Acta Geologica Polonica, Vol. 58 (2008), No. 2, pp. 249-255

When the "primitive" shark *Tribodus* (Hybodontiformes) meets the "modern" ray *Pseudohypolophus* (Rajiformes): the unique co-occurrence of these two durophagous Cretaceous selachians in Charentes (SW France)

ROMAIN VULLO[1] & DIDIER NÉRAUDEAU[2]

[1]*Unidad de Paleontología, Departamento de Biología, Calle Darwin, Universidad Autónoma de Madrid, Cantoblanco, 28049-Madrid, Spain. E-mail: romain.vullo@gmail.com*
[2]*Université de Rennes I, UMR CNRS 6118, Campus de Beaulieu, avenue du général Leclerc, 35042 Rennes cedex, France. E-mail: didier.neraudeau@univ-rennes1.fr*

ABSTRACT:

VULLO, R. & NÉRAUDEAU, D. 2008. When the "primitive" shark *Tribodus* (Hybodontiformes) meets the "modern" ray *Pseudohypolophus* (Rajiformes): the unique co-occurrence of these two durophagous Cretaceous selachians in Charentes (SW France). *Acta Geologica Polonica*, **58** (2), 249-255. Warszawa.

The palaeoecology and palaeobiogeography of two Cretaceous selachian genera, *Tribodus* BRITO & FERREIRA, 1989 and *Pseudohypolophus* CAPPETTA & CASE, 1975, are briefly discussed. These two similar-sized taxa developed an analogous pavement-like grinding dentition, characterized by massive teeth with a rhomboidal to hexagonal occlusal surface. Although both genera appear to have been euryhaline forms, the hybodont *Tribodus* occurred in fresh/brackish water habitats (e.g. deltas) to shallow marine lagoons, whereas the ray *Pseudohypolophus* lived in brackish water to coastal marine environments. Palaeobiogeographically, their global distribution displays two distinct but adjoined areas, with *Tribodus* being present in the northern part of Gondwana (Brazil and North Africa), and *Pseudohypolophus* occurring on both sides of the North Atlantic (North America and Western Europe). However, the two genera coexisted during Cenomanian times within a small overlap zone, localized in western France. A trophic competition may have arisen from this situation between these two selachians belonging to the same trophic guild. This peculiar situation is well documented within the Cenomanian transgressive series of Charentes (SW France), where a turnover between the two forms is observed (replacement of *Tribodus* by *Pseudohypolophus*).

Key words: Hybodontiformes, *Tribodus*, Rajiformes, *Pseudohypolophus*, Palaeoecology, Palaeobiogeography, Cenomanian, SW France.

INTRODUCTION

The Cretaceous period constituted a fundamental stage in the evolution of selachians. Indeed, the late Mesozoic corresponds to the rise of modern sharks (neoselachians) and marks the extinction of the primitive group of hybodont sharks just before the K/T boundary (CAPPETTA 1987a, KRIWET & BENTON 2004, UNDERWOOD 2006). The present study deals with the unusual co-occurrence of the hybodont *Tribodus* and the rajiform *Pseudohypolophus* in the Cenomanian of Charentes (SW France), two benthic durophagous selachians that have elsewhere distinct palaeogeographic distributions.

THE HYBODONTIFORM GENUS *TRIBODUS* (Text-fig. 1A)

This hybodont shark was originally described by BRITO & FERREIRA (1989), on the basis of almost complete skeletons from the Santana Formation (Albian) in Brazil. In 1992, BRITO provided additional information on *Tribodus*, including figures of its particular massive teeth. Further studies on the anatomy of *Tribodus* revealed that it displays an unusual mosaic of characters (e.g. ray-like dentition), with features present either among hybodont sharks or among neoselachians (MAISEY & CARVAHLO 1997, MAISEY 2005). Before the first detailed description and illustration of oral teeth by BRITO (1992), isolated teeth of *Tribodus* from the Cenomanian of Egypt and France had been erroneously assigned to myliobatiform rays by WERNER (1989) and LANDEMAINE (1991), respectively. These teeth were referred to several genera (*Distobatus*, *Aegyptobatus*, *Protohypolophites*), which subsequently were considered as junior synonyms of *Tribodus* (WERNER 1994, CAPPETTA & CASE 1999).

AUTECOLOGY: The ray-like dentition of *Tribodus*, consisting of polygonal teeth forming a flat grinding pavement (MAISEY & CARVAHLO 1997) is very informative. Such durophagous feeding adaptations suggest that this shark preyed on shelled invertebrates like bivalves, gastropods or crustaceans. Further information about the feeding behaviour of *Tribodus* could be inferred from the well-preserved, complete skeletons from Brazil. These data confirm that *Tribodus* was a benthic feeder (MAISEY & CARVAHLO 1997). Its various occurrences indicate a large range of habitats, from fluvio-deltaic to shallow coastal environments, in subtropical and equatorial zones (see below for references).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: ?Valanginian-Barremian (Loia Series) of Congo (described as ?*Hylaeobatis* sp. by CASIER 1961, MAISEY 2000); Albian (Chenini Formation) of Tunisia (CUNY & *al.* 2004); Albian (Tiout Formation) of Algeria (LANDEMAINE 1991); Albian (Santana Formation) and Albian-Cenomanian (Alcântara Formation; oral teeth described as *Myliobatis*) of Brazil (BRITO & FERREIRA 1989, DUTRA & MALBARBA 2001); Cenomanian (Kem Kem Beds) of Morocco (DUTHEIL 1999); ?Cenomanian (In Abangharit Beds) of Niger (DUTHEIL 2001), Cenomanian (Draa Ubari Formation) of Libya (NESSOV & *al.* 1998, RAGE & CAPPETTA 2002); Cenomanian (Bahariya Formation) of Egypt (WERNER 1989); ?Cenomanian (Wadi Milk Formation) of Sudan (described as *Asteracanthus aegyptiacus* by WERNER 1994); Cenomanian of France (LANDEMAINE 1991, VULLO & *al.* 2007).

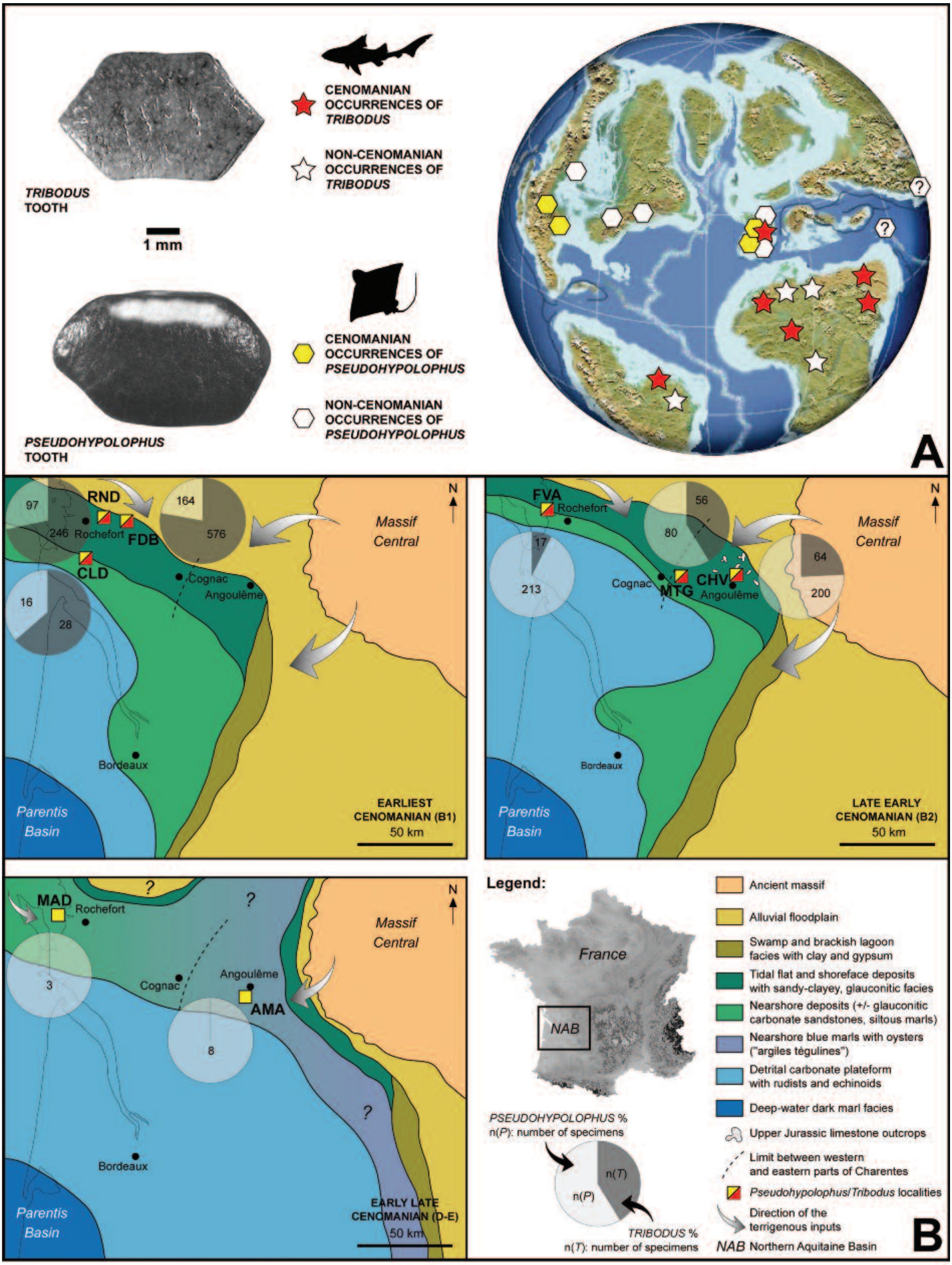
THE RAJIFORM GENUS *PSEUDOHYPOLOPHUS* (Text-fig. 1A)

The genus *Pseudohypolophus* was erected by CAPPETTA & CASE (1975) for teeth from the mid-Cretaceous (?Aptian-Albian and Cenomanian) of Texas, previously compared and referred to hypolophids (MCNULTY 1964, THURMOND 1971). This form is known only by isolated teeth.

AUTECOLOGY: *Pseudohypolophus* belongs to a specialized group of Cretaceous rajiforms that developed a grinding-type dentition, similarly to some myliobatiforms (CAPPETTA 1992). This ray regularly occurs in shallow marine detrital facies, indicating it was a demersal form living near the coast, in temperate and subtropical zones (see below for references). Brackish water habitats were also suggested for this genus (THURMOND 1971).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: Barremian and Cenomanian of France (BIDDLE & LANDEMAINE 1988, LANDEMAINE 1991, VULLO & *al.* 2007); Barremian, Albian, and Cenomanian of Spain (CANUDO & *al.* 1996, KRIWET 1999, BERNARDEZ 2002); ?Albian-Cenomanian of Portugal (R. VULLO, personal observations); various ?Aptian to Maastrichtian formations of North America (Georgia, Maryland, Nebraska, New Mexico, North Carolina, South Dakota, Texas, Wyoming) (see CAPPETTA 1987b, CAPPETTA & CASE 1999, BECKER & *al.* 2004). A few teeth from the Albian of Uzbekistan (NESSOV & UDOVICHENKO 1986) and the Santonian of Jordan (MUSTAFA & *al.* 2002) have been referred to *Pseudohypolophus*, but these assignments remain very doubtful (personal communication of H. CAPPETTA, 10/2007).

Fig. 1. A – Teeth of *Tribodus* (*T. morlati*) and *Pseudohypolophus* (*P. mcnultyi*) (early Cenomanian of "Les Renardières" quarry, Charente-Maritime) in occlusal views, showing a similar hexagonal grinding surface, and global distribution of the two genera during Cretaceous times (palaeogeographic globe from BLAKEY 2007). B – Spatial and temporal variations of *Pseudohypolophus*/*Tribodus* ratios in Charentes through the Cenomanian (palaeogeographic maps modified from PLATEL 1996; see text for locality abbreviations)


TRIBODUS TOOTH
1 mm
PSEUDOHYPOLOPHUS TOOTH
CENOMANIAN OCCURRENCES OF TRIBODUS
NON-CENOMANIAN OCCURRENCES OF TRIBODUS
CENOMANIAN OCCURRENCES OF PSEUDOHYPOLOPHUS
NON-CENOMANIAN OCCURRENCES OF PSEUDOHYPOLOPHUS
?
?
A
97
246
RND
FDB
CLD
164
576
16
28
Rochefort
Cognac
Angoulême
Bordeaux
Massif Central
N
Parentis Basin
EARLIEST CENOMANIAN (B1)
50 km
FVA
Rochefort
56
80
17
213
64
200
Cognac
MTG
CHV
Angoulême
Bordeaux
Massif Central
N
Parentis Basin
LATE EARLY CENOMANIAN (B2)
50 km
MAD
Rochefort
?
?
?
3
Cognac
Angoulême
AMA
8
Bordeaux
Massif Central
N
Parentis Basin
EARLY LATE CENOMANIAN (D-E)
50 km
Legend:
France
NAB
PSEUDOHYPOLOPHUS %
n(P): number of specimens
n(T)
n(P)
TRIBODUS %
n(T): number of specimens
Ancient massif
Alluvial floodplain
Swamp and brackish lagoon facies with clay and gypsum
Tidal flat and shoreface deposits with sandy-clayey, glauconitic facies
Nearshore deposits (+/- glauconitic carbonate sandstones, siltous marls)
Nearshore blue marls with oysters ("argiles tégulines")
Detrital carbonate plateform with rudists and echinoids
Deep-water dark marl facies
Upper Jurassic limestone outcrops
Limit between western and eastern parts of Charentes
Pseudohypolophus/Tribodus localities
Direction of the terrigenous inputs
NAB Northern Aquitaine Basin
B

THE *TRIBODUS-PSEUDOHYPOLOPHUS* ASSOCIATION IN THE CENOMANIAN OF CHARENTES (SW FRANCE)

Western France (Touraine, Poitou and Charentes regions) is the only place where the *Tribodus-Pseudohypolophus* association can be observed, with the species *T. morlati* (LANDEMAINE, 1991) and *P. mcnultyi* (THURMOND, 1971). The present study focuses on Cenomanian paralic deposits of Charentes (northern Aquitaine Basin), that yielded a rich and diverse selachian fauna (LANDEMAINE 1991; VULLO & *al.* 2003, 2005, 2007). The Cenomanian series of Charentes consists of estuarine, deltaic and lagoon deposits near the base and more marine sediments higher up in the section (MOREAU 1977, 1996; NÉRAUDEAU & *al.* 2005), and thus corresponds to a transgressive sequence of the northern shoreline of the Mediterranean Tethys. The genera *Tribodus* and *Pseudohypolophus* co-occur in several localities of early Cenomanian age (B1 and B2 units *sensu* NÉRAUDEAU & *al.* 1997): Font-de-Benon (FDB); Cadeuil (CDL); Les Renardières (RND); Fouras-Vauban (FVA); Montagan (MTG); Les Chauvauds (CHV). Two early late Cenomanian localities (D and E units *sensu* NÉRAUDEAU & *al.* 1997), with *Pseudohypolophus* but no *Tribodus* records, are included in this study: Madame Island (MAD); L'Amas (AMA). In each locality, teeth have been collected from the same stratigraphic horizon. Most of the material shows a slight post-mortem abrasion, indicating that these teeth were autochthonous elements or have undergone a short-distance water transport. This suggests that *Tribodus* and *Pseudohypolophus* probably lived in the same area, or that their biotopes overlapped. In the northern Aquitaine Basin, these two forms may have fed mainly on small oysters, particularly abundant in the lower part of the series (VULLO & *al.* 2003, VIDET 2004). Because they are the only two selachian forms in the Cenomanian of Charentes having such a dentition, a rather equal body size and a similar supposed ecology, the proportion between *Tribodus* and *Pseudohypolophus* teeth collected has been directly compared. Based on about 1750 isolated teeth, the variations of the *T. morlati*/*P. mcnultyi* species ratio in space (western and eastern parts of Charentes) and time (early Cenomanian through late Cenomanian) in such a transgressive context are illustrated in Text-fig. 1B.

EARLIEST CENOMANIAN: The first shallow marine facies of the Charentes series yielded numerous teeth of *Tribodus* and *Pseudohypolophus*, especially at FDB. In the two most proximal localities (FDB and RND), it is worth noting that about three-quarters of the teeth collected belong to *T. morlati*. In these assemblages, *Tribodus* is one of the three most abundant vertebrate taxa (with two other sharks: the orectolobiform *Cantioscyllium* sp. and the lamniform "*Carcharias*" *amonensis*), and is obviously the dominant grinding-toothed selachian. In the most distal locality (CDL), the dominance of *T. morlati* is slightly less marked (about 64%). Unfortunately, no data from the eastern part of Charentes are available due to the lack of vertebrate localities of earliest Cenomanian age.

LATE EARLY CENOMANIAN: Overlying the marine detrital limestone from the upper part of the B1 unit, a coastal greensand facies (B2gl subunit *sensu* NÉRAUDEAU & *al.* 1997) developed during the late early Cenomanian. These shallow deposits bear a rather similar vertebrate fauna (including numerous continental taxa) to that identified in the B1 unit (VULLO 2007, VULLO & NÉRAUDEAU 2008). However, an inversion of the *Tribodus*/*Pseudohypolophus* ratio is observed, and differences can be noted between the western and the eastern localities. *Tribodus morlati* becomes a quite rare, marginal element within the FVA assemblage, whereas *P. mcnultyi*, which seems to have been well adapted to marine environments (see above), is here the second most abundant vertebrate taxon. This trend is less marked in the two eastern localities (MTG and CHV), where *T. morlati* remains a relatively common taxon. It can be supposed that the shallow area of eastern Charentes, with possibly less marked marine influence, has constituted a "refuge" for *T. morlati* after the first transgressive pulse.

EARLY LATE CENOMANIAN: These two localities (MAD and AMA) have yielded only a few teeth of *P. mcnultyi*. The selachian fauna is dominated by pelagic lamniforms, while nektobenthic forms, like *P. mcnultyi*, become rarer. So far, no teeth of *Tribodus* have been collected in the late Cenomanian deposits of Charentes. The complete vertebrate assemblage, without any continental forms, indicates deeper and more distal marine conditions. Durophagous fishes are mainly represented by large pycnodontiforms (VULLO 2007).

CONCLUSION

A unique and well-documented *Tribodus-Pseudohypolophus* association was studied in detail. The fine space and time scale analysis of the ratio variations of such an association provides a precise example of an ecological competition between a hybodont shark and a neoselachian. It also illustrates the influence of palaeoenvironmental changes (e.g. a marine transgression) on the local extinction of some highly adapted selachians, like *Tribodus*. Trophic factors, such as prey availabilities and responses, may have also occurred (e.g. the general size increase observed in *Rhynchostreon suborbiculatum*, the most abundant oyster in the early Cenomanian of Charentes and probably one of the main preys of the selachians dealt with herein; see VIDET & NÉRAUDEAU 2003, VIDET 2004). Lastly, climatic and oceanographic factors must be considered. The minor shelf-sea cooling event observed in Europe in the middle Cenomanian (VOIGT & *al.* 2004) has certainly affected populations of the French endemic *Tribodus morlati*, which appears to have been the northernmost species of the genus. Such a short time scale climatic change would have shrunk the distribution area of this shark, restricting it to lower latitudes (northern Gondwanan shores; see above), in warm water habitats.

Similarly to the present study, the fish faunal evolution from freshwater to marine palaeoenvironments in NW Africa has been analysed by CAVIN & *al.* (2001) on the basis of material from the Cenomanian-Turonian of SE Morocco. Interestingly, they also noted the local disappearance of *Tribodus* during the Cenomanian. The global extinction of *Tribodus*, which has not been found in post-Cenomanian deposits, is certainly related to the important Cenomanian-Turonian transgression, resulting in a significant reduction of paralic habitats.

Acknowledgements

We thank H. CAPPETTA (Montpellier) for providing rare documentation and helpful taxonomic comments. We are grateful to J. KRIWET (Berlin) for his critical and constructive review. This work is a contribution to the French ANR Project AMBRACE (no. BLAN07-1-184190), and to the Spanish project CGL2005-01121 of the "Ministerio de Educación y Ciencia."

REFERENCES

BECKER, M.A., CHAMBERLAIN, JR., J.A. & TERRY, JR., D.O. 2004. Chondrichthyans from the Fairpoint Member of the Fox Hills Formation (Maastrichtian), Meade County, South Dakota. *Journal of Vertebrate Paleontology*, **24**, 780-793.

BERNARDEZ, E. 2002. Los dientes de selaceos del Cretacico de la Depresion Central Asturiana. Unpublished Ph.D. dissertation, University of Oviedo, pp. 1-476. Oviedo.

BIDDLE, J.-P. & LANDEMAINE, O. 1988. Contribution à l'étude des sélaciens du Crétacé du Bassin de Paris. Découverte de quelques nouvelles espèces associées à une faune de type wealdien dans le Barrémien supérieur (Crétacé inférieur) des environs de Troyes (Aube). *Musée de Saint-Dizier, Cahier,* **2**, 1-22.

BLAKEY, R.C. 2007. Global paleogeographic views of Earth history – Late Precambrian to Recent. http://jan.ucc.nau.edu/~rcb7/globaltext2.html.

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

BRITO, P.M. & FERREIRA, P.L.N. 1989. The first hybodont shark *Tribodus limae* nov. gen., nov. sp., from the Lower Cretaceous of Chapada do Araripe (North-East Brazil). *Anais de Academia Brasileira de Ciências*, **61**, 53-57.

CANUDO, J.I., CUENCA-BESCÓS, G. & RUIZ-OMEÑACA, J.I. 1996. Tiburones y rayas (Chondrichthyes, Elasmobranchii) del Barremiense superior (Cretacico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas*, **15**, 35-57.

CAPPETTA, H. 1987a. Extinctions et renouvellements fauniques chez les sélaciens post-jurassiques. *Mémoires de la Société Géologique de France*, **150**, 113-131.

— 1987b. Chondrichthyes II - Mesozoic and Cenozoic Elasmobranchii. *In*: H.-P. SCHULTZE (*Ed.*), Handbook of Paleoichthyology. *Gustav Fischer Verlag*; Stuttgart - New York, **3B**, 1-193.

— 1992. Nouveaux Rhinobatoidei (Neoselachii, Rajiformes) à denture spécialisée du Maastrichtien du Maroc. Remarques sur l'évolution dentaire des Rajiformes et des Myliobatiformes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **187**, 31-52.

CAPPETTA, H. & CASE, G.R. 1975. Sélaciens nouveaux du Crétacé du Texas. *Geobios*, **8**, 303-307.

— & — 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur-Campanien). *Palaeo Ichthyologica*, **9**, 5-111.

CASIER, E. 1961. Matériaux pour la faune ichthyologique éocrétacique du Congo. *Annales du Musée Royal d'Afrique Centrale, série 8, Sciences Géologiques*, **39**, 1-96.

CAVIN, L., BOUDAD, L., DUFFAUD, S., KABIRI, L., LE LŒUFF, J., ROUGET, I. & TONG, H. 2001. L'évolution paléoenvironnementale des faunes de poissons du Crétacé supérieur du bassin du Tafilalt et des régions avoisinantes (Sud-Est du Maroc): implications paléobiogéographiques. *Comptes Rendus de l'Académie des Sciences, Paris, série IIa*, **333**, 677-683.

CUNY, G., OUAJA, M., SRARFI, D., SCHMITZ, L., BUFFETAUT, E. & BENTON, M.J. 2004. Fossil sharks from the Early Cretaceous of Tunisia. *Revue de Paléobiologie*, volume spécial **9**, 127-142.

Dutheil, D.B. 1999. An overview of the freshwater fish fauna from the Kem Kem beds (Late Cretaceous: Cenomanian) of southeastern Morocco. *In*: G. Arratia & H.-P. Schultze (*Eds*), Mesozoic Fishes 2 - Systematics and Fossil Record. *Verlag Dr. Friedrich Pfeil*, München, 553-563.

— 2001. New freshwater fish from the Late Cretaceous (Cenomanian) of Niger. *Journal of Vertebrate Paleontology*, **21** supplement 3, 46A.

Dutra, M.F.A. & Malabarba, M.C.S.L. 2001. Peixes do Albiano-Cenomaniano do Grupo Itapecuru, Estado do Maranhão, Brasil. *In*: D.F. Rossetti, A.M. Góes & W. Truckenbrodt (*Eds*), O Cretáceo na Bacia São Luís-Grajaú, pp. 191-208, *Museu Paraense Emilio Goeldi*; Belém.

Kriwet, J. 1999. Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). *Palaeo Ichthyologica*, **9**, 113-142.

Kriwet, J. & Benton, M.J. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **214**, 181-194.

Landemaine, O. 1991. Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des élasmobranches. Société Amicale des Géologues Amateurs (MNHN, Paris), *SAGA information*, hors-série **1**, 1-45.

McNulty, C.L. 1964. Hypolophid teeth from the Woodbine Formation, Tarrant County, Texas. *Eclogae Geologicae Helvetiae*, **57**, 537-541.

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

— 2005. The hybodont shark *Tribodus*: trying to be modern? *In*: F.J. Poyato-Ariza (*Ed.*), Fourth International Meeting on Mesozoic Fishes - Systematics, Homology, and Nomenclature, pp. 179-181. Madrid.

Maisey, J.G. & Carvahlo, M.R. de 1997. A new look at old sharks. *Nature*, **385**, 779-780.

Moreau, P. 1977. Les environnements sédimentaires marins dans le Cénomanien du Nord du Bassin de l'Aquitaine. *Bulletin de la Société géologique de France*, **19**, 281-288.

— 1996. Analyse de la transgression cénomanienne sur la bordure nord-occidentale du Bassin de l'Aquitaine. *Géologie de la France*, **1**, 3-16.

Mustafa , H., Case, J.R. & Zalmout, I.S. 2002. A new selachian fauna from the Wadi Umm Ghudran Formation (Late Cretaceous) - central Jordan. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **226**, 419-444.

Néraudeau, D., Thierry, J. & Moreau, P. 1997. Variation in echinoid biodiversity during the Cenomanian-Early Turonian transgressive episode in Charentes. *Bulletin de la Société géologique de France*, **168**, 51-61.

Néraudeau, D., Vullo, R., Gomez, B., Perrichot, V. & Videt, B. 2005. Stratigraphie et paléontologie (plantes, vertébrés) de la série paralique Albien terminal-Cénomanien basal de Tonnay-Charente (Charente-Maritime, France). *Comptes Rendus Palevol*, **4**, 79-93.

Nessov, L.A. & Udovichenko, N.I. 1986. New findings of Cretaceous and Paleogene vertebrate remains of Soviet Middle Asia. *Voprosy Paleontologii*, **9**, 129-136. [*In Russian*]

Nessov, L.A., Zhegallo, V.I. & Averianov, A.O. 1998. A new locality of Late Cretaceous snakes, mammals and other vertebrates in Africa (western Libya). *Annales de Paléontologie*, **84**, 265-274.

Platel, J.-P. 1996. Stratigraphie, sédimentologie et évolution géodynamique de la plate-forme carbonatée du Crétacé supérieur du nord du bassin d'Aquitaine. *Géologie de la France*, **4**, 33-58.

Rage, J.-C. & Cappetta, H. 2002. Vertebrates from the Cenomanian, and the geological age of the Draa Ubari fauna (Libya). *Annales de Paléontologie*, **88**, 79-84.

Thurmond, J.T. 1971. Cartilaginous fishes of the Trinity group and related rocks (Lower Cretaceous) of North Central Texas. *Southeastern Geology*, **13**, 207-227.

Underwood, C.J. 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology*, **32**, 215-235.

Videt, B. 2004. Dynamique des paléoenvironnements à huîtres du Crétacé supérieur nord-aquitain (SO France) et du Mio-Pliocène andalou (SE Espagne): biodiversité, analyse séquentielle, biogéochimie. Ph.D. dissertation of the University of Rennes 1, *Mémoires de Géosciences Rennes*, **108**, 1-263.

Videt, B. & Néraudeau, D. 2003. Variabilité et hétérochronies chez l'exogyre *Rhynchostreon suborbiculatum* (Lamarck, 1801) (Bivalvia : Ostreoidea : Gryphaeidae) du Cénomanien et du Turonien inférieur des Charentes (SW France). *Comptes Rendus Palevol*, **2**, 563-576.

Voigt, S., Gale, A.S. & Flögel, S. 2004. Midlatitude shelf seas in the Cenomanian-Turonian greenhouse world: Temperature evolution and North Atlantic circulation, *Paleoceanography*, **19**, PA4020, doi: 10.1029/2004PA001015.

Vullo, R. 2007. Les vertébrés du Crétacé supérieur des Charentes (Sud-Ouest de la France): biodiversité, taphonomie, paléoécologie et paléobiogéographie. Ph.D. dissertation of the University of Rennes 1, *Mémoires de Géosciences Rennes*, **125**, 1-302.

Vullo, R. & Néraudeau, D. 2008 (in press). Cenomanian vertebrate assemblages from southwestern France: a new insight into the European mid-Cretaceous continental fauna. *Cretaceous Research*, **29**.

Vullo, R., Cappetta, H. & Néraudeau, D. 2007. New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Palaeontologica Polonica,* **52**, 99-116.

VULLO, R., NÉRAUDEAU, D. & VIDET, B. 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). *Annales de Paléontologie*, **89**, 171-189.

VULLO, R., NÉRAUDEAU, D., ALLAIN, R. & CAPPETTA, H. 2005. Un nouveau gisement à microrestes de vertébrés continentaux et littoraux dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, **4**, 95-107.

WERNER, C. 1989. Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenomanan) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica*, **5**, 5-112.

— 1994. Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk Formation). *Berliner Geowissenschaftliche, Abhandlungen* (E), **13**, 221-249.

Manuscript submitted: 5th November 2007
Revised version accepted: 15th April 2008