

# Sharks and rays (chondrichthyes) from the Upper Cretaceous red beds of the south-central Pyrenees (Lleida, Spain): indices of an India–Eurasia connection

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## Abstract

Six chondrichthyan taxa are recorded in Late Cretaceous (Maastrichtian) red beds of the south-central Pyrenees (Tremp Formation, Lleida, Spain), indicating marine influence in the palaeoenvironment. Two ray species found in Spain have been previously described in India. One ray species conforms to the Gondwanan genus *Igdabatis* and the endemic Indian species *Igdabatis indicus* Prasad and Cappetta, 1993 [Prasad, G.V.R., Cappetta, H., 1993. Late Cretaceous selachian from India and the age of the Deccan traps. *Palaeontology* 36 (1), 231–248.] The other ray from the Tremp Formation is also close to the Indian material assigned to *Rhombodus* sp. 2. The limited dispersal abilities of benthic rays points to a shallow trans-Tethyan connection between Eurasia and India at the end of the Cretaceous. The data increase the evidence of a biogeographical relationship between Eurasia and Gondwanan continents at the Cretaceous–Tertiary boundary.

**Keywords:** Elasmobranchii; rays; Late Cretaceous; south-central Pyrenees; India; palaeobiogeography

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## 1. Introduction

The palaeogeographic relationship between Eurasia, Africa and India at the end of the Mesozoic seems well established by geodynamical data. Tethyan (since the Early Triassic) and Indian (since the Cretaceous) oceanic barriers are claimed to separate these continental plates, isolating them until the India–Eurasia collision in the Early–Middle Eocene (Patriat and Achache, 1984; Besse and Courtillot, 1988; Dewey et al., 1989; Treloar and Coward, 1991; Klootwijk et al., 1992; Dercourt et al., 1993).

Palaeogeographical study of continental fauna and flora, both terrestrial and strictly shelf organisms, shows differences between Gondwanan (Africa and India) landmasses and those of Eurasia, because of the Tethyan barrier. However, palaeontological data point to a connection between the Gondwanan and Eurasian continents at the end of the Mesozoic. Pollen, dinosaurs, crocodiles and mammals from Africa and Europe show strong affinities during the Late Cretaceous and early Tertiary (Gheerbrandt, 1987; Gheerbrandt and Russell, 1989; Buffetaut, 1989; Méon, 1990; Russell, 1993; Prasad et al., 1995, and references therein). In addition, charophytes, ostracodes, toads, lizards, crocodiles and mammals indicate a relationship between India and

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Eurasia at this epoch (Shani et al., 1982; Jaeger et al., 1989; Briggs, 1990; Prasad et al., 1995). Although some of these data have been challenged (Patterson and Owen, 1991; Thewissen and McKenna, 1992), the Late Cretaceous palaeobiogeography strongly suggests that migrations through Tethyan shelf or shoals were possible between Eurasian, African and Indian landmasses.

Different ways of connecting the margins of the Tethys by shallow shelves have been inferred: through the western Tethys, the eastern Tethys or the Indian Ocean (Chatterjee and Hotton, 1986; Gheerbrandt, 1987; Gheerbrandt and Russell, 1989; Jaeger et al., 1989). We present here additional evidence which supports the hypothesis of a close palaeogeographical relationship between Europe and India in the Late Cretaceous, based on new findings of fossil rays with Gondwanan affinities in Spain.

## 2. Geological setting

Coastal and continental deposits of the Cretaceous–Tertiary (K/T) transition reaching near 1000 m thickness occur in excellent outcrops on both sides of the Pyrenees. In the south-central Pyrenees (Trempe–Graus basin, Spain), Late Cretaceous and early Tertiary deposits are represented mainly by sandstone (Arén Formation) and red beds (Trempe Formation) interfingering along east–west exposures (Nagtegaal et al., 1983; Díaz Molina, 1987). The whole Arén Formation and the lower part of the Trempe Formation are of Maastrichtian age, the upper part of the Trempe Formation has an early Tertiary age. The age is based on the fossil content, including foraminifera (Caus and Gómez Garrido, 1989), molluscs (Bataller et al., 1953; Pons, 1977), ostracodes (Liebau, 1973), charophytes (Feist and Colombo, 1983; Galbrun et al., 1993), pollen (Médus et al., 1992; Galbrun et al., 1993), fishes (Soler-Gijón and De la Peña, 1995; Soler-Gijón and López-Martínez, 1995; De la Peña and Soler-Gijón, 1996), dinosaurs (Llombart, 1979; Llombart et al., 1984; Casanovas et al., 1987; Alvarez-Sierra et al., 1994; Sanz et al., 1995), and mammals (Alvarez-Sierra et al., 1994; López-Martínez et al., 1995). The succession represents a regressive–transgressive cycle: the Late Cretaceous Arén Formation and the base of the Trempe

Formation are interpreted as the deposits of a barrier island–lagoon system (Nagtegaal et al., 1983; Díaz Molina, 1987); afterwards around the K/T boundary interval, most of the Trempe Formation is interpreted as a deposit of continental waters (flood plains, fluvial channels and ponds; Rosell and Llombart, 1988; Puigdefàbregas et al., 1989); and, finally, some marine influence is detected at the top of the Trempe Formation (Late Paleocene; Krauss, 1990) just before the Ilerdian Pyrenean transgression (earliest Eocene).

The basin is tectonically broken into many parts so that correlation and palaeogeographic reconstruction are difficult. Two of the major parts are the Trempe and the Ager synclines which are divided by the Montsec thrust. They bear the four main localities (Orcau 2, Suterranya, Julí and Fontllonga 6, Lleida province; Fig. 1) containing fossil chondrichthyans. The first two localities outcrop at the northern flank of the Trempe syncline, and are situated at the base of the Trempe Formation. In particular, Orcau 2 is a greyish marl lying above a charophyte limestone bank with dinosaur footprints (Llombart et al., 1984) and underlain by a rudist bank with *Praeradiolites boucheroni* (Bayle) in life position. The Suterranya sample, slightly younger, comes from a gypsiferous marl containing oyster shells. It lies a few metres above a rudist level with broken, resedimented shells appearing in channel fill sandstones. Coal beds with abundant *Melanopsis* shells lie above the sampled level. The two sites are 3.5 km away from each other separated by a deep palaeocanyon (Díaz Molina, 1987).

The third locality, Julí, near Isona (Lleida), is a dark marl with complete shells of *Melanopsis* near the base of the 'Xulí' beds of Liebau (1973), lying above La Posa section. Ostracodes data allow this author to assign a 'middle Maastrichtian' age for the top of La Posa section which corresponds to the lower Trempe Formation.

The fourth locality, Fontllonga 6, is situated in the Ager syncline (Fig. 1), 20 km south of Trempe but probably affected by about 15 km of thrust shortening (Garrido-Mejías and Ríos Aragües, 1972; ECORS team, 1988). The Trempe Formation at the Ager syncline shows a different facies from that of the Trempe syncline. The lower part of the Trempe Formation at the Ager syncline has a 70 m thick limestone unit with algae (freshwater charophytes,

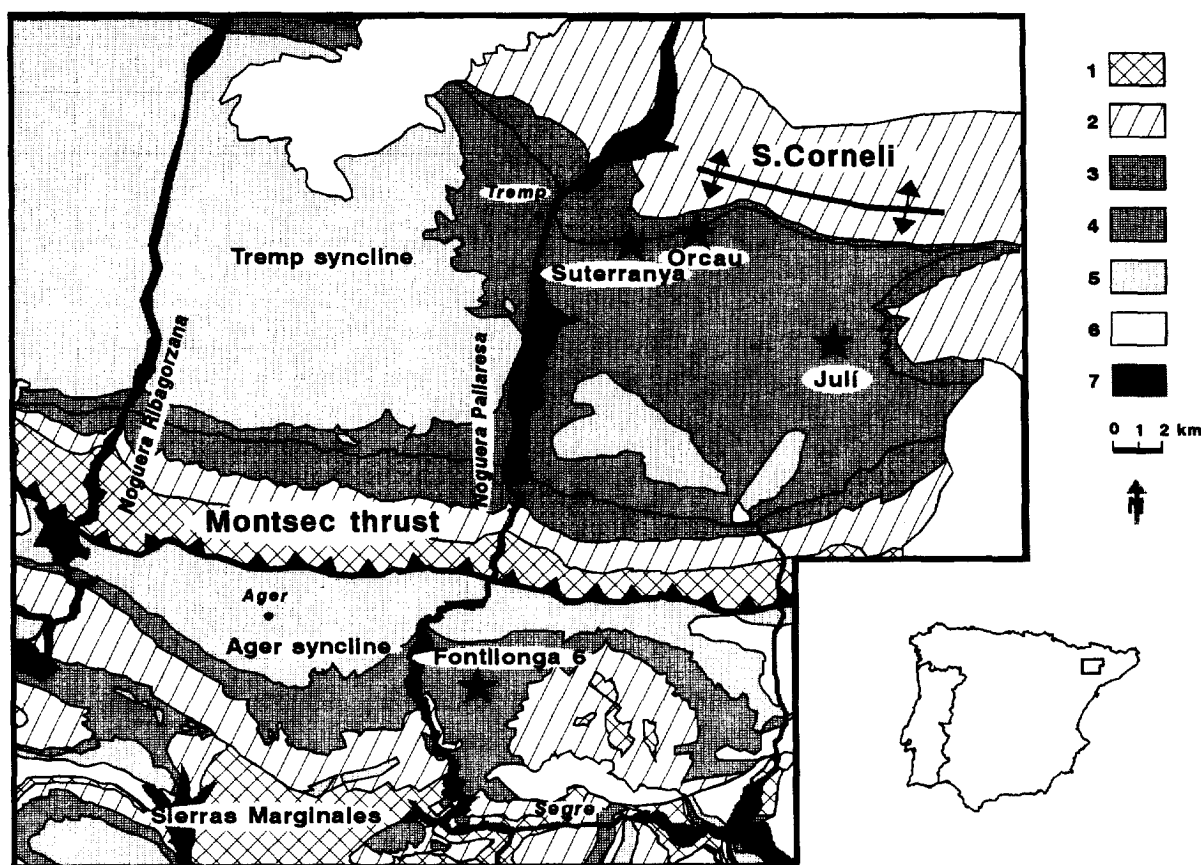


Fig. 1. Geological map of the Tremp and Ager areas (Lleida; data from Losantos et al., Generalitat de Catalunya) and location of the chondrichthyes samples. Legend: 1, pre-Upper Cretaceous–Mesozoic; 2, Upper Cretaceous; 3, Arenisca de Arén Fm., 4, Tremp Fm., 5, Lower Eocene; 6, Upper Palaeogene; 7, recent fluvial valleys.

marine *Girvanella*) and foraminifera, underlying red-dish beds containing a thickening–coarsening sequence of sandstone bodies with a tidal influence (units 1 and 2; Galbrun et al., 1993; Alvarez-Sierra et al., 1994). The sample with ray teeth is a grey clay with oncolites located in unit 2, 25 m above the base. It also contains remains of dinosaur, crocodiles, fishes, ostracodes and charophytes. Palaeomagnetic measurements situate this locality just in the lower part of the chron 31R (Galbrun et al., 1993). An early Maastrichtian age was suggested by Alvarez-Sierra et al. (1994) based on the presence of dinosaur eggshells similar to those of southern France (*Megaloolithus aureliensis*, *M. petralta*, *Prismatolithus tenuis* and *P. matellensis*; see Vianey-Liaud and López-Martínez, 1997). The re-

cent recalibration of the Campanian/Maastrichtian boundary confirm the correspondence of both data, around 70.5 Ma (Gradstein et al., 1995). The underlying rudist assemblages have a late Campanian–early Maastrichtian age (Pons, 1977). The Fontllonga section was extensively sampled for iridium traces with negative results (Galbrun et al., 1993).

### 3. Chondrichthyes

The chondrichthyans are represented by isolated teeth of 1 cm to less than 200  $\mu$ m. They occur together with other microfossils recovered by washing and screening large marl and clay samples (75 to 750 kg).

Six taxa have been identified, three sharks (*Lis-*

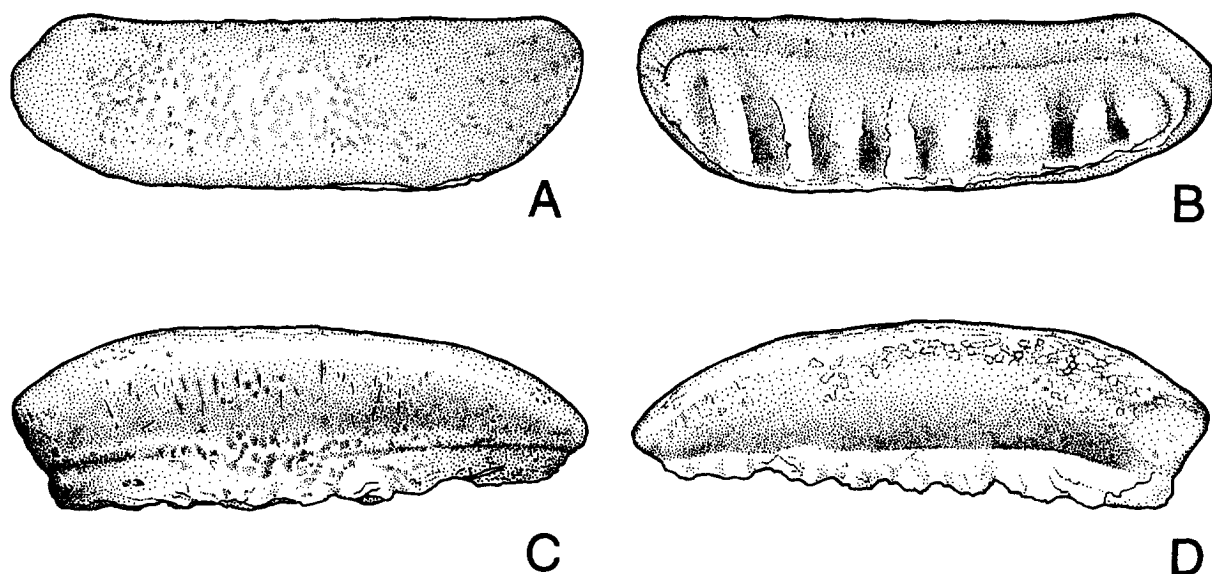


Fig. 2. *Igdabatis indicus* Prasad and Cappetta, 1993. Late Cretaceous (Maastrichtian) from Fontllonga 6 (Lleida, Spain). Median tooth, FONT6-7005. (A) Occlusal view. (B) Basal view. (C) Lingual view. (D) Labial view. Size 17.75 mm wide, 5.37 mm long and 5.50 mm high. Scale bar represents 0.5 cm.

*sodus* sp., *Hemiscyllium* sp. and Lamnidae indet.) and three rays (*Rhinobatos* sp., *Igdabatis indicus* and *Rhombodus* sp.; Soler-Gijón and López-Martínez, 1995; see Figs. 2 and 3). The three sharks come from the Orcau 2 sample, the only sample containing shark teeth. *Lissodus* (family Hybodontidae) is a genus with 33 species that becomes extinct at the Cretaceous–Tertiary boundary (Duffin, 1985, 1989; Duffin and Sigogneau-Russell, 1993). The genus *Hemiscyllium* (family Hemiscylliidae) was reported from Late Paleocene to recent times (Cappetta, 1987); however, Kriwet (1995) reports this genus from the Barremian of the Iberian Range. It contains species small in size (less than 1 m long) having a benthic life, eating small bottom fishes and invertebrates. *Rhinobatos* (family Rhinobatidae), recorded at Orcau 2, is a benthic ray living in shelves from 200 m depth to the intertidal zone. This genus is recorded from the Aptian to Recent (Cappetta, 1987).

The family Myliobatidae is represented in Fontllonga 6 and Suterranya by the Gondwanan genus *Igdabatis*, only known before from the Maastrichtian of Niger (*I. sigmodon*) and India (*I. indicus*; Courtillot et al., 1986; Cappetta, 1987; Prasad, 1989; Prasad and Cappetta, 1993).

The Spanish specimens are assigned to *Igdabatis* because the following features which are diagnostic at generic level, are present (Cappetta, 1987): the crown width varies in thickness of the middle to the lateral parts (lingual view); occlusal face is ornamented with fine pits; lateral and lingual faces bear folds; the lingual bulge is well marked; polyaulacorrhize root.

At specific level, the specimens of Fontllonga 6 and Suterranya are assigned to *Igdabatis indicus*. A total of 202 median and lateral teeth have been studied: 132 teeth from Fontllonga (1 complete and 2 fragmentary median teeth, and 129 lateral teeth) and 70 teeth from Suterranya (1 fragmentary median tooth and 69 lateral teeth). The ratio between median and lateral teeth is similar in both Fontllonga and Suterranya samples and the Indian sample: Prasad and Cappetta (1993) recorded 190 lateral teeth but six median teeth only. In addition, 51 small teeth from Fontllonga and Suterranya belonging probably to juvenile individuals have also been studied (see below).

The best preserved complete median tooth found in Fontllonga (specimen FONT6-7005; Fig. 2) clearly shows the diagnostic features of the Indian

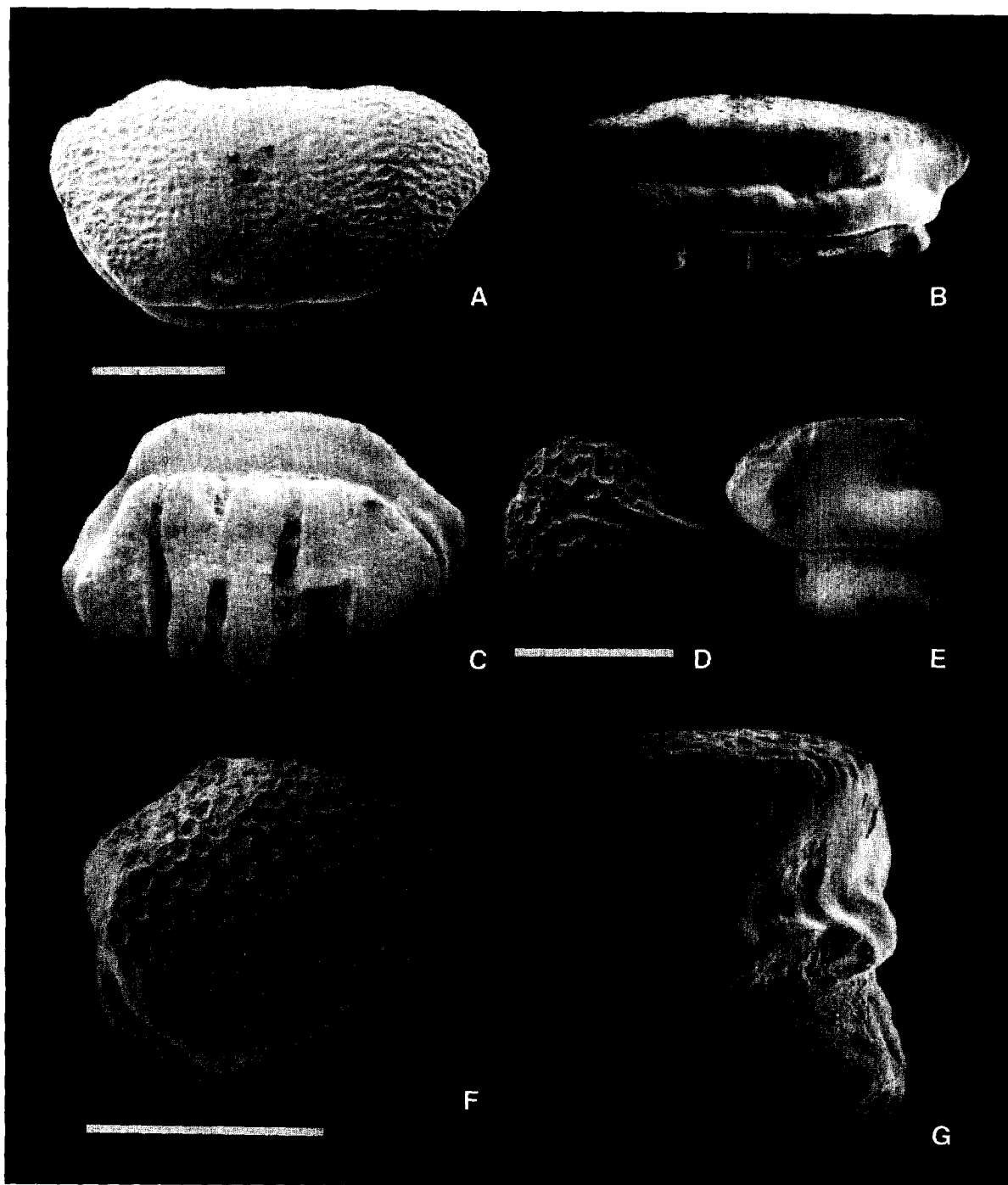


Fig. 3. *Igdabatis indicus* Prasad and Cappetta, 1993. Late Cretaceous (Maastrichtian) from Fontllonga 6 (Lleida, Spain). A, B — FONT6-7001, lateral tooth: (A) occlusal view; (B) lingual view. (C) FONT6-7003, lateral tooth: basal view. D, E — FONT6-7004, tooth of a young specimen: (D) occlusal view; (E) profile. F, G — *Rhombodus* sp. Late Cretaceous (Maastrichtian) from Fontllonga 6 (Lleida, Spain), FONT6-7006: (F) occlusal view; (G) lingual view. Scale bars represent 1 mm.

species. The size is similar to the largest tooth from the Indian sample. The occlusal surface is partially worn but the characteristic pitted ornamentation is still well preserved in some areas. The contour of the crown is arcuated in occlusal view; the lingual border is convex whereas the labial border is slightly concave. The crown also shows an acute lateral angle pointing labially. The lingual bulge exhibits a corrugate surface. The preserved root presents nine lobes of variable width and eight grooves. The lateral teeth from the Pyrenees (Fig. 3A–C) are also closely similar in size and morphology to those from India. They share the following features: size does not exceed 5 mm width; in occlusal view, the crown shows hexagonal or subtrapezoidal outline and rugose-pitted ornamentation; the root, less high than the crown has lobes of variable width. The 51 juvenile teeth (Fig. 3D,E) are about 1 mm wide. The crown projects lingually forming a cusp. The root is bilobate. Similar small teeth, ranging from 0.9 to 1.5 mm in width, have been described in India by Prasad and Cappetta (1993).

The Spanish teeth clearly differ in size and shape from *I. sigmodon* Cappetta, 1972 from the Maastrichtian of Niger. The teeth from Spain are smaller (17 mm wide for the median teeth and less than 5 mm for the lateral teeth, against 26 mm and 10 mm, respectively, in *I. sigmodon*). In *I. sigmodon* the teeth differentiate a sort of uvula in the lingual bulge above every root groove (see for example the holotype, Cappetta, 1972, pl. 8, fig. 3), which is absent in the Spanish and Indian teeth. Moreover, the Spanish and Indian teeth lack the sigmoidal contour, the specific character of *I. sigmodon*.

The teeth from Fontllonga and Suterranya are distinct of those from *Garabatis*, a ray from the Paleocene (Thanetian) of Morocco (Ouarzazate basin) which appears to be similar in several aspects to *Igdabatis* (Cappetta, 1993). The Paleocene ray is much smaller than the Cretaceous ones (2.5 mm maximum width, 1 mm height in the median tooth from *G. atlasi*, against more than 10 mm in width and 5 mm in height from Fontllonga; 1.5 mm for the lateral teeth of *Garabatis* against more than 3 mm in Fontllonga and Suterranya). Morphologically, *G. atlasi* differs from the Spanish and Indian material in having smooth labial and lingual crown faces.

*Rhombodus* sp. from Fontllonga 6, Suterranya

and Julí, belongs to the extinct Cretaceous family Rhombodontidae. Their living closest relatives are the Myliobatidae, habitants of shallow tropical seas. No member of this family is known to ascend rivers, as some rays of the family Dasyatidae do. This supports the inference of a marine influence in the lower part of the Tresp Formation at the Tresp and Ager synclines (Alvarez-Sierra et al., 1994). The genus *Rhombodus* has a wider geographic distribution than *Igdabatis*. In addition to the Indian specimens classified as *Rhombodus* sp. 1 and *Rhombodus* sp. 2 (Prasad and Cappetta, 1993), numerous teeth comprising five species have been described: *R. levis* (early Maastrichtian of New Jersey, USA); *R. binkhorsti* (Maastrichtian of northern Europe, Near East, Africa and South America); *R. meridionalis*, *R. microdon* and *R. andriesi* (Maastrichtian of Morocco) (Cappetta, 1987; Noubhani and Cappetta, 1994).

The isolated teeth of the Pyrenees assigned here to *Rhombodus* sp. (see Fig. 3F,G) present the following features common to the genus: high, massive and rhombic crown in occlusal view; flat or slightly convex occlusal surface with rugose and pitted ornamentation; salient lingual bulge lacking an uvula; bilobate root with a flat basal face (cf. Cappetta, 1987; Noubhani and Cappetta, 1994). The Spanish *Rhombodus* sp. resembles the Indian specimens *Rhombodus* sp. 2 more than any other species. Both are similar in size (1.4–4 mm wide for the Indian specimens, 1.04–4.05 mm for the Spanish material, 1.94 mm average from 28 specimens) and morphology (U-shaped, broad and smooth lingual bulge; margino-lingual faces smooth, lacking dense and marked vertical wrinkles). Other species differ from the Spanish *Rhombodus* sp. in size and/or morphology. *R. microdon* is similar in size and crown-root ratio but differs in the lingual bulge, with an angled outline in occlusal view, and the margino-lingual faces having vertical wrinkles. *R. binkhorsti*, *R. meridionalis* and *R. andriesi* differ in the same features and are also of a larger size. *R. levis* clearly differs because of its larger size, the smooth-crowned condition and the reduced development of the lingual bulge.

The mode of life of fossil taxa is inferred on the base of that of their Recent relatives, as are physiology and function. The differences in size and shape

allow us to distinguish between small benthic and large pelagic forms. Most rays have benthic habits during their complete lifespan, lacking the adaptive features of pelagic elasmobranch (oil-filled liver for buoyancy, fusiform body and powerful tail for navigation). Only two Tertiary families (Myliobatidae and Mobulidae) have adopted a more pelagic mode of life during the Neogene. Most of the skates and rays are found in shallow waters; exceptionally they descend to the bathyal zone near 1500 m depth, 3000 m being their deepest record. From their ecology and distribution it seems that they do not cross deep ocean basins (Springer, 1982). Therefore, sharing of ray species by two continents is generally considered as a good indication for a shelf connection. Conversely, the endemic species give a key for oceanic barriers and continental isolation. Long (1994), for example, documents a settlement of skates in Antarctica during the Palaeogene migrating through continental margins and corridors; later on, skate species became endemic because of their isolation in the Neogene by deep and wide basins formed around Antarctica.

#### 4. Results

The shark and ray teeth recovered from the Late Cretaceous deposits of the Pyrenees document a rather diversified marine fauna. Six taxa are found in a rather limited sample of about hundred specimens from four localities. No chondrichthyan record was available before from this area and epoch. These new finds have important consequences for the interpretation of the palaeoenvironment as well as the palaeogeography.

##### 4.1. Palaeoenvironment

The Late Cretaceous Pyrenean basin is reconstructed either as a foreland basin or as a remnant basin (Nijman, 1989) setting, north of the Ebro Massif which emerged during the Mesozoic. A major source area for the deposits of the Arén and Tremp formations was situated in the south and southeast, the basin being situated to the northwest (Nagtegaal et al., 1983). Thrust-related anticlines, like San Corneli anticline (Fig. 1) started to grow and emerge

south of the axial zone of the incipient Pyrenees during the Late Cretaceous. The palaeoshoreline was situated just south of S. Corneli, oriented east–west and prograded westwards (Díaz Molina, 1987).

The lower part of the Tremp Formation at Orcau and Suterranya contains palaeontological evidence of a marine influence other than sharks and rays, which includes oysters and rudist banks. In the neighbouring Isona area (La Posa section), Liebau (1973) interpreted the rudist levels interbedded with coal beds as marine episodic transgressions flooding a coastal swamp. Nagtegaal et al. (1983) and Díaz Molina (1987) interpreted these facies as lagoonal sediments of a barrier island–lagoon complex prograding from the southeast towards the northwest. The sandstone bodies of the Arén Formation would represent the successive positions of these barrier islands.

Most of the Tremp Formation is supposed to consist of non-marine red beds in origin (fluvial plain red clays, channel fill sandstones and lacustrine limestones). In particular, the Julí beds and units 1 and 2 in the Ager syncline at Fontllonga are generally interpreted as devoid of marine influence (Liebau, 1973; Puigdefábregas et al., 1989; Galbrun et al., 1993). Tidal influence has, however, been detected in the channel fill sandstones from the upper part of unit 2 (Llompарт and Krauss, 1982; Alvarez-Sierra et al., 1994), but the lower part of the unit contains mainly clays and limestones with few thin detrital oncolite beds, which are not indices of typical fluvial estuarine conditions.

In such a situation, the finding of diverse marine fish remains in the Julí beds and in the lower part of unit 2 at Fontllonga 6 indicates that coastal environments with an important marine influence extended more than 35 km landwards from the inferred Late Cretaceous shoreline. Also the unit 1 limestones were found to contain *Girvanella*-type algae and benthic foraminifera, suggestive of marine influence (Alvarez-Sierra et al., 1994). Consequently, we interpret the Tremp Formation at the Ager syncline as probably part of a large coastal plain some kilometres south from the lagoon–barrier island. The marine influence was not apparently limited to tidal currents in fluvial channels, as low-energy clay and limestone deposits also contain marine taxa. Thus, we infer for the lower part of the Tremp Formation a type of landscape similar to the modern Everglades

(Florida, USA): a large, flat coastal plain landwards of the lagoons with a fuzzy shoreline. This would explain the co-occurrence of taxa with freshwater and marine inhabitants of the region.

#### 4.2. Palaeogeography

The Indian rays *Igdabatis indicus* and *Rhombodus* sp. recorded in the Pyrenees raises again the question of the isolation of India during the Cretaceous, and whether the Tethys ocean acted as an effective barrier for shelf organisms.

*Igdabatis* was considered a Gondwanan endemic genus, indicating isolation of the ancient continent. In addition, the two species, *I. sigmodon* and *I. indicus*, restricted to Africa and India, respectively, would reflect the biotic consequences of the tectonic splitting of Gondwana. However, the record of *I. indicus* in the Pyrenees challenges the accepted palaeogeographical picture (Fig. 4). We examine below other arguments relevant to the hypothesis of a trans-Tethyan connection in the Late Cretaceous. The alternative hypothesis of a modification in the mode of life of rays through time seems less probable, as that would need strong changes in the

anatomy and physiology of these organisms leaving no evidence in the recent nor fossil record of taxa.

Besides the ray *Igdabatis indicus*, the record of related continental-shelf taxa in Eurasia and India during the Late Cretaceous includes pelobatid and discoglossid frogs, anguid lizards, alligatorid crocodiles and palaeoryctid mammals, as well as ostracodes and charophytes, none of these organisms being able to dispersal over oceanic barriers (Prasad et al., 1995). The authors suggest a direct connection between India and Eurasia through the Himalayan region during the Late Cretaceous, whereas an oceanic barrier of some 1000 km width is suggested by plate reconstructions (Besse and Courtillot, 1988; Dercourt et al., 1993).

Continental Gondwanan taxa common in Africa, South America and India, such as titanosaurid and abelisaurid dinosaurs, are recorded in the Late Cretaceous of Europe (France, Spain, Rumania; see Sanz and Buscalioni, 1987; Buffetaut, 1989; Le Loeuff, 1991; Weishampel et al., 1991). Also terrestrial crocodiles, birds (such as ratite and phorusrhacid birds) and mammals (ant-eater edentates) with Gondwanan affinities appear in the lower Tertiary of Europe (Antunes, 1975; Storch, 1986, 1990; Buffe-

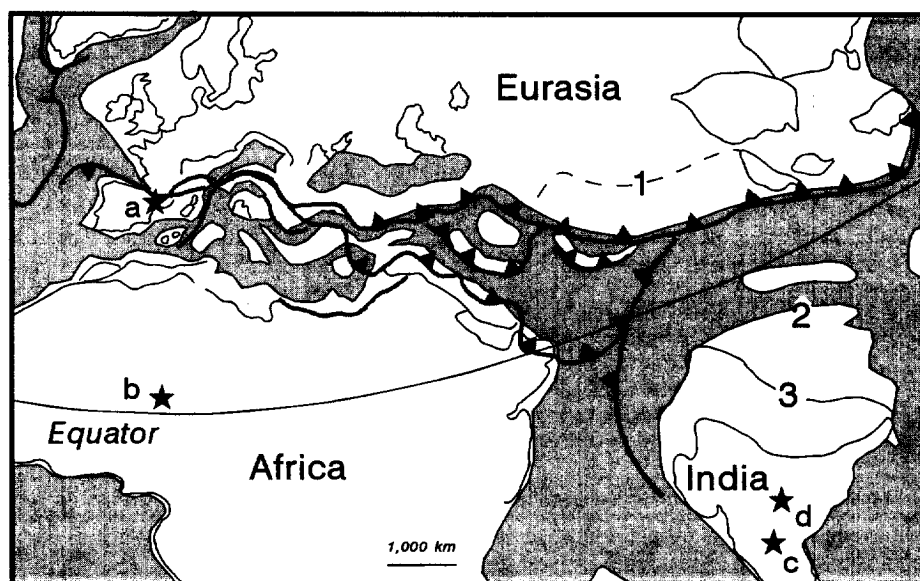


Fig. 4. Palaeogeography of the Tethys region during the late Maastrichtian. Shaded areas, oceanic basins; white areas, emerged land and shallow seas. Data from Dercourt et al. (1993); 1, fit of the Indian continent after collision; 2, contour estimate of Greater India after Lee and Lawver (1995), and 3, after Treloar and Coward (1991). Stars indicate the localities with *Igdabatis* rays: a, Trep-Ager basin (Spain); b, Mont Igdaman (Niger); c, Marepalli; d, Asifabad (India).



taut, 1988; Peters and Storch, 1993; Ortega et al., 1993). Moreover, mammals with Eurasian affinities are recorded in the Paleocene of Morocco (Gheerbrandt, 1987; Gheerbrandt and Russell, 1989) and in the Cretaceous of India (Prasad et al., 1995). Additionally, palaeobotanists recognize strong European affinities in the African flora around the K/T boundary (see Méon, 1990 and references therein). The similarity between African, Indian and European terrestrial taxa indicates a close palaeobiogeographical relationship between both sides of the Tethys during the Late Cretaceous–early Tertiary. A western closure was suggested as the most probable trans-Tethyan way between Africa and Europe (Chatterjee and Hotton, 1986; Briggs, 1990). Continental margin collision may locally have occurred along the Alpine belt in the Late Cretaceous by interaction of several blocks (e.g. the Alborán microcontinent domain, the Apulian ‘African promontory’, etc.; Coward et al., 1989; Ziegler, 1989; see Fig. 4). The Tethyan straight in the Gibraltar region, reconstructed as an en-échelon series of pull-apart basins by Andrieux et al. (1989) was shrunk since at least 85 Ma. Thus it was probably a narrow and shallow basin at the Cretaceous–Tertiary boundary, making probable the migration of continental organisms.

However, the relation between Europe and Africa does not explain that between Europe and India. On the other hand, a connection between Africa and India at this epoch as proposed by some authors (Krause and Maas, 1990; Briggs, 1990; Russell, 1993) is hardly compatible with current plate kinematic reconstructions (Courtillet et al., 1986; Besse and Courtillet, 1988; Klootwijk et al., 1992). The western junction thus cannot account for the Indian–Eurasian affinities, and consequently an eastern bridge across the Tethys seems necessary. The timing of the Eurasia–India collision has been estimated to ca. 45 Ma (Middle Eocene; Dewey et al., 1989; Rowley, 1996) or ca. 54 Ma (Early Eocene; Patriat and Achache, 1984; Treloar and Coward, 1991). Jaeger et al. (1989) favoured an earlier contact between India and Asia, around the Cretaceous–Tertiary boundary, through the landmass of ‘Sundaland’ (Yunnan, Indochina, Thailand and Shan), then situated north of India in an intermediate position. During the Tertiary, Sundaland would then become extruded from there a thousand km towards the southeast (Tap-

ponnier et al., 1986; Lin and Watts, 1988; Sengör, 1993; see Dewey et al., 1989, against this view).

A early continental contact between Asia and India was probably favoured by an important northern extension of India (the ‘Greater India’; see Boulin, 1981) now shortened and subducted in the Himalaya and under the Tibetan plateau. It has been estimated to be about 500 km by Coward and Butler (1985) and about 1500 km by Powell et al. (1988) and Lee and Lawver (1995). Fig. 4 shows the estimation of Greater India by Lee and Lawver (1995) and that by Treloar and Coward (1991).

Ophiolite obduction and olistolite deposits in an anoxic basin during the Late Cretaceous–early Tertiary have been recorded between Asia and India (Cannat and Mascle, 1990; Searle et al., 1997), both signals of tectonic uplift probably indicating the starting collision (but see Coward, 1994). Lee and Lawver (1995) detect indices of an early contact between India and Asia by mid-Paleocene (58 Ma), when the convergence rate drops to 11 cm/year after an exceptionally 17 cm/year high rate around the Cretaceous–Tertiary boundary. This is the ‘soft collision’ stage, the ‘hard collision’ being when convergence dropped to about 6 cm/year in the Middle Eocene (45 Ma).

The dispersal route between India and Asia was probably favoured by intermediate continental fragments, such as the Gondwanan Mount Victoria, Sikuleh, Natal, Semitau and southwest Borneo, now included in southeast Asia after collision with it during the Late Mesozoic to form ‘Sundaland’ (Metcalfe, 1991).

## 5. Conclusions

The diversified shark and ray assemblages recovered from the Late Cretaceous presumed continental red beds of the south-central Pyrenees (Lleida, Spain) have two consequences for the palaeoenvironmental and palaeogeographical reconstructions.

The non-marine environment generally accepted for these red beds has to be reassessed, in view of the presence of ray teeth several tens of kilometres landwards from the inferred palaeoshoreline. The occurrence of other marine organisms in these beds, such as foraminifera and *Girvanella* algae, points to

a transitional environment, where marine forms are mixed with freshwater forms.

The presence of a ray species and another close relative to Indian rays in the Pyrenees is additional evidence confirming the occurrence of similar terrestrial and shelf organisms in Europe and India by the Late Cretaceous. The current palaeogeographical reconstructions do not hold for this biogeographical relationship. Shallow connections across the ocean barriers between the northern and southern Tethyan margins are necessary to explain the observed palaeontological data.

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