W., Konishi, T., Chiappe, L.M., 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. PloS one 5, 1–10.

Liu, J., 2013. On the taxonomy of *Xinpusaurus* (Reptilia: Thalattosauria). Vertebrata PalAsiatica 51, 17–23.

Lingham-Soliar, T., Plodowski, G., 2007. Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs. Naturwissenschaften 94, 65–70.

Lingham-Soliar, T., Reif, W.-E., 1998. Taphonomic evidence for fast tuna-like swimming in Jurassic and Cretaceous ichthyosaurs. Neues. Jahrb. Geol. Palaontol.–Abh. 207, 171–183.

Lyson, T.R., Bever, G.S., Scheyer, T.M., Hsiang, A.Y., Gauthier, J.A., 2013. Evolutionary origin of the turtle shell. Current Biology 23, 1113–1119.

Massare, JA., 1994. Swimming capabilities of Mesozoic marine reptiles: a review. In Mechanics and Physiology of Animal Swimming (eds Maddock L, Bone Q, and Rayner JMV), pp. 133-149. Cambridge University Press. New York, NY.

Massare, J.A., 1997. Part VI. Faunas, behavior, and evolution. Introduction, in: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, San Diego, pp. 401–421.

Mazin, J.M., 2001. Mesozoic marine reptiles: an overview. In: Mazin J-M, de Buffrénil V, eds. *Secondary adaptation of tetrapods to life in water*. Munich: Verlag Dr. Friedrich Pfeil, 95–117.

Maisch, M.W., 2010. Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. Palaeodiversity 3, 151–214.

Martin, J.E., Fischer, V., Vincent, P., Suan, G., 2012. A longirostrine *Temnodontosaurus* (Ichthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and disparity. Palaeontology 55, 995–1005.

Maxwell, E.E., Fernández, M.S., Schoch, R.R., 2012. First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. PLoS ONE 7, e41692.

Maxwell, E.E., Kear, B.P., 2013. Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. GFF.

McGowan, C., 1974. A revision of the latipinnate ichthyosaurs of the Lower Jurassic of England (Reptilia, Ichthyosauria). Life Science Contributions, Royal Ontario Museum 100, 1–30.

McGowan, C., 1992. The ichthyosaurian tail: sharks do not provide an appropriate analogue. Palaeontology 35, 555–570.

McGowan, C., 1995. A remarkable small ichthyosaur from the Upper Triassic of British Columbia, representing a new genus and species. Can. J. Earth Sci. 32, 292–303.

McGowan, C., 1997. A Transitional Ichthyosaur Fauna, In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, San Diego, California, pp. 61–80.

McGowan, C., Motani, R., 2003. Part 8 Ichthyopterygia. Verlag Dr. Friedrich Pfeil, München.

Meylan, P.A., 2006a. Introduction to the Sea Turtles: Family Cheloniidae. Chelonian Research Monographs 3, 72–73.

Meylan, P.A., 2006b. Introduction to the Leatherback Turtles: Family Dermochelyidae. Chelonian Research Monographs 3, 142–143.

Modesto, S.P., 2010. The postcranial skeleton of the aquatic parareptile *Mesosaurus tenuidens* from the Gondwanan Permian. Journal of Vertebrate Paleontology 30, 1378–1395.

Moody, R.T., 1997. The paleogeography of marine and coastal turtles of the North Atlantic and trans-saharan regions, In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient marine reptiles: Academic Press, San Diego, pp. 259-278.

Motani, R., 1999a. On the evolution and homologies of ichthyosaurian forefins. J. Vertebr. Paleontol. 19, 28–41.

Motani, R., 1999b. Phylogeny of the Ichthyopterygia. J. Vertebr. Paleontol. 19, 473–496.

Motani, R., 2005. Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. Annual Review of Earth and Planetary Sciences 33, 395–420.

Motani R. 2009. The evolution of marine reptiles. Evolution: Education.

Motani, R., Minoura, N., Ando, T., 1998. Ichthyosaurian relationships illuminated by new primitive skeletons form Japan. Nature 393, 255–257.

Müller, J., 2005. The anatomy of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio and the interrelationships of thalattosaurs (Reptilia, Diapsida). Canadian Journal of Earth Sciences 42, 1347–1367.

Müller, J., 2007. First record of a thalattosaur from the Upper Triassic of Austria. Journal of Vertebrate Paleontology 27, 236–240.

Müller, J., Renesto, S., Evans, S.E., 2005. The marine diapsid reptile *Endennasaurus* from the Upper Triassic of Italy. Palaeontology 48, 15–30.

Neenan, J.M., Klein, N., Scheyer, T.M., 2013. European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. Nature Communication, 4:1621 | DOI: 10.1038/ncomms2633.

Nicholls, E. L., 1976. The oldest known North American occurrence of Plesiosauria (Reptilia: Sauropterygia) from the Liassic (Lower Jurassic) Fernie Group, Alberta, Canada. Canadian Journal of Earth Sciences 13(1):185–188.

Nicholls, E.L., 1997. Introduction, In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient marine reptiles: Academic Press, San Diego, pp. 219–223.

Nicholls, E.L., 1999. A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia: Diapsida). PaleoBios 19, 1–29.

Nicholls, E.L., Brinkman, D., 1993. New thalattosaurs (Reptilia: Diapsida) from the Triassic Sulphur Mountain Formation of Wapiti Lake, British Columbia. Journal of Paleontology 67, 263–278.

Nicholls, E.L., Manabe, M., 2004. Giant ichthyosaurs of the Triassic-A new species of *Shonisaurus* from the Pardonet Formation (Norian: Late Triassic) of British Columbia. J. Vertebr. Paleontol. 24, 838–849.

Nicholls, E. L., Russell, A. P. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeogr., Palaeoclimatol., Palaeoecol. 79, 149-169.

O’Keefe F.R. 2001. Ecomorphology of plesiosaur flipper geometry. J. Evol. Biol. 14: 987-991.

O’Keefe F.R. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). Paleobiology 28, 101–112.

Ogg, J.G., Gradstein, F.M., Chunduru, N.V., Gangi, P., Lugowski, A., Ault, A., 2012. TS Creator visualization of Geologic Time Scale 2012 database. Version 6.0. Available at http://www.tscreator.org

Palci, A., Caldwell, M.W., 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. Journal of Vertebrate Paleontology 27, 1-7.

Palci, A., Caldwell, M.W., 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. Journal of Vertebrate Paleontology 30, 94-108.

Parham, J.F., Pyenson, N.D., 2010. New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the cretaceous. Journal of Paleontology 84, 231–247.

Parmley, D., Devore, M., 2005. Palaeophid Snakes from the Late Eocene Hardie Mine Local Fauna of Central Georgia. Southeastern Naturalist 4, 703-722.

Patterson C. (1983). Aims and methods in biogeography. In: Sims R.W., Price J.-H. & Whalley P.E.S. (eds), Evolution, Time and Space: the emergence of the Biosphere, 1-28, Systematical Association special volume, 23, Academic Press, Londont & NewYork..

Pérez-García, A., 2012. High diversity of pancryptodiran turtles in the Lower Cretaceous of Europe. Cretaceous Research 36, 67–82.

Pérez-García, A., in press. A new interpretation of the holotype of "*Hispaniachelys prebetica*", a plesiochelyid turtle (Testudines, Pan-Cryptodira) from the Late Jurassic of Spain. Acta Palaeontologica Polonica. doi: http://dx.doi.org/10.4202/app.2012.0115.

Pérez-García, A., Scheyer, T.M., Murelaga, X., 2013. The turtles from the uppermost Jurassic and Early Cretaceous of Galve (Iberian Range, Spain): anatomical, systematic, biostratigraphic and palaeobiogeographical implications. Cretaceous Research 44, 64–82.

Pol, D., Gasparini, Z., 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. Journal of Systematic Palaeontology 7, 163–197.

Prasad, G.V.R., Rage, J.-C., 1995. Amphibians and squamates from the Maastrichtian of Naskal, India. Cretaceous Research 16, 95-107.

Rage, J.C., 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments. 93, 517-534.

Rage, J.-C., Wouters, G., 1979. Découverte du plus ancien Palaeopheide (Reptilia, Serpentes) dans le Maestrichtien du Maroc. Géobios 12, 293-296.

Rees, J., Lindgren J., 2005. Aquatic birds from the Upper Cretaceous (Lower Campanian) of Sweden and the biology and distribution of Hesperornithiforms. Palaeontology 48, 6, 1321–1329.

Reisz, R., Head, J.J., 2008 Turtle origins out to sea. Nature 456, 450–451.

Reynoso, V.H., 2000. An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayua Formation (Albian), Central Mexico. Journal of Paleontology 74, 133–148.

Rieppel, O., 1987. *Clarazia* and *Hescheleria*: a re-investigation of two problematical reptiles from the Middle Triassic of Monte San Giorgio (Switzerland). Palaeontographica Abteilung A 195, 101–129.

Rieppel, O., 1989. *Helveticosaurus zollingeri* Peyer (Reptilia, Diapsida) skeletal paedomorphosis, functional anatomy and systematic affinities. Palaeontographica Abteilung A 208, 123–152.

Rieppel O. 2000. Sauropterygia I. Handbuch der Paläoherpetologie 12A. München: Verlag Dr. Friedrich Pfeil; 134 pp.

Rieppel O. 2002. Feeding mechanics in Triassic stem group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. Zoological Journal of the Linnean Society 135, 33–63.

Rieppel, O., Hagdorn, H., 1998. Fossil reptiles from the spanish Muschelkalk (Mont-ral and Alcover, province Tarragona). Historical Biology 13, 77–97.

Rieppel, O., Reisz, R.R., 1999: The origin and early evolution of turtles. Annual Review of Ecology & Systematics 30, 1–22.

Rieppel, O., Sander, P.M., Storrs, G.W., 2002. The skull of the pistosaur Augustasaurus from the Middle Triassic of northwestern Nevada. Journal of Vertebrate Paleontology 22, 577–592.

Rieppel, O., Li, C., Fraser, N.C., 2008. The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, southern China. Journal of Vertebrate Paleontology 28, 95–110.

Rosen, B.R., 1988. Biogeographic patterns: a perceptual overview. In: Myers, A.A., Giller, P.S. (Eds), Analytical Biogeography: an integrated Approach to the Study of Animal and Plant Distribution, 23-55, Champan & Hall, London.

Sander, P.M., 1989. The large ichthyosaur *Cymbospondylus buchseri*, sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe, J. Vertebr. Paleontol. University of Oklahoma : Norman, OK, United States, United States, pp. 163–173.

Sander, M.P., Rieppel, O.C., Bucher, H., 1994. New marine vertebrate fauna from the Middle Triassic of Nevada. Journal of Paleontology 68, 676–680.

Sander, P.M., Chen, X., Cheng, L., Wang, X., 2011. Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. PLoS ONE 6, e19480.

Scheyer T.M. 2007. Skeletal histology of the dermal armor of Placodontia: the occurrence of ‘postcranial fibro cartilaginous bone’ and its developmental implications. J Anat. 211, 6, 737–753.

Scheyer T.M., Neenana J.M., Renesto S., Saller F., Hagdorn H., Furrer H., Rieppel O. & Tintori A. 2012. Revised paleoecology of placodonts–with a comment on ‘The shallow marine placodont *Cyamodus* of the central European Germanic Basin: its evolution, paleobiogeography and paleoecology’ by C.G. Diedrich. Historical Biology, 24: 257–267.

Sennikov, A.G., Arkhangelsky, M.S., 2010. On a typical Jurassic sauropterygian from the Upper Triassic of Wilczek Land (Franz Josef Land, Arctic Russia). Paleontological Journal 44, 567–572.

Shimada, K., Hooks, G.E., 2004. Shark-bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama. Journal of Paleontology 78, 205–210.

Smith, P.L., 1983. The Pliensbachian ammonite Dayiceras dayiceroides and Early Jurassic Paleogeography. Can. J. Earth Sci. 20, 86–91.

Smith, A.S., Dyke, G.J., 2008. The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. Naturwissenschaften 95, 975–980.

Storrs, G.W., 1991. Note on a second occurrence of thalattosaur remains (Reptilia: Neodiapsida) in British Columbia. Canadian Journal of Earth Sciences 28, 2065–2068.

Storrs G.W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. American Journal of Science 293–1, 63–90.

Storrs, G.W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). Zoological Journal of the Linnean Society 112, 217–259.

Sun, Z.Y., Maisch, M.W., Hao, W.C., Jiang, D.Y., 2005. A Middle Triassic thalattosaur (Reptilia: Diapsida) from Yunnan (China). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2005, 193–206.

Thorne, P.M., Ruta, M., Benton, M.J., 2011. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. Proc. Natl. Acad. Sci. U. S. A. 108, 8339-8344.

Tong, H., Meylan, P., 2013. Morphology and relationships of *Brachyopsemys tingitana* gen. et sp. nov. from the early Paleocene of Morocco and recognition of the new eucryptodiran turtle family: Sandownidae, In: Brinkman, D. Holroyd, P., Gardner J. (Eds.), Morphology and Evolution of Turtles: Vertebrate Paleobiology and Paleoanthropology, Springer, pp. 187-212.

Torsvik, T.H., Cocks, R.M., 2012. From Wegener until now: the development of our understanding of Earth’s Phanerozoic evolution. Geologica Belgica 15/3, 181-192

Vignaud, P., 1995. Les Thalattosuchia, crocodiles marins du Mesozoique□: systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. (Paléontologie). Ph D Thesis, University of Poitiers, 271 pp.

Vincent, P., Bardet, N., Bouya, B., Amaghzaz, M., Meslouh, S., 2011. *Zarafasaura oceanis*, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. Gondwana Research 19, 1062–1073.

Vincent, P., Martin, J.E., Fischer, V., Suan, G., Khalloufi, B., Sucheras-Marx, B., Lena, A., Janneau, K., Rousselle, B., Rulleau, L., 2013a. A marine vertebrate fauna from the

Toarcian-Aalenian succession of southern Beaujolais, Rhône, France. Geological Magazine 150, 822–834.

Vincent, P., Bardet, N., Houssaye, A., Amaghzaz, M., Meslouh, S., 2013b. New plesiosaur specimens from the Maastrichtian Phosphates of Morocco and their implications for the ecology of the latest Cretaceous marine apex predators. Gondwana Research 24, 796–805.

Wallace, A.R., 1876. The Geographical Distribution of Animals. Macmillan, London.

Wallace, A.R., 1880. Island Life. Macmillan, London.

Wegener, A., 1912. Die Entstehung der Kontinente. Geologische Rundschau 3, 276-292.

Wegener, A., 1915. Die Entstehung der Kontinente und Ozeane. Vieweg, Brunswick.

Westermann, G.E.G., 1993. Global bio-events in Mid-Jurassic ammonites controlled by seaways. In: House, M.R. (Ed.), Ammonoidea: Environment, Ecology, and Evolutionnary Change, 187-226. Oxford University Press, Oxford.

Wilberg, E.W., 2012. Phylogenetic and morphometric assessment of the evolution of the longirostrine crocodylomorphs. Ph D Thesis, University of Iowa, 250 pp.

Young, M.T., De Andrade, M.B., 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. Zoological Journal of the Linnean Society 157, 551–585.

Young, M.T., Brusatte, S.L., Ruta, M., De Andrade, M.B., 2010. The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. Zoological Journal of the Linnean Society 158, 801–859.

Zhao, L.J., Sato, T., Liu, J., Li, C., Wu, X.C., 2010. A new skeleton of *Miodentosaurus brevis* (Diapsida: Thalattosauria) with a further study of the taxon. Vertebrata PalAsiatica 48, 1–10.

Zhao, L.-J., Liu, J., Li, C., He, T., 2013. A new thalattosaur, *Concavispina biseridens* gen. et sp. nov. from Guanling, Guizhou, China. Vertebrata PalAsiatica 51, 24–28.

Zammit, M., 2012. Cretaceous ichthyosaurs: dwindling diversity, or the Empire strikes back? Geosciences 2, 11–24.

Figure Captions

Figure 1 – Schematic phylogenetical relationships of Mesozoic marine reptiles. Blue color indicates the presence of marine representatives for each clade. Mesozoic marine reptiles were all diapsids, with the possible exception of turtles and ichthyosaurs (depending of the authors). Mesosaurids belong to a distinct clade. Time-scale built and modified from TS-Creator (Ogg et al., 2012). For fossil record and ages, see text except for dyrosaurid crocodylomorphs (Buffetaut and Lauverjat, 1978; Jouve et al., 2008). The dashing indicates that the occurrence of thalattosaurs during the Lower Triassic remains uncertain. Reconstructions of the mesosaurid *Mesosaurus* modified from Modesto (2010), the testudinata *Caretta* from Pérez-García (this paper), the ichthyosaur *Ophthalmosaurus* from McGowan and Motani (2003), the thalattosaur *Askeptosaurus* from Müller (2005), the sauropterygian plesiosaur *Rhomaleosaurus* from Smith and Dyke (2008), the rhynchocephalian *Palaeopleurosaurus* from Carroll (1985), the mosasauroid squamate *Platecarpus* from Lindgren et al. (2010), and the thalattosuchian crocodylomorph *Metriorhynchus* from Hua and Buffetaut (1997). Reconstructions not at scale.

Figure 2 – Ichthyosauria palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent the main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 1 and Appendix. **A, Early Triassic** – 1: Canada (British Columbia), *Parvinatator*, *Grippia*, *Gulosaurus*. 2: Norway (Svalbard), *Grippia*, *Pessopteryx*, *Quasianosteosaurus*. 3: Japan, *Utatsusaurus*; 4: China (Anhui), *Chaohusaurus*. 5: Thailand, *Thaisaurus*. **B, Middle Triassic –** 1: Canada (British Columbia), *Phalarodon, Parvinatator*; 2: Norway (Svalbard), *Phalarodon*. 3: USA (Nevada), *Phalarodon, Cymbospondylus, Thalattoarchon*. 4: China (Panxian), *Phalarodon,*

Barracudasauroides. 5: German Basin, *Contectopalatus*, *Phantomosaurus*. 6: Switzerland and Italy, *Besanosaurus, Mikadocephalus*, *Cymbospondylus*, *Mixosaurus, Wimanius, Phalarodon*. 7: Timor, *Mixosaurus*. 8: Saudi Arabia, Ichthyosauria indet. **C, Late Triassic** – 1: Canada (British Columbia), *Shonisaurus, Macgowania*, *Hudsonelpidia*, *Callawayia, Shastasaurus*. 2: USA (California), *Toretocnemus*, *Shastasaurus*, *Shonisaurus*. 3: France, Shastasauridae indet. 4: China (Ghizou), *Guizhouichthyosaurus*, *Qianichthyosaurus*, *Shastasaurus*/*Guanlingsaurus*. 5: Tibet, *Himalayasaurus*. 6: New Caledonia, cf. Shastasauridae. 7: Italy (Sicily), Shastasauridae indet. **D, Early Jurassic** – 1: England, *Stenopterygius*, *Hauffiopteryx, Eurhinosaurus, Temnodontosaurus, Leptonectes, Ichthyosaurus*, *Excalibosaurus*. 2: Germany, Belgium, Switzerland and Luxemburg, *Ichthyosaurus*, *Leptonectes*, *Stenopterygius*, *Hauffiopteryx*, *Suevoleviathan*, *Eurhinosaurus*, *Temnodontosaurus*. 3: France, *Suevoleviathan, Eurhinosaurus, Temnodontosaurus*, Stenopterygiidae indet. 4: Canada (Alberta), Ichthyosauria indet. 5: New Zealand, Ichthyosauria indet. 6. Argentina (Mendoza), Ichthyosauria indet. **E, Middle Jurassic** – 1: England, *Ophthalmosaurus*. 2: Germany, *Stenopterygius*. 3: France, Stenopterygiidae indet. 4: Argentina (Neuquén), *Stenopterygius*/*Chacaicosaurus*, *Mollesaurus*, Ophthalmosauridae indet. 5: Alaska, Ophthalmosaurinae indet. 6: USA (Wyoming), *Ophthalmosaurus*. 7: Western Russia, Ophthalmosauridae indet. **F, Late Jurassic** – 1: Canada (Melville), *Arthropterygius*. 2: Norway (Svalbard), *Cryopterygius*, *Palvennia*, *Brachypterygius*. 3: USA (Wyoming), *Ophthalmosaurus*. 4: England and France, *Ophthalmosaurus*, *Brachypterygius, Nannopterygius*. 5: Southern Germany, *Aegirosaurus*. 6: Western Russia, *Ophthalmosaurus*/*Paraophthalmosaurus*, *Brachypterygius*/*Otschveia*, *Undorosaurus*. 7: Mexico, *Ophthalmosaurus*, *Brachypterygius*. 8: Argentina (Neuquén), *Arthropterygius*; ‘*Ophthalmosaurus*’, *Caypullisaurus*. 9: Madagascar, Ophthalmosauridae indet.

Figure 3 – Thalattosauria palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps

represent the main outcrops. For each genus, For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 2 and Appendix. **A, Early–Middle Triassic –** 1: Canada (British Columbia), Early–Middle Triassic, *Agkistrognathus*, *Paralonectes*; Middle Triassic, *Thalattosaurus*, Thalattosauria indet. 2: USA (Nevada), Anisian, Thalattosauria indet. 3: Spain, Ladinian, Thalattosauria indet. 4: Switzerland, Anisian-Ladinian boundary, *Askeptosaurus*, *Clarazia*, *Hescheleria*. 5: China (Yunnan), Ladinian, *Anshunsaurus*. **B, Late Triassic –** 1: USA (Alaska), Norian, *Nectosaurus* sp. 2: USA (California), Carnian, *Nectosaurus*, *Thalattosaurus*. 3: USA (Nevada), Carnian, Thalattosauria indet. 4: Italy and Austria, Norian, *Endennasaurus*, Thalattosauroidea indet., Thalattosauria indet. 5: China (Guizhou), Carnian, *Anshunsaurus*, *Concavispina*, *Miodentosaurus*, *Wayaosaurus*, *Xinpusaurus*.

Figure 4 – Sauropterygia palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 3 and Appendix. **Early Triassic -** 1: USA (Wyoming), Olenekian, *Corosaurus*. 2: Italy, Induen, *Placodus*. 3: Israel, Olenekian, *Placodus, Psephosaurus*. 4: China (Guangxi, Guizhou, Yunnan), Early Triassic, *Diandongosaurus*, *Kwangsisaurus*, *Wumengosaurus*. **Middle Triassic -** 1: USA (Nevada) Anisian, *Augustasaurus*. 2: Central Europe (Austria, Germany, Hungary, Poland, and Slovenia), Anisian to Ladinian, *Anarosaurus, Cyamodus, Cymatosaurus, Dactylosaurus, Germanosaurus, Neusticosaurus, Nothosaurus, Pistosaurus, Placodus, Psephosaurus, Simosaurus.* 3: Western Europe (France, Netherland, Switzerland), Anisian to Ladinian, *Anarosaurus, Cyamodus, Lariosaurus, Nothosaurus, Neusticosaurus, Paraplacodus, Palatodonta, Placodus, Serpianosaurus, Simosaurus*. 4: Eastern Europe, Anisian-Ladinian

boundary, *Dactylosaurus.* 5: Southern Europe (Bulgaria, Italia), *Lariosaurus, Nothosaurus, Paraplacodus, Pistosaurus, Placodus.* 6: Turkey, Ladinian, *Psephosaurus*. 7: Israël, Egypt, Sinai Peninsula and Saudi Arabia, Anisian and Ladinian, *Nothosaurus*, *Simosaurus*, *Placodus*, *Psephosaurus*, *Psephosauriscus*, Pachypleurosauroids indet. 8: China (Guizhou, Jiangxi, southwestern), Anisian and Ladinian, *Chinchenia, Dianopachysaurus*, *Hanosaurus*, *Keichousaurus*, *Largocephalosaurus, Sanchiasaurus, Yunguisaurus*. **Late Triassic -** 1: Russia (Arctic Russia), *Alexeyisaurus*. 2: Western Europe (United Kingdoms, France), Rhaetian-Hettangian?, *Psephoderma, Simosaurus, Eurycleidus*, *Thalassiodracon.* 3: Central Europe (Austria, Germany, Hungary), Carnian to Rhaetian, *Macroplacus*, *Placochelys, Henodus*. 4: Southern Europe (Italy), Carnian to Rhaetian, *Bobosaurus*, *Nothosaurus, Placochelys, Protenodontosaurus*, *Psephoderma.* 5: China (Guizhou), Carnian, *Psephochelys*, *Sinocyamodus*. **Early Jurassic -** 1: Norway (Svalbard), Toarcian, *Tricleidus*. 2: Canada (Alberta), Sinemurian, Plesiosauria indet. 3: Central Europe (Germany), Early Jurassic, *Hauffiosaurus, Hydrorion, Meyerasaurus*, *Plesiopterys*, *Seeleyosaurus, Westphaliasaurus*. 4: Western Europe (France, United Kingdoms), *Anningasaura*, *Archaeonectrus, Attenborosaurus*, *Avalonnectes*, *Cryonectes*, *Eoplesiosaurus*, *Eretmosaurus*, *Hauffiosaurus, Macroplata*, *Microcleidus*, *Occitanosaurus, Plesiosaurus*, *Rhomaleosaurus*, *Stheneosaurus, Stratesaurus*. 5: Southern Europe (Portugal), Early Jurassic, *Lusonectes*. 6: China (Sichuan), Toarcian?, *Bishanopliosaurus*. 7: Chile, Sinemurian, Plesiosauria indet. 8: Australia (Queensland), Sinemurian, Plesiosauria indet. **Middle Jurassic -** 1: Canada (Northwest Territories), Callovian, *Borealonectes*. 2: Western Europe (United Kingdom, France, Switzerland), Bathonian-Callovian, *Cryptoclidus*, *Liopleurodon, Marmonectes, Muraenosaurus*, *Pachycostasaurus*, *Peloneustes*, *Pliosaurus*, *Simolestes*, *Tricleidus*. 3: Central Europe (Germany), Callovian, *Liopleurodon*, *Peloneustes*. 4: China (Chongqing), Callovian, *Yuzhoupliosaurus*. 5: Argentina (Neuquén), Bajocian, *Maresaurus*. 6: Australia (Western Australia) Aalenian-Bajocian, Plesiosauria indet. **Late Jurassic -** 1: Norway (Spitsbergen), Tithonian, *Colymbosaurus*, *Djupedalia*, *Pliosaurus*, *Spitrasaurus*. 2: Russia

(Saratov, Chuvashia), Tithonian, *Pliosaurus*. 3: USA (Wyoming), Oxfordian, *Cimoliosaurus*, *Pantosaurus*, *Tatenectes*. 4: Western Europe (United Kingdom, France), Late Jurassic, *Colymbosaurus*, *Kimmerosaurus*, *Pliosaurus*. 5: Central Europe (Germany, Poland), Late Jurassic, *Pliosaurus*, *Liopleurodon*. 6: Cuba, Oxfordian, *Gallardosaurus*, *Vinialesaurus*. 7: Mexico, Kimmeridgian, *Pliosaurus.* 8: Argentina (Neuquén), Tithonian, *Pliosaurus*. **Early Cretaceous -** 1: Canada (Alberta), Albian, *Nichollsia*, *Wapuskanectes*. 2: USA (Montana), Albian, *Edgarosaurus*. 3: Russia (Chuvashia), Hauterivian, *Abyssosaurus*. 4: Europe (England, Germany, Switzerland), Berriasian to Barremian, *Brancasaurus*, *Hastanectes*, *Leptocleidus*, *Vectocleidus*. 5: Colombia (Boyaca), Barremian-Aptian, *Callawayasaurus*, *Brachauchenius.* 6: South Africa (Eastern Cape), Valanginian, *Leptocleidus*. 7: Australia (Queensland), Albian, *Eromangasaurus*, *Kronosaurus*. 8: Australia (northern South, Western), Hauterivian to Aptian, *Leptocleidus*, *Kronosaurus*, *Umoonasaurus*. **Late Cretaceous -** 1: Canada (Northwest territories), Campanian, *Dolichorhynchops*. 2: Canada (Manitoba, Saskatchewan), Coniacian and Campanian, *Dolichorhynchops*, *Terminonatator*, *Trinacromerum*. 3: USA (Nebraska), Campanian, *Hydralmosaurus*. 4: USA (Colorado, Montana, Wyoming, Utah, South Dakota, California), Cenomanian to Maastrichtian, *Brachauchenius*, *Dolichorhynchops*, *Eopolycotylus*, *Hydralmosaurus*, *Hydrotherosaurus*, *Palmula*, *Pahasapasaurus*, *Plesiopleurodon*, *Thalassomedon*, *Trinacromerum*. 5: USA (Kansas, Texas, Alabama), Cenomanian to Campanian, *Albertonectes*, *Brachauchenius*, *Dolichorhynchops*, *Elasmosaurus*, *Megacephalosaurus*, *Polycotylus*, *Polytptycodon*, *Styxosaurus*, *Trinacromerum*. 6: Russia (Penza), Coniacian, *Georgiasaurus*. 7: Japan, Coniacian, *Futabasaurus*. 8: Morocco, Turonian and Maastrichtian, *Libonectes*, *Manemergus*, *Thililua*, *Brachauchenius*, *Zarafasaura*. 9: Chile, Campanian-Maastrichtian, *Aristonectes*, *Mauisaurus*. 10: Angola, Maastrichtian, cf. *Tuarangisaurus*. 11: Argentina (Chubut), Campanian, *Aristonectes*, *Sulcusuchus*. 12: New Zealand, Late Cretaceous, *Kaiwhekea*, *Mauisaurus*, *Tuarangisaurus*. 13: Antarctica, Campanian-Maastrichtian, *Aristonectes*, *Mauisaurus*.

Figure 5 – Testudinata palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent the main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 4 and Appendix. **A, Late Triassic -** 1: China (Guizhou), Early Carnian, *Odontochelys*. **B, Late Jurassic -** 1: Argentina (Neuquén), Tithonian, *Neusticemys*, *Notoemys*. 2: Cuba, Oxfordian, *Caribemys*. 3: England, Kimmeridgian-Tithonian, *Pelobatochelys*, *Plesiochelys*, *Portlandemys*, *Tholemys*. 4: Europe (France, Germany, Spain, Switzerland), Oxfordian to Tithonian, *Platychelys*, *Craspedochelys*, *Plesiochelys*, *Thalassemys*, *Tropidemys*, *Achelonia*, *Anaphotidemys*, *Euryaspis*, *Eurysternum*, *Hydropelta*, *Idiochelys, Palaeomedusa*, *Solnhofia*. 5: Portugal, Kimmeridgian-Tithonian, *Plesiochelys*, *Craspedochelys*. **C, middle Cretaceous -** 1: USA (Nebraska, South Dakota, Kansas), Turonian, *Desmatochelys*. 2: USA (Texas), Aptian, new unnamed Sandownidae. 3: Brazil (Ceara), Aptian-Albian, *Santanachelys*. 4: England, Aptian to Turonian, *Sandownia*, *Lytoloma*, *Cimochelys*, *Rhinochelys*. 5: France, Albian to Turonian, *Rhinochelys*. 6: Italy, Cenomanian-Turonian, *Protosphargis*. 7: SW Russia (Belgorod, Volgograd, Saratov), Albian, *Teguliscapha*. 8: Uzbekistan, Turonian, *Oxemys*. 9: Angola, Turonian, *Angolachelys*. 10: Japan, Turonian, *Desmatochelys*. 11: Australia (Queensland), Albian, *Bouliachelys*, *Cratochelone*, *Notochelone*. **D, Late Cretaceous -** 1: Canada (Alberta), Coniacian-Santonian, *Nichollsemys*, *Toxochelys*. 2: Canada (Manitoba), Coniacian-Santonian, *Toxochelys*, *Protostega*. 3: USA (South Dakota, Wyoming), Campanian-Maastrichtian, *Toxochelys*, *Archelon*. 4: USA (Kansas, Colorado), Coniacian-Maastrichtian, *Ctenochelys*, *Porthochelys*, *Toxochelys*, *Prionochelys*, *Archelon*, *Chelosphargis*, *Microstega*, *Protostega*. 5: USA (Texas), Campanian, *Terlinguachelys*. 6: USA (Arkansas, Tennessee, Alabama), Coniacian-Maastrichtian, *Ctenochelys*, *Porthochelys*, *Thinochelys*, *Toxochelys*, *Prionochelys*, *Zangerlchelys*, *Calcarhichelys*, *Chelosphargis*, *Protostega*, *Corsochelys*. 7: USA (New

Jersey, North Carolina), Campanian-Maastrichtian, *Bothremys*, *Taphrosphys*, *Catapleura*, *Glyptochelone*, *Peritresius*, *Atlantochelys*. 8: Mexico (Cohuila), Campanian, *Euclastes*. 9: Argentina (Río Negro), Campanian-Mastrichtian, *Euclastes*. 10: England, Coniacian-Campanian, *Ctenochelys*. 11: Europe (Netherlands, Belgium, Germany), Maastrichtian, *Allopleuron*, *Glaucochelone*, *Glyptochelone*, *Platychelone*, *Tomochelone*. 12: Syria, Maastrichtian, *Taphrosphys*. 13: Jordan, Santonian-Maastrichtian, *Bothremys*, *Gigantatypus*. 14: Kazakhstan, Campanian, *Turgaiscapha*. 15: Morocco, Maastrichtian, *Ocepechelon*, *Alienochelys*. 16: Egypt, Maastrichtian, *Arenila*, *Zolhafah*, *Taphrosphys*. 17: Niger, Maastrichtian, *Nigeremys*. 18: Japan, Santonian-Maastrichtian, *Protostega*, *Mesodermochelys*.

Figure 6 – Crocodyliformes palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent the main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 5 and Appendix. **A, Early Jurassic –** 1: Europe (France, England, Germany, Portugal), Sinemurian-Toarcian, *Pelagosaurus*, *Platysuchus*, *Steneosaurus*. 2: Chile, Sinemurian, Thalattosuchia indet. 3: Argentina (Neuquén), Sinemurian, Thalattosuchia indet. 4: Madagascar, Toarcian, *Steneosaurus* sp. 5: India (Maharashtra), Piensbachian?, Thalattosuchia indet. 6: China (Sichuan), Toarcian, *Peipehsuchus*, *Teleorhinus*. **B, Middle Jurassic –** 1: Europe (France, England, Germany, Switzerland?, Italy, Spain), Aalenian-Callovian, *Steneosaurus*, *Metriorhynchus*, *Gracilineustes*, *Suchodus*, *Teleosaurus*, *Neptunidraco*, *Teleidosaurus*, *Eoneustes*. 2: Chile (Antofagasta, Atacama), Bajocian and Callovian, *Purranisaurus*, Metriorhynchoidea indet. 3. Argentina (Neuquén), Bathonian, Metriorhynchoidea indet. 4: Madagascar, Bathonian, *Steneosaurus.* 5: India (Gujarat), Callovian, *Steneosaurus*. 6: Dagestan, Callovian, *Steneosaurus*. 7: Mexico (Guerrero), Callovian, Thalattosuchia indet. 8: North Africa (Morocco, Tunisia), Bathonian, *Steneosaurus.* 9: USA (Oregon), Aalenian-

Bajocian, *Zoneait*. **Late Jurassic –** 1: Europe (Germany, France, Portugal, Spain, England, Switzerland, Poland), Oxfordian-Tithonian, *Steneosaurus*, *Machimosaurus, Dakosaurus, Rhacheosaurus*, *Cricosaurus*, *Geosaurus*, *Metriorhynchus*, *Gracilineustes*, *Torvoneustes*, *Suchodus*. 2: Chile (Antofagasta), Tithonian, *Cricosaurus* sp. 3: Argentina (Mendoza, Neuquén), Tithonian, *Dakosaurus*, *Cricosaurus*, *Purranisaurus*. 4: Ethiopia, Oxfordian, *Machimosaurus*. 5. Mexico, Kimmeridgian-Tithonian, *Cricosaurus*, *Dakosaurus*. 6: Russia (Volga), Kimmeridgian-Tithonian, *Dakosaurus*, *Steneosaurus*. 7: Cuba, Oxfordian, *Cricosaurus*. 8: Tunisia, Oxfordian-Kimmeridgian, Thalattosuchia.

Figure 7 – Rhynchocephalia palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent the main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 6 and Appendix. **A, Early Jurassic** – 1: Germany, Toarcian, *Palaeopleurosaurus*. 2: Germany, Toarcian, *Palaeopleurosaurus*. **B, Late Jurassic** – 1: France, Kimmeridgian-Tithonian boundary, *Pleurosaurus*. 2: France, Tithonian, *Pleurosaurus*. 3: Germany, Tithonian, *Pleurosaurus*.

Figure 8 – Squamata palaeobiogeographical distribution during the Mesozoic. Palaeogeographical maps used by courtesy of R. Blakey. The numbers indicated on the maps represent the main outcrops. For each genus, we provide the stage (or stratigraphic interval) in which it has been found, the country of origin (and the state / province when relevant), as well as bibliographical references in the corresponding Table 7 and Appendix. **A, middle Cretaceous –** 1: USA (Texas, Kansas), Cenomanian-Turonian, *Coniasaurus*, *Dallasaurus*, *Russellosaurus*. 2: Mexico (Cohuila), Turonian, *Vallecillosaurus*. 3: Columbia, Turonian, *Yaguarasaurus*. 4: Angola, Turonian, *Angolasaurus*, *Tylosaurus*. **B, Late Cretaceous –** 1: USA (Texas, Kansas, Alabama, Tennessee, Missourri), Coniacian to Maastrichtian,

Coniasaurus, *Tylosaurus*, *Plesioplatecarpus*, *Platecarpus*, *Selmasaurus*, *Clidastes*, *Eonatator*, *Globidens*, *Ectenosaurus*, *Latoplatecarpus*, *Plioplatecarpus*, *Mosasaurus*. 2: Italy, Turonian-Santonian, *Romeosaurus*. 3: USA (South Dakota, Colorado, Wyoming), Coniacian to Campanian, *Coniasaurus*, "*Platecarpus*" (*somenensis*), *Clidastes*, *Tylosaurus*, *Globidens*, *Latoplatecarpus*, *Plioplatecarpus*, *Prognathodon*. 4: Mexico, Santonian, *Amphekepubis*. 5: South Africa (Pondoland), Santonian, *Tylosaurus*. 6: Europe (Belgium, Netherlands, France, Spain, England, Sweden, Poland, Bulgaria, Germany, Denmark), Santonian to Maastrichtian, *Tylosaurus*, *Hainosaurus*, *Platecarpus*, "*Platecarpus*" (*somenensis*), *Clidastes*, *Eonatator*, *Globidens*, *Plioplatecarpus*, *Prognathodon*, *Mosasaurus*, *Halisaurus*, *Carinodens*. 7: Canada (Alberta, British Columbia, Manitoba, Saskatchevan), Santonian-Campanian, *Kourisodon*, *Clidastes*, *Tylosaurus*, *Latoplatecarpus*, *Plioplatecarpus*, *Prognathodon*. 8: Japan, Santonian-Campanian, *Kourisodon*, *Taniwhasaurus*. 9: New Zealand, Campanian, *Taniwhasaurus*, *Tylosaurus*, *Prognathodon*. 10: Antarctica, Campanian, *Taniwhasaurus*. 11: Morocco, Maastrichtian, *Prognathodon*, *Mosasaurus*, *Globidens*, Nov. gen. *"ptychodon"*, *Eremiasaurus*, *Halisaurus*, *Carinodens*, *Palaeophis*. 12: Middle East (Syria, Jordan, Israel), Maastrichtian, *Prognathodon*, *Mosasaurus*?, *Globidens*, Nov. gen. *"ptychodon"*, *Eremiasaurus*, *Halisaurus*, *Carinodens*. 13: Egypt, Maastrichtian, *Prognathodon*, *Mosasaurus*, *Globidens*, *Igdamanosaurus*, *Halisaurus*. 14: USA (New Jersey), Maastrichtian, *Prognathodon*, *Mosasaurus*, *Plioplatecarpus*, *Halisaurus*, *Carinodens*. 15: USA (California), Maastrichtian, *Prognathodon*, *Plesiotylosaurus*, *Plotosaurus*. 16, Turkey, Maastrichtian, *Mosasaurus*. 17, Angola, *Mosasaurus*, *Prognathodon*, *Globidens*, Nov. gen. *"ptychodon"*, *Halisaurus*. 18, Brazil (Pernambuco), *Mosasaurus* , *Eremiasaurus*, *Carinodens*. 19, Africa (Niger, Nigeria), Maastrichtian, *Globidens*, *Igdamanosaurus*, *Halisaurus*, *Goronyosaurus*. 20, Asia (Russia, Ukraine), Maastrichtian, *Carinodens*. 21, India, Maastrichtian, *Indophis*. 22, Madagascar, Maastrichtian, *Kelyophis*. **C, middle Cretaceous (Mediterranean Tethys) –** 1: Croatia, Cenomanian, *Aigialosaurus*, *Adriosaurus*, *Pontosaurus*. 2: Slovenia, Cenomanian, *Mesoleptos*, *Carsosaurus*, *Komensaurus*, *Adriosaurus*, *Acteosaurus*, *Eidolosaurus*. 3:

Palestine, Cenomanian, *Mesoleptos*, *Haasiasaurus*, *Haasiophis*, *Pachyrhachis*. 4: Morocco, Turonian, *Tethysaurus*. 5: Lebanon, Cenomanian, *Aphanizocnemus*, *Pontosaurus*, *Eupodophis*. 6: England, Cenomanian, *Coniasaurus*. 7: Germany, Cenomanian, *Coniasaurus*, *Dolichosaurus*. 8: Spain, Cenomanian, *Carentonosaurus*, *Coniasaurus*, *Simoliophis*. 9: Bosnia-Herzegovina, Cenomanian, *Mesophis*, *Pachyophis*. 10: France, Cenomanian-Turonian, *Carentonosaurus*, "Pythonomorph from Touraine", *Simoliophis*. 11: Portugal, Cenomanian, *Simoliophis*. 12: Libya, Cenomanian, *Simoliophis*. 13: Morocco, Cenomanian, *Simoliophis*.

CV and Photographs of Authors

Nathalie BARDET is a permanent researcher of the CNRS (CR2P, CNRS-MNHN-UPMC) at the *Muséum National d'Histoire Naturelle* of Paris (France). She is a specialist of Mesozoic marine reptiles. Her main interest is the impact of global environmental changes on the diversity fluctuations and palaeobiogeographical distributions of these clades through time.

Jocelyn FALCONNET is currently Collection Technician at the *Muséum National d'Histoire Naturelle* of Paris (France). His research focuses mainly on the origination and early diversification of amniote vertebrates during the Palaeozoic and on the impact of the Permian-Triassic mass extinction on terrestrial tetrapod faunas.

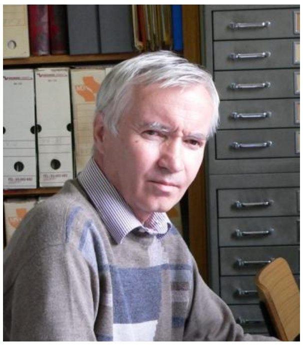
Valentin FISCHER is a teaching assistant at the *Université de Liège*, Belgium and associate researcher at the *Institut Royal des Sciences Naturelles de Belgique* (Belgium). He is investigating the fluctuations of ancient biodiversity, focusing on the evolutionary history and extinction phases of Mesozoic marine reptiles. A particular emphasis is put on Eurasian ichthyosaurs and the influence of climate change in shaping their biodiversity.

Alexandra HOUSSAYE is a postdoctoral fellow (UMR 7179 MNHN-CNRS) at the *Muséum National d'Histoire Naturelle* of Paris (France). She is specialized in the morphofunctional and physiological analysis of the process of secondary adaptation to an aquatic life. Most of her work deals with microanatomical and histological features of extant and fossil amniotes that secondarily adapted to an aquatic life and with Cretaceous varanoids and snakes.

Stéphane JOUVE is an assistant curator at the *Muséum d'Histoire Naturelle* of Marseille (France) and an associate researcher of the *Muséum National d'Histoire Naturelle* of Paris, France. His research activities focus on the anatomy, systematics, palaeobiogeography, and evolution of the crocodyliformes.

Xabier PEREDA SUBERBIOLA is a permanent researcher at the *Universidad del País Vasco / Euskal Herriko Unibertsitatea* of Bilbao (Spain). Most of his research projects are devoted to Mesozoic vertebrate palaeontology, more specifically on archosauromorphs, including ornithischian dinosaurs, pterosaurs and crocodylomorphs.

Adán PÉREZ-GARCÍA is a postdoctoral researcher at the *Universidad Complutense* of Madrid (Spain), and a member of the *Grupo de Biología Evolutiva* of the UNED. His research activities focus on the phylogeny, evolution, palaeobiogeography and palaeoecology of Mesozoic and Cenozoic turtles, especially the European record.



Jean-Claude RAGE is Emeritus Research Director of the CNRS (CR2P, CNRS-MNHN-UPMC) at the *Muséum National d'Histoire Naturelle* of Paris (France). His major research interests lie in the evolution of lissamphibians and squamates, and in palaeobiogeography.

Peggy VINCENT is a permanent researcher of the CNRS (CR2P, CNRS-MNHN-UPMC) at the *Muséum National d'Histoire Naturelle* of Paris (France). Her research activities sit at the frontier of earth and biological sciences with a peculiar emphasis on the anatomy, systematics, palaeoecology, palaeobiology and evolution of Mesozoic marine reptiles.

Manuscript Table of Contents

1. Introduction

2. Material and Methods

- **2.1. Material**
- **2.2. Methods**
- **2.3. Potential Biases**

3. Overview of the biogeographic history of Mesozoic marine reptiles

- **3.1. Ichthyosauria (Fig. 2, Table 1 in Appendix)**
- **3.2. Thalattosauria (Fig. 3, Table 2 in Appendix)**
- **3.3. Sauropterygia (Fig. 4, Table 3 in Appendix)**
- **3.4. Testudinata (Fig. 5, Table 4 in Appendix)**
- **3.5. Crocodyliformes (Fig. 6, Table 5 in Appendix)**
- **3.6. Rhynchocephalia (Fig. 7, Table 6 in Appendix)**
- **3.7. Squamata (Fig. 8, Table 7 in Appendix)**

4. Discussion

5. Conclusion

Acknowledgments

References

Figure 1 to 8 captions

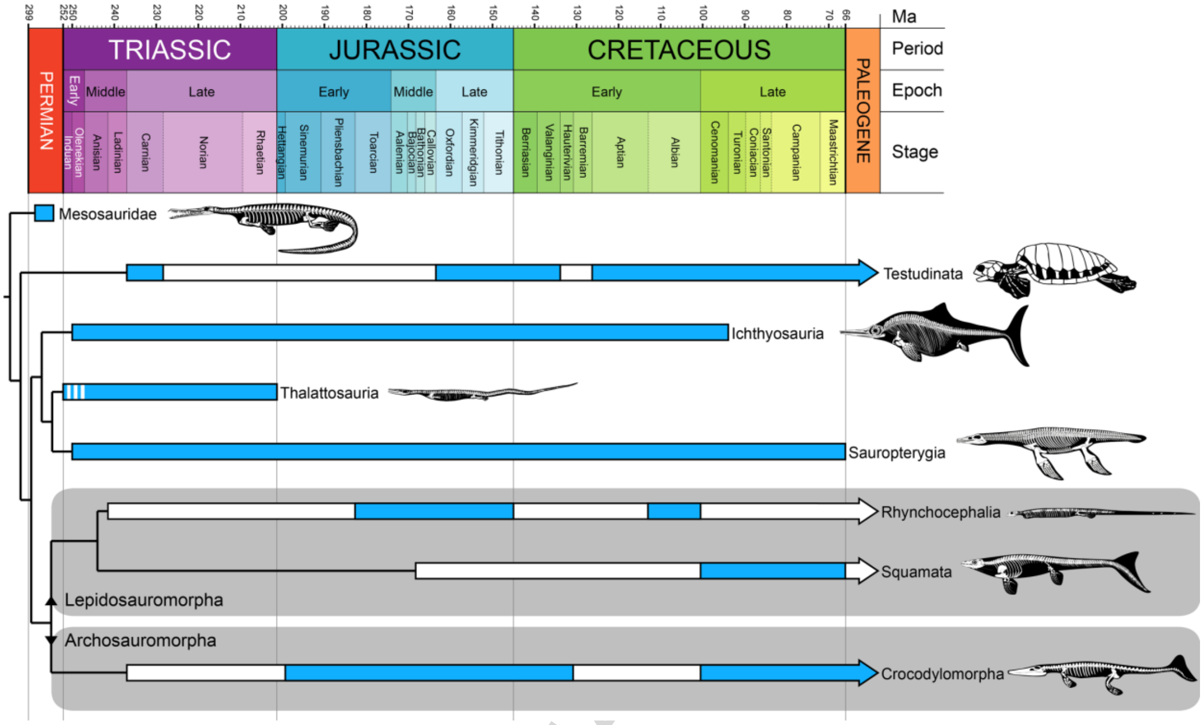

Ma
299
252
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
66
Period
Epoch
Stage
PERMIAN
TRIASSIC
JURASSIC
CRETACEOUS
PALEOGENE
Early
Middle
Late
Early
Middle
Late
Early
Late
Induan
Olenekian
Anisian
Ladinian
Carnian
Norian
Rhaetian
Hettangian
Sinemurian
Pliensbachian
Toarcian
Aalenian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithonian
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastrichtian
Mesosauridae
Testudinata
Ichthyosauria
Thalattosauria
Sauropterygia
Rhynchocephalia
Squamata
Lepidosauromorpha
Archosauromorpha
Crocodylomorpha

Figure 1

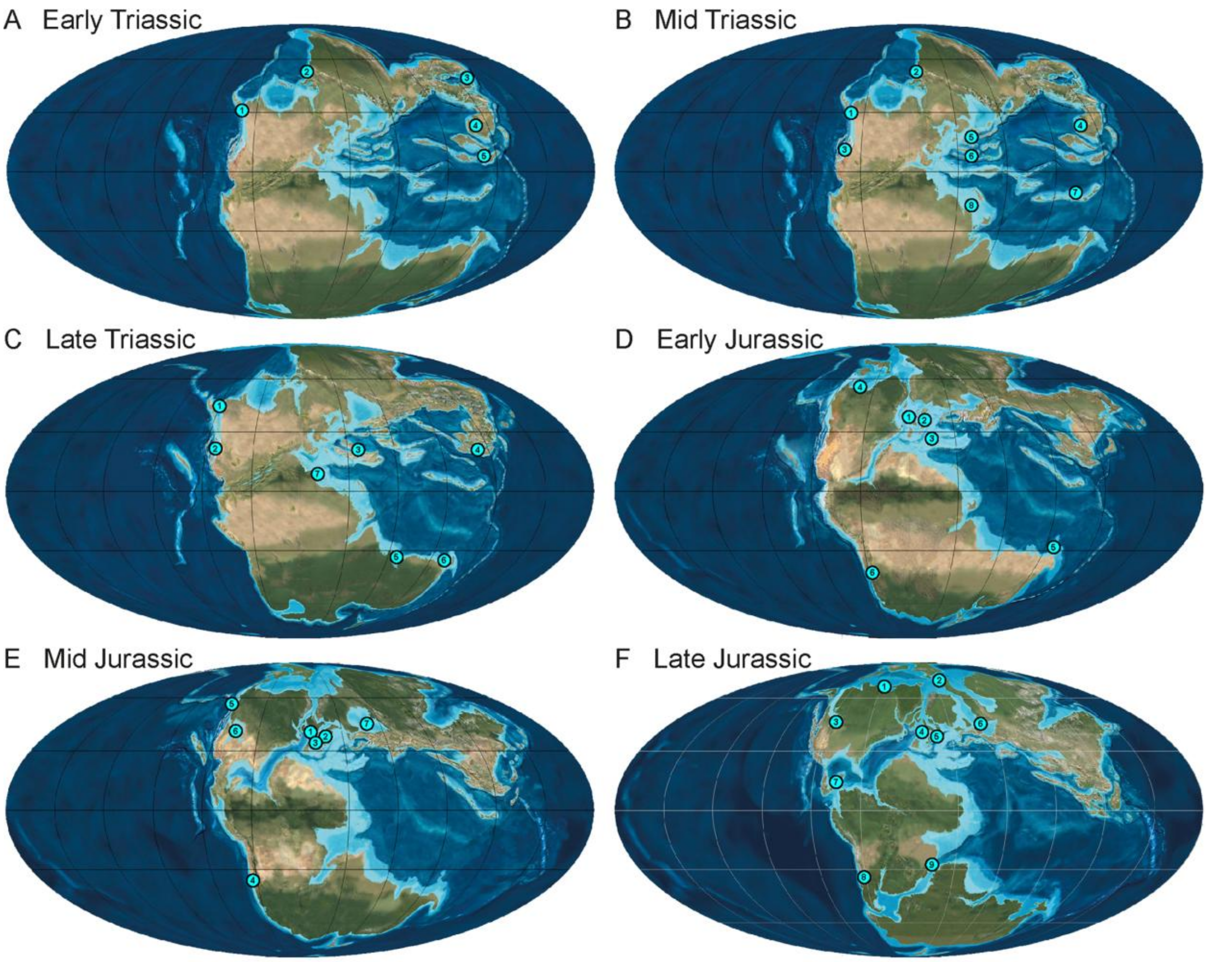

A Early Triassic
B Mid Triassic
C Late Triassic
D Early Jurassic
E Mid Jurassic
F Late Jurassic

Figure 2

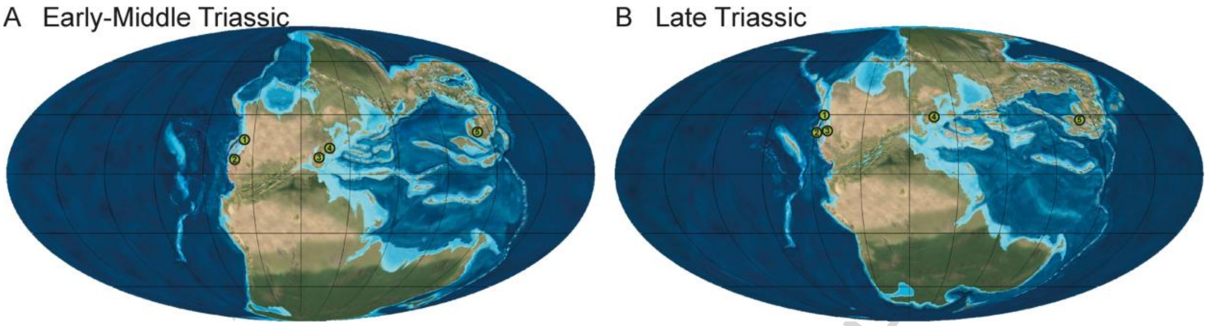


Figure 3

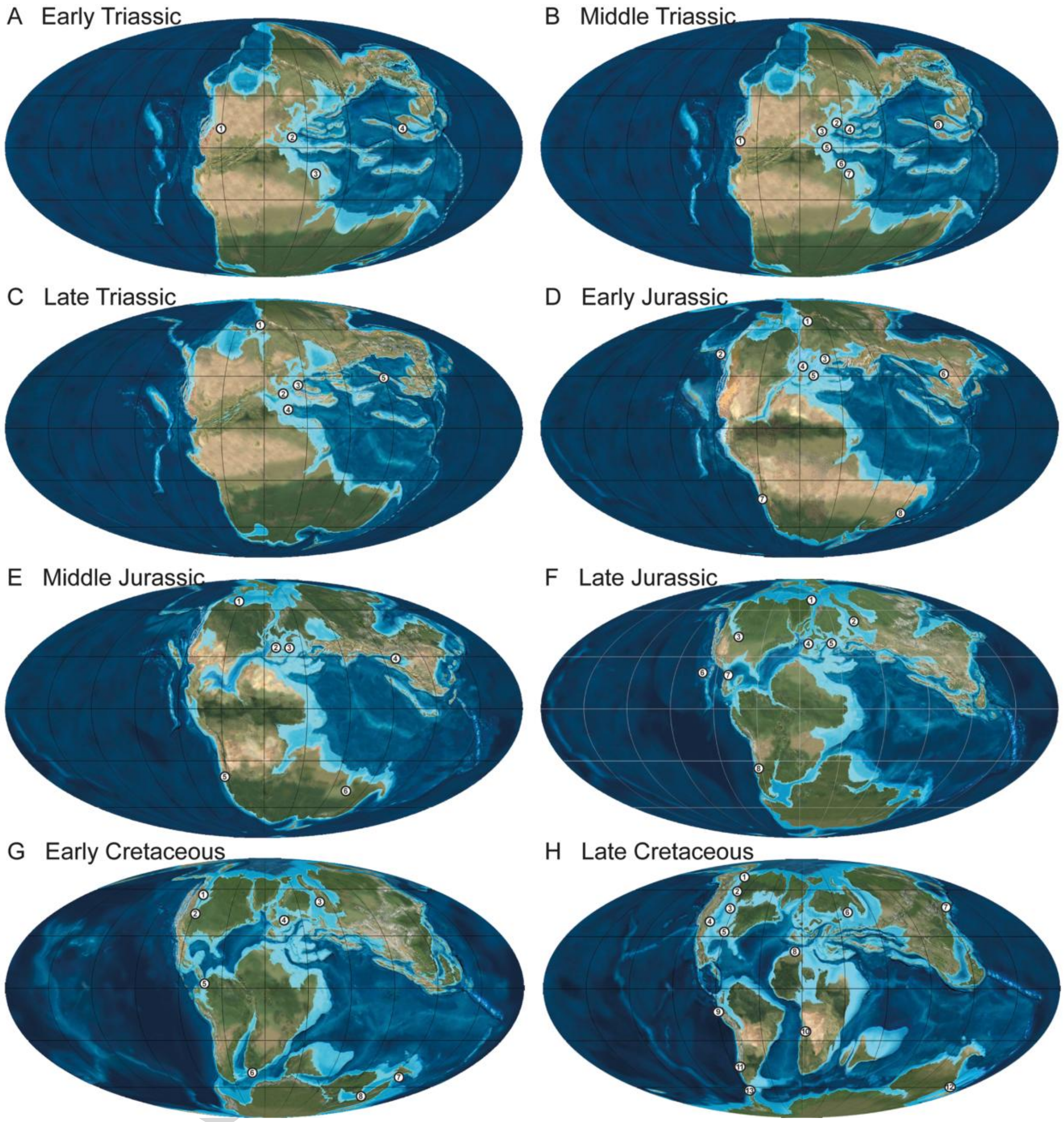

A Early Triassic
B Middle Triassic
C Late Triassic
D Early Jurassic
E Middle Jurassic
F Late Jurassic
G Early Cretaceous
H Late Cretaceous

Figure 4

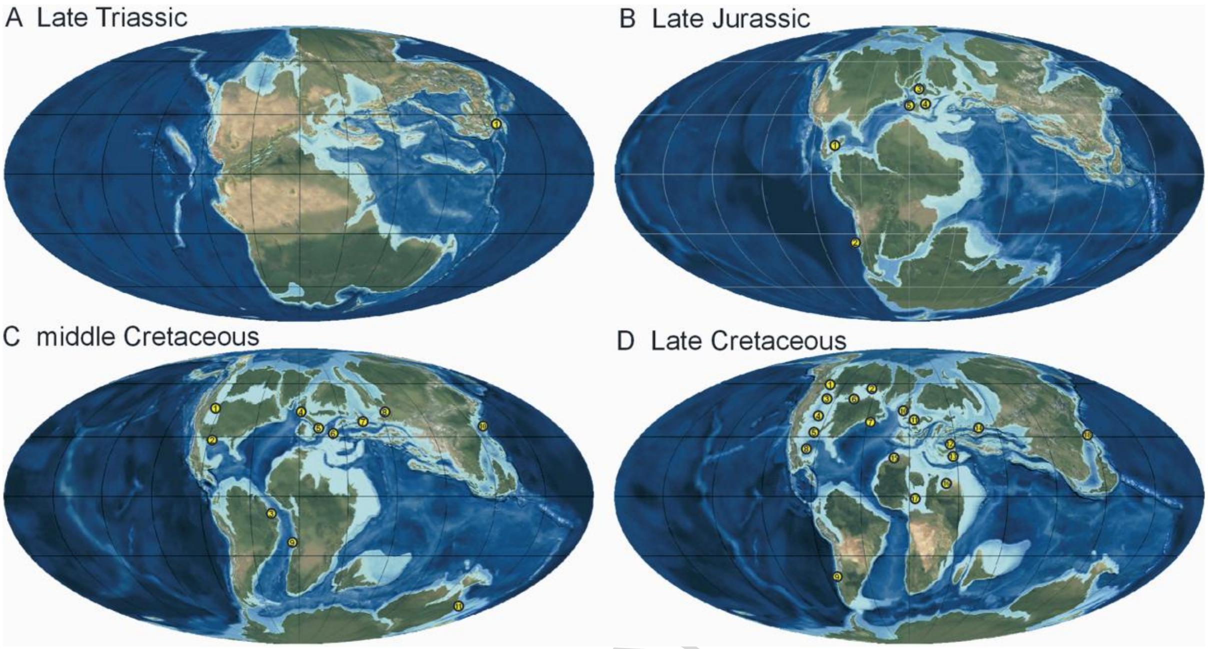

A Late Triassic
B Late Jurassic
C middle Cretaceous
D Late Cretaceous

Figure 5

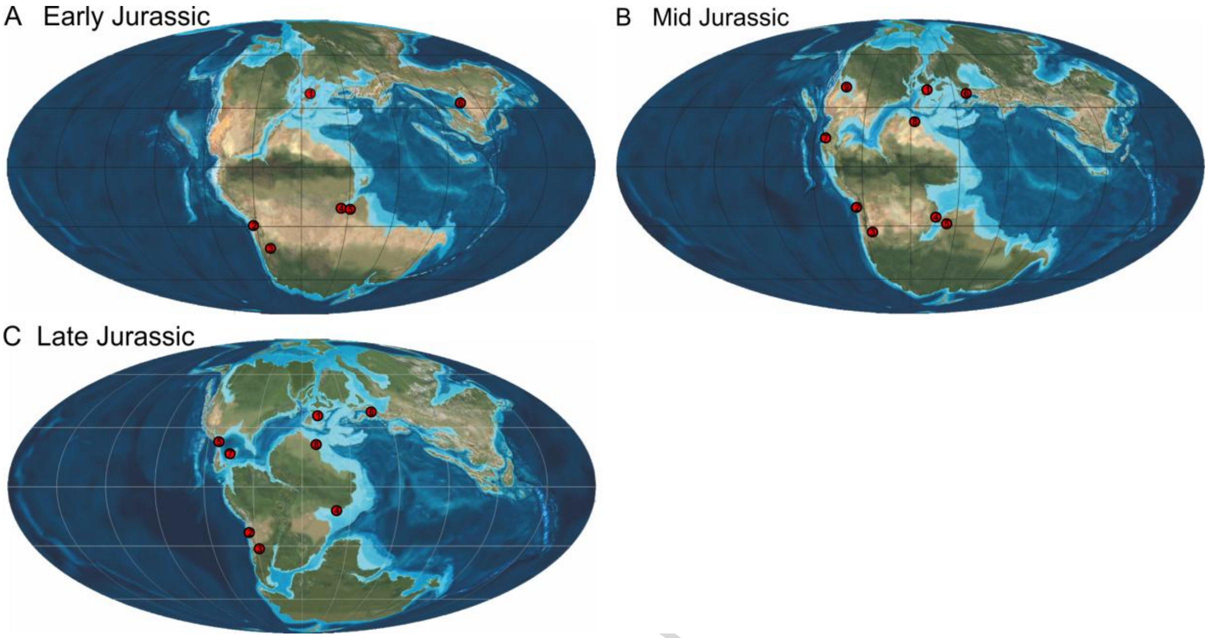


Figure 6

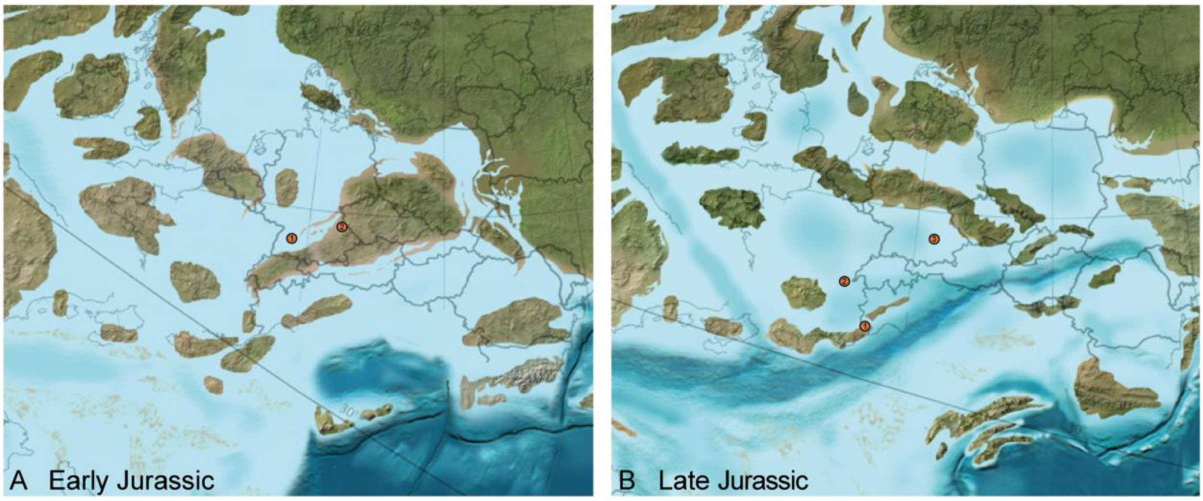


Figure 7

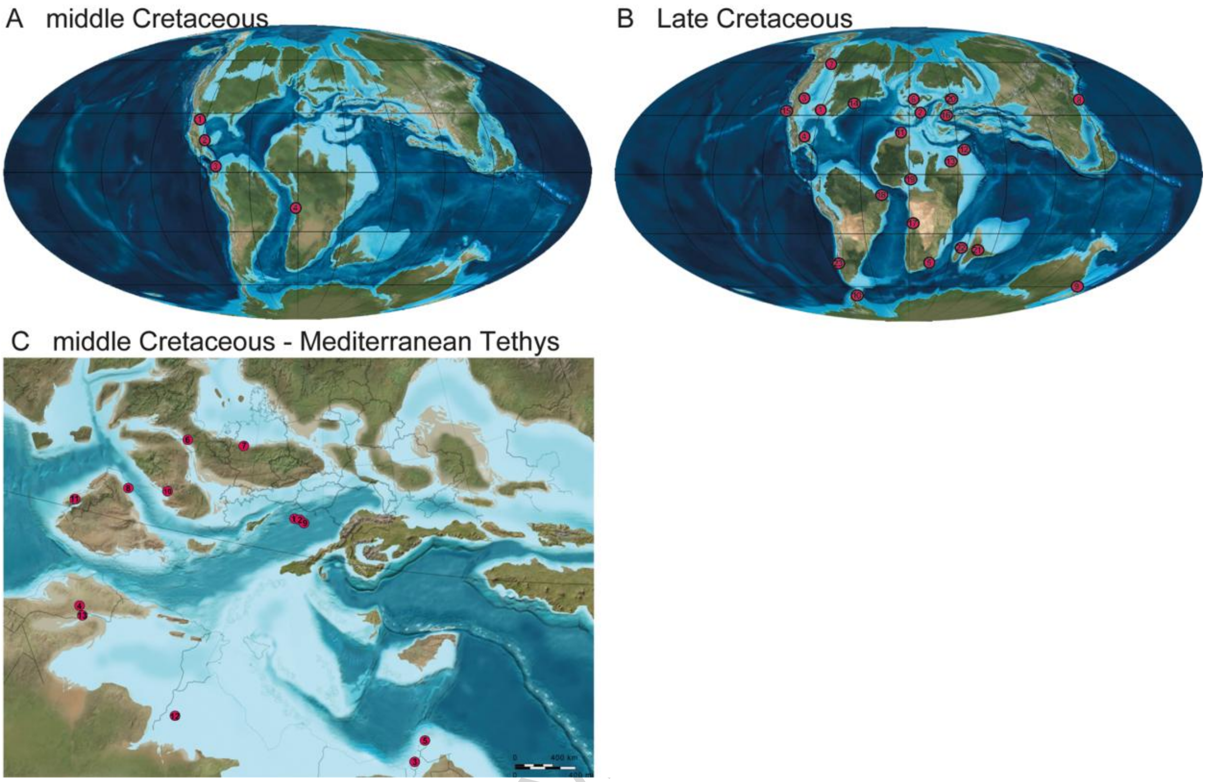
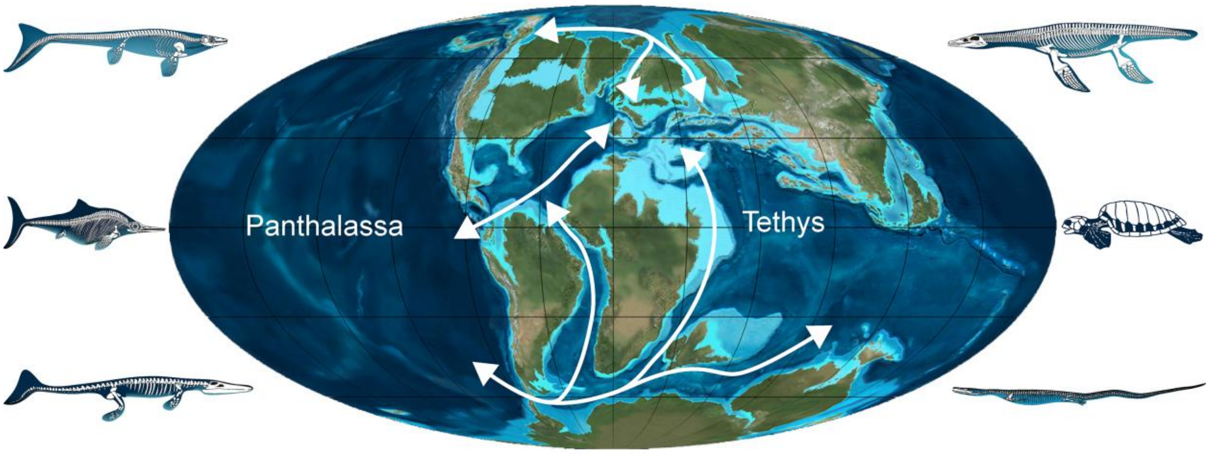

A middle Cretaceous
B Late Cretaceous
C middle Cretaceous - Mediterranean Tethys

Figure 8



Graphical abstract

Research Highlights

Reptiles underwent a spectacular return to an aquatic life during the Mesozoic.
Their palaeobiogeographical distribution closely followed the break-up of Pangaea.
They globally used the marine corridors created by this break-up to disperse.