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Middle Triassic sharks from the Catalan Coastal ranges (NE Spain) and faunal colonization patterns during the westward transgression of Tethys

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ABSTRACT

Palaeogeographic changes that occurred during the Middle Triassic in the westernmost Tethyan domain were governed by a westward marine transgression of the Tethys Ocean. The transgression flooded wide areas of the eastern part of Iberia, forming new epicontinental shallow-marine environments, which were subsequently colonized by diverse faunas, including chondrichthyans. The transgression is recorded by two successive transgressive–regressive cycles: (1) middle–late Anisian and (2) late Anisian–early Carnian. Here, we describe the chondrichthyan fauna recovered from several Middle Triassic stratigraphic sections (Pelsonian-Longobardian) located at the Catalan Coastal Basin (western-most Tethys). The assemblage consists of isolated teeth of the species *Hybodus plicatilis*, *Omanoselache bucheri*, *O. contrarius* and *Pseudodalatias henarejensis*. Our data complement a series of recent studies on chondrichthyan faunas from Middle-Late Triassic marine basins of the Iberian Peninsula, allowing us to evaluate patterns of faunal colonization. Sharks that reached East Iberia during the first transgressive pulse (Anisian) show strong affinities with the Sephardic bioprovince (related with the Neotethys Ocean) whereas a later increase in chondrichthyan diversity (during the Ladinian transgressive pulse) is due to the arrival of taxa with affinities to European faunas (Palaeotethys). This contrasts with recently evaluated colonization patterns of invertebrates and conodonts, where Middle–Upper Anisian assemblages are composed of taxa with affinities to the Alpine/Germanic bioprovince whereas faunas from the Sephardic bioprovince only reached the shallow waters of the Iberian peninsula during the second (Ladinian) transgressive pulse. The differences between chondrichthyans vs. invertebrate and conodonts colonization patterns are explained here on the basis of differing dispersal strategies. Our finding suggests the existence, during the Anisian, of connections between Palaeo- and NeoTethys through the western Cimmerian microcontinent, which served as pathways for the entrance of chondrichthyans from the Sephardic bioprovince.

1. Introduction

The Triassic is a key period to understand the evolutionary history of chondrichthyans, with the decline or extinction of several major Palaeozoic groups (such as xenacanthiforms, symmoriiforms, ctenacanthiformes and non-chimaeroid holocephalans), the increasing dominance of hybodontiforms, and the emergence of the modern sharks (Elasmobranchii). The Triassic was also an important period for the Iberian Peninsula in terms of palaeogeography. During these times, the western Tethys domain was characterised by important palaeogeographic changes and the subsequent advance of the broad westward marine transgression of the Tethys Sea that reached East Iberia during the Middle Triassic (Anisian) (Escudero-Mozo et al., 2015). This transgression, for the first time during the Mesozoic, flooded wide areas of the eastern part of Iberia, connecting some internal basins (i.e. Iberian and Catalan), which until this moment had been independent (e.g. Arche et al., 2004; Galán-Abellán et al., 2013; Escudero-Mozo et al., 2015), causing the demise of continental sedimentation and the consequent deposition of marine carbonates and mixed coastal facies (Muschelkalk).

In East Iberia, this general transgression is recorded by two transgressive-regressive cycles that show important palaeogeographic and fossil content changes (Escudero-Mozo et al., 2015). The first one (middle–late Anisian) took place from the NE to the Catalan Coastal

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Basin reaching the Iberian Basin through a narrow corridor bounded by palaeohighs. The second transgressive-regressive cycle (late Anisian–early Carnian) was characterised by an extensive transgression that covered a wide area of E Iberia including some of the previous topographic highs. After that, during the early Carnian, this area is characterised by the development of an extensive siliciclastic-evaporitic setting of the Keuper. These transgressive events resulted in the evolution of a diversity of epicontinental shallow coastal environments and associated colonization by marine faunas, including chondrichthyans. Accordingly, Middle Triassic faunas from the Iberian Peninsula reflect the transformation from continental settings to a wide variety of coastal and marine depositional environments owing to the Muschelkalk transgression, which occurred in the middle Anisian (Escudero-Mozo et al., 2015).

In this paper, we document for the first time the presence of chondrichthyans in the Middle Triassic rocks of the Catalan Coastal ranges (CCR). This paper is complementary to Pla et al.'s (2013) and Manzanares et al.'s (2018) studies on Middle–Late Triassic chondrichthyans from other areas of the Iberian Peninsula, i.e. the Iberian (IR) and Betic ranges (BR), respectively. Together, these three works give the first general overview of the chondrichthyan communities that inhabited the shallow epicontinental seas of the westernmost Tethys during the Middle to Late Triassic. This allows us to evaluate colonization patterns of the new shallow epicontinental seas of the western Tethys followed by coastal sharks and to compare it with invertebrate faunas. Findings require some adjustments of previous palaeogeographic reconstructions of the westernmost Tethyan realm for the Middle Triassic.

2. Geographical and geological settings

The Catalonian Coastal range is located in the north-eastern Iberian Peninsula (Fig. 1A) and includes two mountain chains that run parallel to the Mediterranean Coast in a NE–SW direction, from the Gerona region toward the Ebro delta, separated by the Prelitoral Depression (Sopeña and de Vicente, 2004; Escudero-Mozo et al., 2015).

The Catalonian Basin constituted an intracratonic basin that was mainly developed during Mesozoic times when it experienced some extensional periods with several *syn*-rift and post-rift phases (Vargas et al., 2009; De Vicente et al., 2009). It is dominated by longitudinal NE–SW faults and to a lesser extent by a conjugated NW–SE fault system (Vegas, 1975); the latter divided this basin into three domains with different subsidence (from SW to NE): Priorat-Baix Ebre, Prades, and Gaiá-Montseny (Marzo, 1980; Calvet and Ramon, 1987; Ramon and Calvet, 1987; Gaspar-Escribano et al., 2004). During the Cenozoic, Alpine compressional tectonics gave rise to the present-day Iberian range and Catalan Coastal range.

In the Catalonian Basin, the succession shows the three typical subdivisions of the Germanic Triassic, namely Buntsandstein, Muschelkalk and Keuper facies. In the Catalan Coastal range, the Muschelkalk facies is represented by two carbonate units ("Lower" and "Upper" Muschelkalk) that record the deposition of shallow to outer carbonate ramps, separated by a mixed evaporite-siliciclastic unit ("Middle Muschelkalk"). This facies, combined with the uppermost part of the Buntsandstein (or Röt) facies and the lower part of the Keuper facies, records two major transgressive–regressive cycles, respectively of middle–late Anisian and late Anisian–early Carnian age (Escudero-Mozo et al., 2014, 2015), each one related to the development of a wide carbonate ramp. The studied sections are constituted from materials of the "Lower Muschelkalk" (L'Ametlla section) from the Gaia–Montseny domain, and "Upper Muschelkalk" (Rasquera-Benifallet and Tivissa sections) from the Priorat-Baix-Ebre (Fig. 1B).

In the Gaia–Montseny domain, the Lower Muschelkalk shows an average thickness of 120 m, showing a sharp lower contact with lutite, carbonate and evaporite units (Röt facies) and a transitional upper contact with the Middle Muschelkalk. The unit was divided by Calvet and Ramon (1987) and Calvet et al. (1990) into four members, which correspond to El Brul (shallow subtidal to supratidal deposits), Olesa (lagoonal bioclastic carbonates), Vilella Baixa (open marine burrowed deposits) and Colldejou (white peritidal dolomite facies). Based on ammonoids, foraminifera, pollen and brachiopods, the Lower Muschelkalk unit is dated as middle–upper Anisian (Calvet and Marzo, 1994; Goy, 1995; López-Gómez et al., 1998; Márquez-Aliaga et al., 2000). Chondrichthyan remains are concentrated in different levels of the Olesa unit.

The L'Ametlla section is located close to the village of L'Ametlla del Vallès in the province of Barcelona, Catalonia, 35 km northeast of Barcelona City (coordinates at the base; 41° 43′ 18″ N and 2° 15′ 26″ W; Fig. 1A). The section and its fossil record have been studied previously by Márquez-Aliaga et al. (2000) and Plasencia (2009, and references therein).

In the Baix-Ebre Priorat domain, the Upper Muschelkak carbonates show a gradual to sharp lower contact with the "Middle" Muschelkalk and a gradual upper contact with the Keuper, and show an average thickness of 140 m. In this area, the carbonate unit was divided by Calvet et al. (1987) into several members from base to top that are: 1) Rojals Member (shallow subtidal to supratidal oolitic limestone and dolostone); 2) Benifallet Member (low energy subtidal bioturbated limestone and dolostone); 3) Rasquera Member (outer to middle ramp limestone, dolostone and shales with *Daonella*); 4) Tivissa Member (outer to inner ramp carbonates); and 5) Capafons Member (peritidal dolomites, marls and shales). Based on the ammonoids yielded by the Rasquera and Tivissa members and the sequence stratigraphic analysis, the Upper Muschelkalk has been dated as late Illyrian–late Longobardian (Goy, 1995; Escudero-Mozo et al., 2015). Conodonts from the same samples confirm a Ladinan age (Plasencia, 2009).

Both the Rasquera–Benifallet and Tivissa sections expose sediments of the five members as defined by Calvet et al. (1987). These sections are located in the province of Tarragona, Catalonia (Fig. 1A). The Rasquera–Benifallet section is along the road of Rasquera to Benifallet villages (coordinates at the base 40° 59′ 38″ N and 0° 32′ 22″ W), and the Tivissa section is close to Tivissa village (coordinates at the base 41° 02′ 33″ N and 0° 44′ 48″ W). Samples that have yielded chondrichthyan remains came from both the Rasquera and Tivissa members (Fig. 1B). Conodonts from the same samples confirm a Ladinan age (Plasencia, 2009).

3. Methodology

The specimens studied here were obtained by acid etching in 5–10% acetic acid, of more than 60 Kg of limestones (in samples of around 1.5 kg each) from the Rasquera–Benifatell, Tivissa and Ametlla sections. After dilution residues were sieved with sieves meshes of 2, 0.125 and 0.063 mm respectively, which created three fractions refer as the "total sample". Fig. 1B shows the stratigraphic position of all samples that have yielded chondrichthyan remains. Fossils were picked under a binocular microscope and photographed with an HITACHII S-4800 Electronic Microscope hosted at the Microscopy Services of the University of Valencia. The archived specimens are mainly isolated teeth and scales, housed in the Museum of Natural History of the University of Valencia (former Geological Museum of Valencia University), Spain (MGUV-36111 to MGUV-36113; and MGUV-36117 to MGUV-36131).

4. Results

The chondrichthyan assemblage found in the Middle Triassic of the Catalan Basin includes four species belonging to three different genera; i.e. *Pseudodalatias henarejensis*, *Omanoselache bucheri*, *O. contrarius* and *Hybodus plicatilis* (Fig. 2). A detailed Systematic Palaeontology section is provided as Supplementary material.

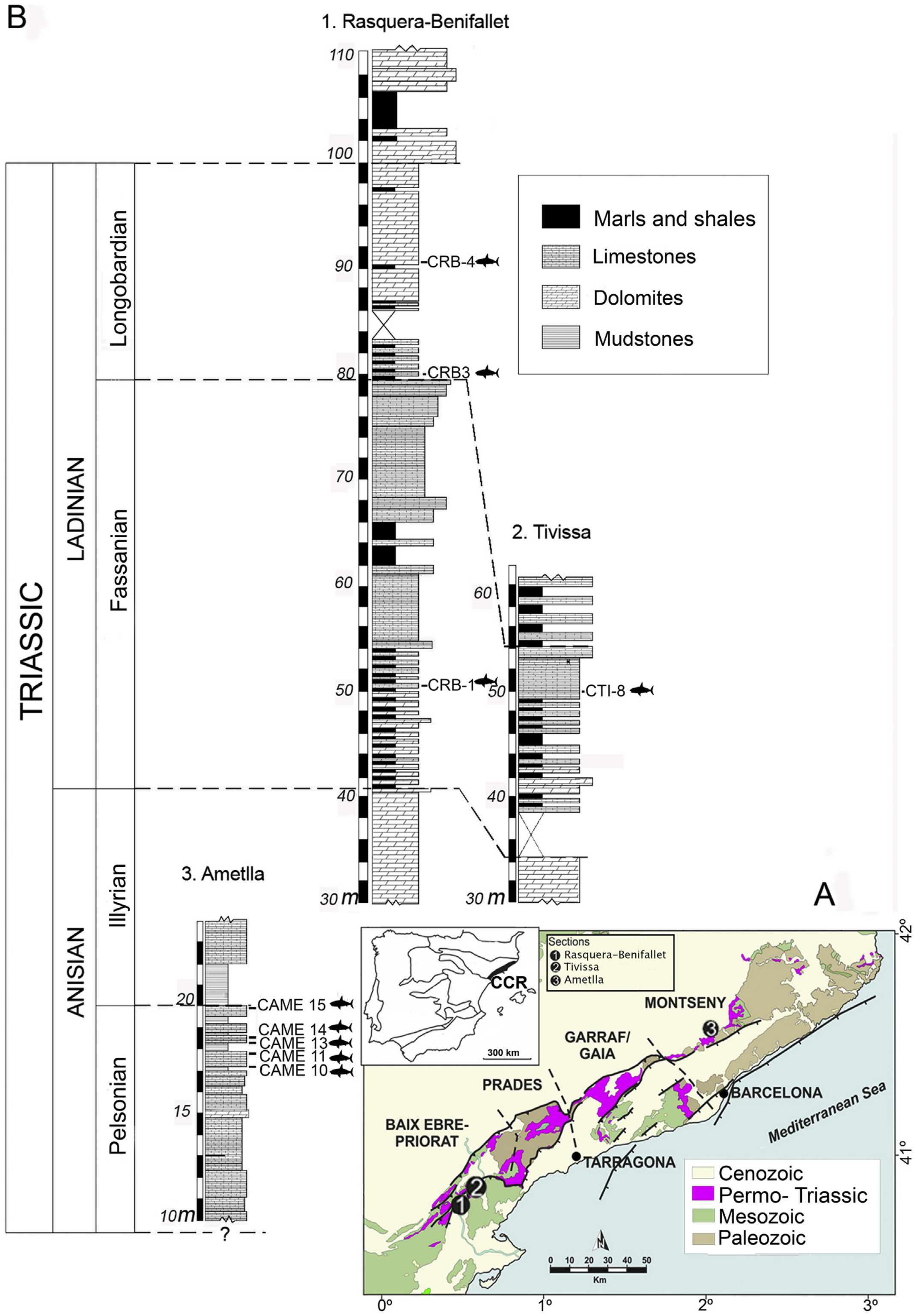

Fig. 1. Geographical and geological settings. A) Geographical setting of Catalonian Coastal Range (CCR) with location of sections studied here, modified from Escudero-Mozo (2015); B) Stratigraphic columns of the sections studied. Only levels where chondrichthyans remains were recovered are marked in the columns; for complete columns see Plasencia (2009).

5. Discussion

5.1. Middle Triassic sharks from the Catalan Basin in the context of the Iberian Peninsula

This association is similar to, but less diverse than, the chondrichthyan faunas recently described by Pla et al. (2013) and Manzanares et al. (2018) from other Middle-Late Triassic basins of the Iberian Peninsula (see also Botella et al., 2009; Ferrón et al., 2014; Manzanares et al., 2017). In fact, *P. henarejensis*, *O. bucheri*, *O. contrarius* and *H. plicatilis* are a typical selection of Middle Triassic forms from Iberia being also present in the Ladinian of both the Iberian and Betic

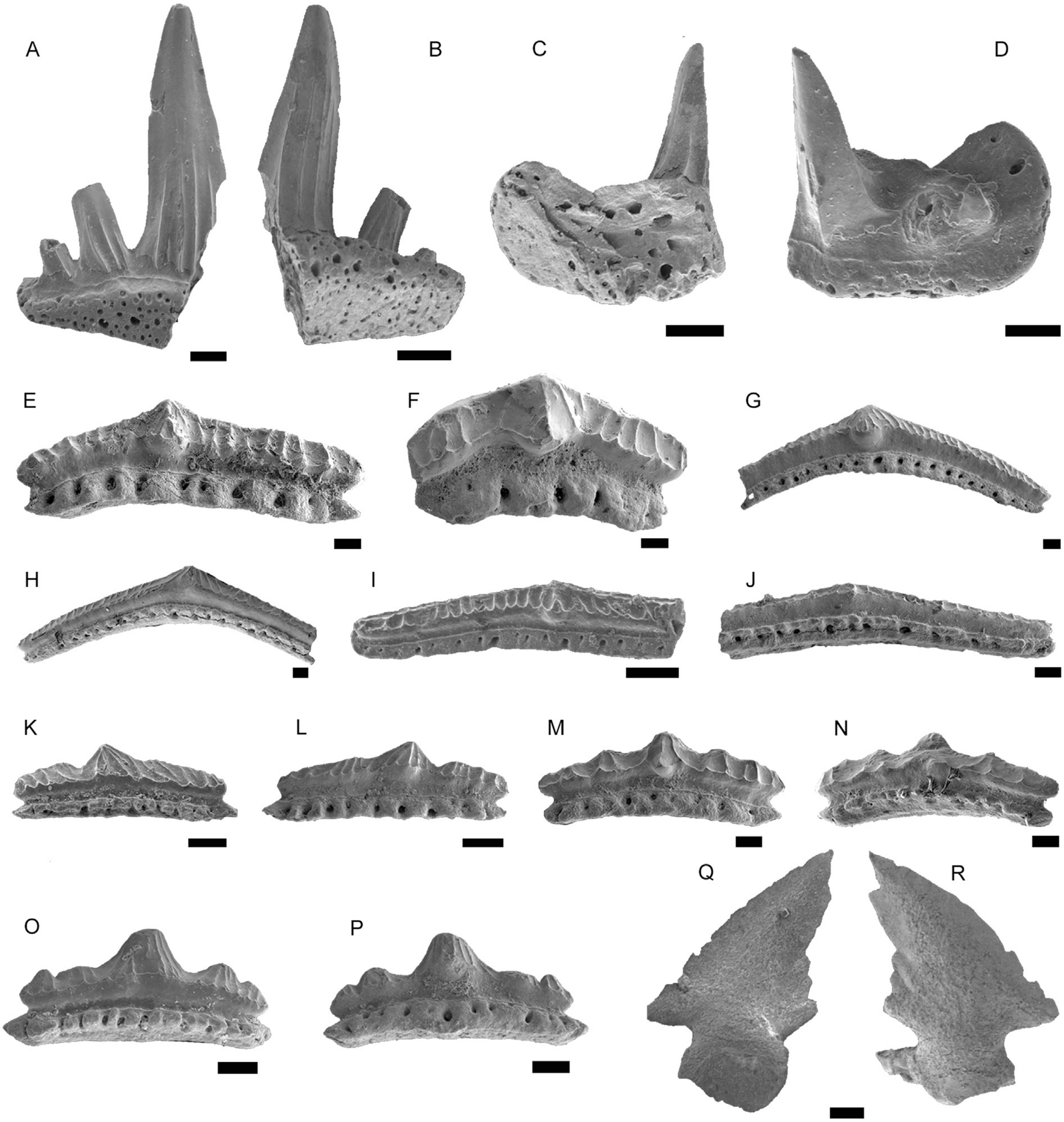

Fig. 2. Chondrichthyan teeth from the Middle Triassic of the Catalan Coastal Ranges, Spain. A–D) *Hybodus plicatilis*; A–B) labial and lingual view, MGUV-36111; C–D) basal and occlusal view, MGUV-36112; E–J) *Omanoselache bucheri* E) labial view, MGUV-36121; F) labial view, MGUV-36122; G–H) labial and lingual view, MGUV-36123; I–J) labial and lingual view, MGUV-36127; K–P) *Omanoselache contrarius*; K–L) labial and lingual view, MGUV-36127; M–N) labial and lingual view, MGUV-36120; O–P) MGUV-36118. Q–R) *Pseudodalatias henarejensis* in labial and lingual view, respectively, MGUV-36113. All scale bars equal 100 µm.

Ranges (Fig. 3 B).

In general, the Middle Triassic shark communities from the epicontinental seas of the westernmost margin of the Tethys ocean (i.e. east of the actual Iberian Peninsula) were largely dominated, in terms of diversity of species and abundance, by durophagous sharks with crushing dentitions (i.e. *O. bucheri*, *O. contrarius*, *Lissodus* aff. *L. lepagei*, *Lonchidion derenzii*), well adapted for grabbing and crushing prey with a hardened exoskeleton (e.g. crustaceans and mollusks). The teeth in general are small, suggesting that these sharks were also of small size, possibly in turn subsidiary prey of some of the larger aquatic reptiles, e.g. pachypleurosaurs, nothosaurs or ichthyosaurs, that were common in the same areas (Fortuny et al., 2011; Márquez-Aliaga et al., 2000), being these (most probably) the apex predators of these shallow marine environments.

The stratigraphic distribution of taxa in East Iberia (i.e. Catalonian, Iberian and Betic basins) is summarized in Fig. 3 A. Fig. 3B, providing synthetic information on the specific abundance. Teeth of *O. bucheri, O. contrarius* and *H. plicatilis* from samples of the Olesa Unit in section L'Ametlla represent the first report of Anisian (Pelsonian–lower Illyrian) sharks of the Iberian Peninsula showing that chondrichthyans reached the epicontinental shallow waters of NE Iberia during the first (middle–late Anisian) Triassic transgression. The stratigraphic record of all these three species extends up into the Carnian (Late Triassic) in the Iberian Peninsula, being also the most representative and abundant taxa.

On the other hand, an important increase of the chondrichthyan diversity in the Triassic Iberian basins occurs in the Longobardian, during the second transgressive–regressive cycle, with the appearance

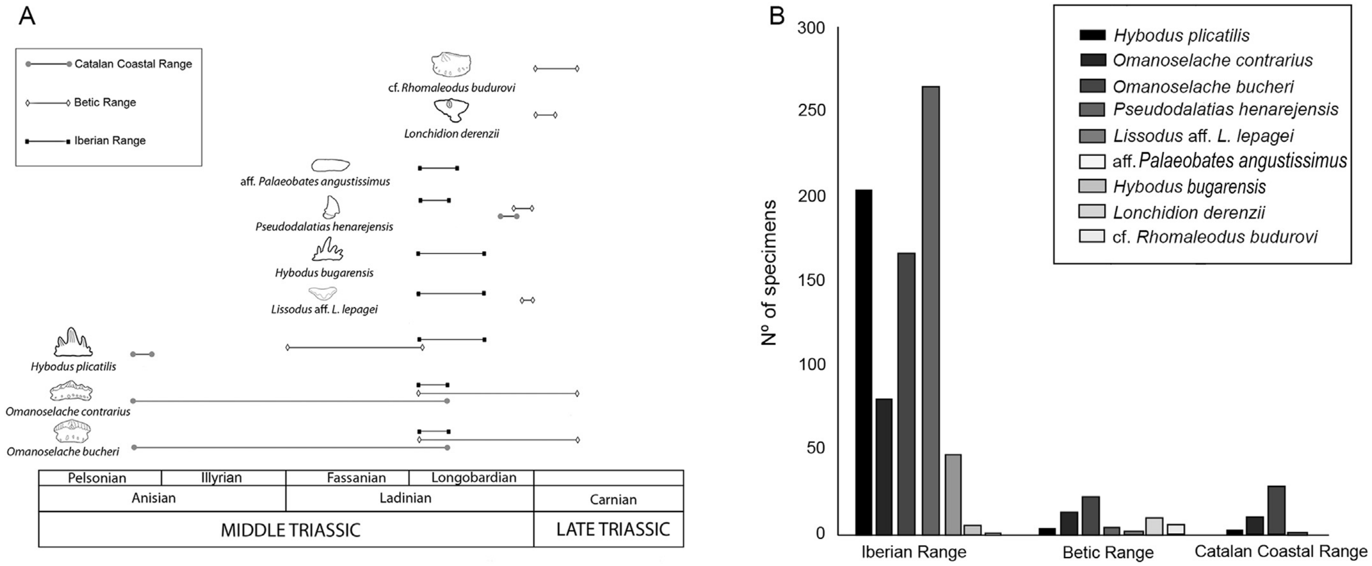

Fig. 3. Stratigraphic distribution and abundance of chondricthyans in Middle-Late Triassic of the Iberian Peninsula A) Stratigraphic distribution of taxa. *H. plicatilis*, *O. bucheri*, *O. contrarius* and *P. henarejensis* are the typical fauna that can be found in any Middle Triassic basin of the Iberian Peninsula. *Lissodus* aff. *L. lepagei* appears only in the Iberian Ranges and Betic Ranges, whereas *Hybodus bugarensis* and *Palaeobates angustissimus* have been only found in the Iberian Ranges. *Lonchidion derenzii* and cf. *Rhomaleodus budurovi* are only present at the Betic Ranges. B) Histograms showing the number of chondrichthyan teeth recovered (for each species) from in the three basins of the Iberian Peninsula considered in this study (the Iberian Range, the Betic Range and the Catalan-Coastal Range).

of several taxa, such as *Palaeobates angustissimus, Lissodus* aff. *L. lepagei, Rhomaleodus,* or *Pseudodalatias henarejensis* (Fig. 3A).

5.2. Biogeographical affinities of chondrichthyan vs. invertebrate faunas from East Iberia during the Triassic westward transgressions of the Tethys Sea

Recent evaluations on the evolution of invertebrate faunas from the Middle Triassic carbonate platforms in eastern Iberia reflect a drastic palaeobiogeographic change during the Upper Anisian. Thus, fossil associations (mainly bivalves, foraminifers, brachiopods and conodonts) from the Landete Formation (Iberian Range) and lower Muschelkalk (Catalan Coastal Range), both dated as Middle–Upper Anisian (Pelsonian–early Illyrian), are almost exclusively composed by taxa with affinities to the Alpine/Germanic bioprovince, related with the Palaeotethys Ocean. This has been interpreted as the Iberian and Catalonian Basins acting as a palaeogeographic gulf opening northwards, only connected with the Palaeotethys. The presence of geographical barriers should have prevented the entrance of faunas from the Sephardy bioprovince, related with the Neotethys (Escudero-Mozo et al., 2015; see fig. 19). In contrast, fossil associations of invertebrates and conodonts from the upper Anisian to upper Ladinian (late Illyrian–Longobardian; i.e. Cañete Fm., Iberian Range and upper Muschelkalk, Catalan Coastal Range) show a mixed origin, where, along with endemic species, typical species of both the Alpine/Germanic and Sephardic bioprovinces appear. This palaeobiogeographical heterogeneity of faunas has been linked to the second and most severe, transgressive–regressive cycle (late Anisian–early Carnian), which allowed for the colonization of shallow waters of the Iberian Peninsula by faunas coming from both Tethys provinces: the Germanic/Alpine to the north and the Sephardic to the south.

Noticeably, the stratigraphic distribution of Middle–Upper Triassic chondrichthyans in the Iberian Peninsula differs from this pattern of colonization. Thus, taxa that reached the new shallow-water environments of NE Iberia during the middle Anisian transgression (i.e. *Hybodus plicatilis, O. bucheri* and *O. contrarius*) do not show the clear Alpine/Germanic affinities reflected in invertebrate and conodont faunas. Only *Hybodus plicatilis* has been reported from other localities in Europe (see supplementary information) including Poland (Niedzwiedzki, 2008); Luxembourg (Delsate and Duffin, 1999); Bulgaria (Stefanov, 1966); Germany and UK (Korneisel et al., 2015). However, this taxon might be a cosmopolitan species from the Tethys realm as teeth assigned to *Hybodus* sp. *aff. Hybodus plicatilis* have been reported from the Middle Triassic of Saudí Arabia (Vickers-Rich et al., 1999). In European localities, *H. plicatilis* occurs in association with other “*Hybodus*”, *Acrodus, Polyacrodus, Lissodus* and some neoselachian species (Niedzwiedzki, 2008; Delsate and Duffin, 1999; Korneisel et al., 2015), which are absent in the Anisian of the Iberian Peninsula. In the same sense, the genus *Omanoselache* has never been reported from the other Triassic localities in Europe apart from the Iberian Peninsula occurrences. *O. contrarius* occurs in the Middle Triassic of Canada (Johns et al., 1997) and in the Middle–Late Triassic of Gualing, China (Chen et al., 2007), whereas *O. bucheri* is known from the Middle Triassic of Nevada, U.S.A. (Rieppel et al., 1996; Cuny et al., 2001). Pla et al. (2013) suggested that this species might have reached the Iberian Peninsula through the Sephardic province (i.e., the southern margin of the Tethys Ocean). The recent discoveries of several new *Omanoselache* species from the Middle Permian (Koot et al., 2013) and Lower Triassic (Koot et al., 2015) of Oman confirm the Sephardic affinities of the genus. Then again, the increase of the chondrichthyan diversity occurred during the second transgressive–regressive cycle (Longobardian, Fig. 3A) is due to the appearance of several taxa with clear affinities with Alpine/Germanic faunas, such as *Palaeobates angustissimus, Lissodus, Rhomaleodus,* or *Pseudodalatias* (Fig. 3).

5.3. Dispersal strategies, oceanic palaeocurrents and readjustment of palaeogeographic reconstructions; an overview

Oceanic currents therefore act as distinctive unidirectional corridors for passive dispersion of organisms with a microscopic pelagic life-stage (Zinsmeister and Emerson, 1979; Jablonski and Lutz, 1983). Consequently, palaeontologists have recognized for a long time that the distribution of some marine fossils are useful for reconstructing ancient marine current patterns. As Jablonski and Lutz (1983) pointed out, low (or high) faunal similarity between regions does not necessarily imply large (or small) geographic disjunctions, but rather it can reflect the prevailing current system.

In this sense, dispersion of bivalves, ammonites and foraminifers was largely determined by the dominant systems of marine currents. Most marine invertebrates include a microscopic, free-living, pelagic life history stage—the larval form. Larvae feed in the plankton (except for lecithotrophs) exhibiting long pelagic durations and high dispersal capacity. Distribution of these taxa is largely determined by ocean currents transporting larvae between distant patches of suitable habitat for adults, often over great distances (Scheltema, 1986; Jablonski and Lutz, 1983; Pechenik, 1999; Kinlan et al., 2005; Trakhtenbrot et al., 2005; Treml et al., 2008; Wangensteen et al., 2017). On the other hand, ammonites underwent a direct development lacking a distinct larval stage (as other, extant cephalopods: nautiluses, cuttlefishes, squids and octopuses) consisting of four ontogenetic stages (embryonic/egg, neanic, juvenile, and adult; see e.g. Westermann, 1996; Klug et al., 2015; Zell and Stinnesbeck, 2016; Tajika et al., 2018). Nevertheless, most authors consider that ammonite hatchlings – the neanic stage – were planktic, with ocean currents enhancing their dispersion. In fact, the patchy yet widespread palaeogeographic distribution of numerous ammonite species suggests that extensive planktic dispersal with ocean currents played an important role in their dispersion patterns (Zell and Stinnesbeck, 2016). The same is valid for foraminifers. Thus, for benthic attached species, such as those fossils found in NE Iberia (L. Marquez pers. comm. (2018), but see also the list of species in Escudero-Mozo et al., 2015), the most common ways of dispersion were, based on living forms (1) release of gametes, zygotes, or of embryonic agamonts/gamonts to the water column, and (2) adaption to a meroplanktonic juvenile stage with passive spread by currents. Moreover, shallow-water taxa can also be transported long distances by floating objects, larger animals and/or by suspended particles (Myers, 1936; Murray, 2006; Nomura et al., 2010; Alve, 1999).

In contrast, chondrichthyans lack any planktic stage but undergo a direct development after internal fertilization. They possess large eggs with a high amount of yolk and produce ovoviviparous or oviparous juveniles (there are some viviparous species). In any case, the distribution of the chondrichthyan species largely depends on the dispersal abilities of adults and much less on marine currents. In this sense, it is well known that the vagility of sharks is directly proportional to body size (e.g. Musick et al., 2004). As a whole, small-bodied coastal sharks present a very low vagility and short forage distances, with oceanic distances, deep channels or strong regional currents acting as dispersal barriers (Musick et al., 2004; Munroe et al., 2015; Whitney et al., 2012). Thus, dispersion of coastal species usually requires continuous appropriate habitats across regionally small geographical scales.

5.4. Palaeogeography and dominant marine currents at the westernmost Tethys

To consider the different dispersal capability of organisms is important in order to evaluate the timing and nature of palaeobiogeographical barriers. Taxa with planktic stages can provide considerable information for reconstructing marine palaeocurrent systems while taxa lacking these stages (or with low-dispersal larvae) can be used to infer continuity among continental shelves, both groups being affected differentially by palaeobiogeographic barriers (see e.g. Shuto, 1974; Jablonski and Lutz, 1983). Following these general rules, the existing differences in the colonizing patterns of invertebrate vs chondrichthyan faunas in the Triassic shallow waters of E Iberia can be reasonably well explained. However, it requires some adjustments of previous palaeogeographic reconstructions of the westernmost Tethyan realm (see Escudero-Mozo et al., 2015; their fig. 19 and references therein).

We suggest that the colonization by bivalves, ammonites and foraminifers, during both the late Pelsonian–early Illyrian and the late Illyrian–Longobardian marine transgressions, was largely determined (or enhanced) by the prevailing marine currents in the westernmost Tethys and by the transgression of the sea itself (Fig. 4).

Thus, in late Pelsonian–early Illyrian times, marine currents from the Palaeotethys enhanced the arrival of planktic organisms to the new Catalan and Iberian marine basins. At this time, the Cimmerian microcontinent, which controlled the regional palaeogeography in the westernmost Tethys (Yin and Song, 2013; Escudero-Mozo et al., 2015), would have acted as a barrier for marine currents (if any) of the incipient Neotethys. However, the occurrence of chondrichthyans from the Sephardic domain indicates the formation of narrow, probably temporary connections (acting as alternative routes for the entrance of sharks) between Palaeo- and Neotethys during the northward displacement of the Cimmerian microcontinent (Fig. 4). During the next greater and more generalized sea level rise (Illyrian–Longobardian transgression), the Tethys sea flooded vast areas of the westernmost Cimmerian microcontinent, such as Alboran, Majorca, Minorca, Sardinia, Corsica, Tuscany, Apulia, Mani (Escudero-Mozo, 2015: fig. 19). Subsequently, the Palaeotethys and Neotethys became broadly connected, allowing for the entrance of planktonic organisms (i.e. bivalve larvae, neatic ammonites and foraminifers, among others) into E Iberia, which were transported by marine currents from the Neotethys (Fig. 4).

Notably, during both colonization events, conodonts follow the same dispersion patterns as invertebrates and not those of chondrichthyans. Conodonts are considered by some authors a basal group of vertebrates (e.g. Donoghue et al., 2000) although their placement in this group is seriously questioned by other authors (e.g. Turner et al., 2010). Little is known about their reproductive strategies (with the finding of putative conodont eggs, von Bitter and Pohl, 2009), although it has been suggested, based on their crown growth and function (see Martínez-Pérez et al., 2014), that conodonts could had developed a larval stage (Shirley et al., 2018). Data here discussed are compatible with conodonts having a passive dispersive planktic stage. Planktic larval stages (or eggs) are present in several osteichthyan (bony fishes; common in teleosteans) but unknown in other fishes. A larval stage is present in agnathan lampreys (but not in mixines) and consists of a large sedentary burrowed larva in freshwater streams (e.g. Kelly and King, 2001), and could to be present in other extinct Palaeozoic agnathan fishes (Ferrón et al., 2018). The cosmopolitanism and high dispersal of Palaeozoic conodonts might also agree with a planktic dispersion drifted by ocean currents; however, further and more extensive studies on this topic are necessary to support this idea.

It should further be noted that, despite that our interpretation are well supported by data from Pla et al., (2013), Manzanares et al. (2018) and here, the number of specimens and taxa in the Iberian Peninsula is relatively low. Moreover, Triassic shark faunas are still poorly known in general. Therefore, new findings could change (or refine) this interpretation in the future.

6. Conclusions

This work completes a series of studies on the chondrichthyan faunas from Middle–Late Triassic of Iberia which has changed the previously inaccurate perception that chondrichthyans were rare, or completely absent, in the Iberian Peninsula. These studies provide now a detailed overview of the evolution of chondrichthyan communities in the new shallow-water environments developed in E Iberia (westernmost Tethys) during the Triassic westward transgression of the Tethys Sea. Chondrichthyan communities were largely dominated by small durophagous coastal sharks with crushing dentitions well adapted for preying on crustaceans and mollusks. Sharks that reach NE Iberia during the first transgressive pulse (middle–late Amirian) of the Tethys Sea show clear affinities with taxa from the Sephardic bioprovince, related to the Neotethys Ocean (i.e. *Omanoselache*). The notable increase in chondrichthyan diversity that occurs in E Iberia during the second transgressive pulse (Ladinian) is due to the arrival of new taxa with clear affinities with European faunas from the Palaeotethys Ocean (i.e. *Paleobates angustissimus, Lissodus, Hybodus, Rhomaleodus,* or *Pseudodalatias*). This colonization pattern is somewhat inverse to those recently evaluated for other fossil groups. Thus, Anisian bivalves, foraminifers, brachiopods and conodont faunas from E Iberia are almost

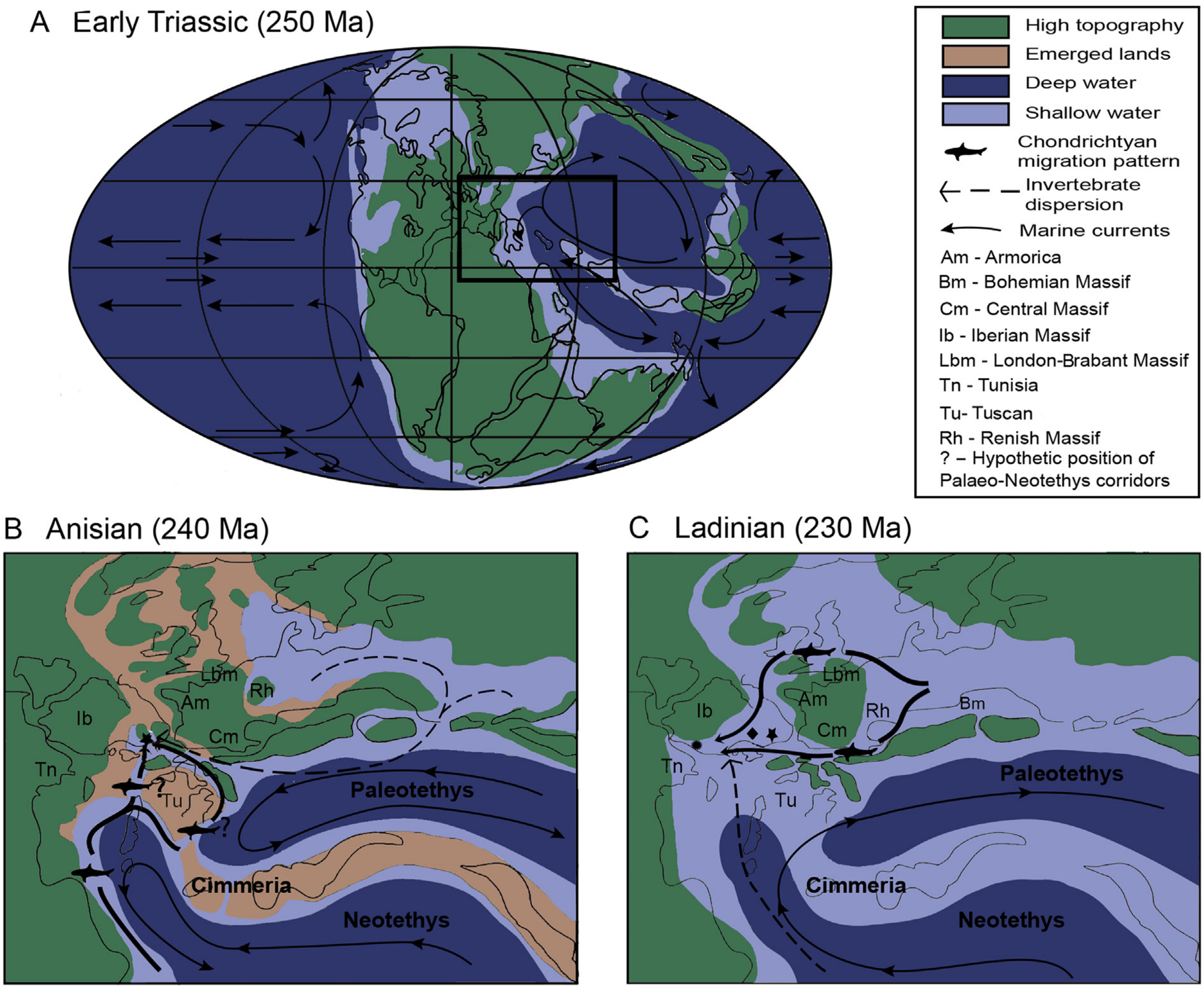

Fig. 4. Faunal colonization patterns of East Iberia during the Anisian and Ladinian westward transgression of the Tethys ocean. A) Global palaeogeographic map, Early Triassic (Induan), with schematic surface-current circulation. B–C) detailed palaeogeographic reconstructions of the westernmost Tethyan realm for the Anisian (B) and Ladinian (C) with interpreted colonization routes for chondrichthyans and invertebrates. Palaeogeographic maps modified from Scotese (1994) (A), Stampfli and Borel (2002) and Escudero-Mozo et al. (2015) (B); oceanic currents interpreted according with Yan and Zhao (2001); Crasquin et al. (2010) and Martindale et al. (2019). The black star marks the position of the Catalan Coastal Range, the black circle marks the Betic Range, the black diamond represents the Iberian Range.

exclusively compose of taxa from the Alpine/Germanic bioprovince. In contrast invertebrate and conodonts from the Sephardic bioprovince reach the shallow waters of the Iberian Peninsula for first time during the second (Ladinian) transgressive pulse.

The existing differences between the colonization patterns of sharks and other groups are explained on the basis of their dissimilar dispersion strategies: dispersion of bivalves, ammonites and foraminifers, is largely determined by oceanic currents whereas dispersion of coastal sharks depends of adult vagility (very low) and requires continuous appropriate habitats. Based on this, we propose some adjustments of previous palaeogeographic reconstructions including: (1) the existence of narrow, probably short-term, shallow-water corridors between Palaeo- and Neo-Tethys during the Anisian; (2) the Cimmerian microcontinent would have acted as a barrier for the oceanic currents in the incipient Neotethys, while currents from the Palaeotethys transported planktic organisms to the new Catalan and Iberian Marine Basins, and (3) during the next sea-level rise (Ladinian), the Tethys sea onlapped vast areas of the westernmost Cimmerian microcontinent allowing marine currents from the Neotethys to extend toward the Palaeotethys reaching E Iberian epicontinental seas.

Declaration of competing interest

We confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.109489.

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