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Non-marine selachians from the basal Cretaceous of Charente, SW France

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ABSTRACT

A gypsum quarry at Cherves-de-Cognac in south-western France exposes a large section of Berriasian (basal Cretaceous) sediments deposited in a lagoonal environment. The sediments have yielded rich vertebrate faunas, but only two species of selachians are present; the lonchidiid hybodont *Parvodus celsucuspus* sp. nov. and the batoid *Belemnobatis variabilis*. The composition of the fauna, including only a single, seemingly endemic, hybodont species from a time when hybodont faunas are relatively well investigated in Europe, indicate that small hybodonts were not able to migrate longer distances. The recorded batoid species also occurs in southern England, demonstrating that these batoids were primarily marine fishes that regularly explored areas with reduced salinity.

1. Introduction

Hybodont sharks have a long history, originating in the Devonian (Ginter et al., 2010), and representing one of the most long-lived selachian clades of all time. They inhabited a wide variety of ecological niches and different environments during the Mesozoic, including both marine and freshwater settings. In Early Cretaceous times, they were apparently very numerous and diverse in non-marine environments throughout the world (e.g., Patterson, 1966; Rees, 2002; Underwood and Rees, 2002; Cappetta et al., 2006; Cuny et al., 2004, 2006, 2008; Klug et al., 2010). Judging by the wide range of dental morphologies found among hybodont sharks and their substantial variation in body size, they were apparently adapted for many different life strategies, from durophagous sharks with crushing dentitions to species with piercing teeth, presumably adapted to a life in open water (e.g., Rees and Underwood, 2008). A few genera (e.g. *Priohybodus* d'Erasmo, 1960, and *Thaiodus* Cappetta et al., 1990) even developed a cutting dentition, allowing them to consume larger prey items (Cappetta et al., 1990, 2006; Duffin, 2001; Duffin and Cuny, 2008; Cuny et al., 2009a; Cappetta, 2012). There are a few external features that appear to be typically hybodont, including large and ornamented dorsal fin spines and, in males, paired cephalic spines above and posterior to the orbits.

The major modern neoselachian groups, including batoids, first began to diversify in the later part of the Early Jurassic (e.g., Underwood, 2006; Kriwet et al., 2009). During the Middle and Late Jurassic, further neoselachian radiation occurred, resulting also in a higher diversity of batoids. Isolated teeth that can be referred to *Spathobatis* Thiollière, 1854 or *Belemnobatis* Thiollière, 1854 are commonly found in marine and non-marine strata from the Middle Jurassic to the Lower Cretaceous of Europe (e.g., Thies, 1983; Underwood and Rees, 2002; Underwood and Ward, 2004; Rees, 2005), and these batoids are also known from complete skeletons (e.g., Cavin et al., 1995). Recently, isolated teeth of *Belemnobatis* have also been found in Thailand (Cuny et al., 2009b). These early batoids had a pointed snout, strongly enlarged pectoral fins and two dorsal fins on the tail, both equipped with a short fin spine. They are the most common neoselachians found in association with hybodonts, forming the typical elements of a selachian fauna from areas where the salinity was considerably lower than in the open ocean (e.g., Underwood and Rees, 2002).

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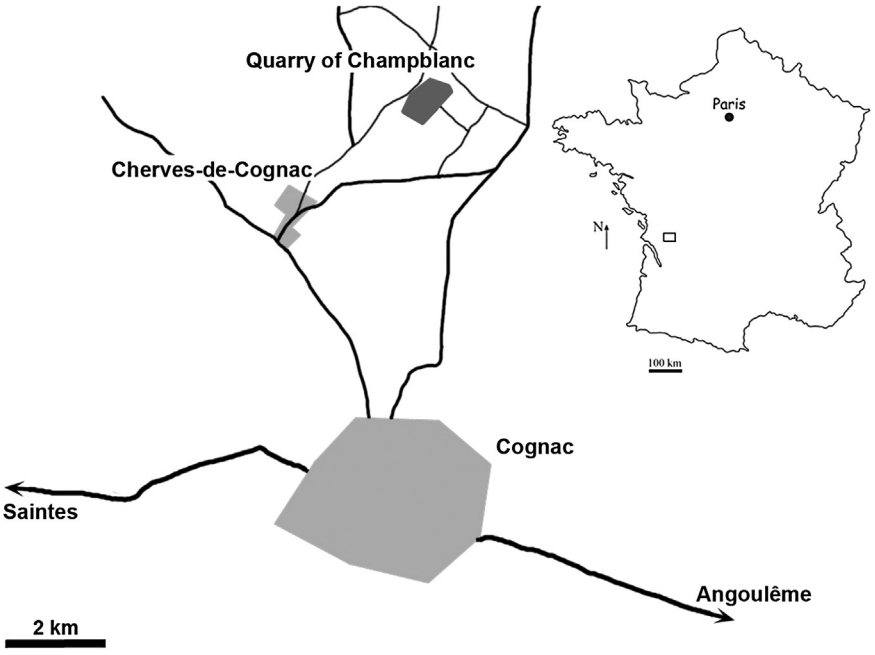

Fig. 1. The village of Cherves-de-Cognac is located 7 km north of the town of Cognac (Charente, south-western France).

2. Geological setting

The village of Cherves-de-Cognac is located in south-western France, on the northern margin of the Aquitaine Basin (Fig. 1). Material was collected from the so-called *Carrière de Champblanc*, a huge gypsum quarry in which a sedimentary series of 81 horizons, comprising carbonates, marls and evaporites, is exposed (Fig. 2). The section at Cherves-de-Cognac represents deposition of non-marine sediments in a lagoonal environment in which two successive lithological units have been identified (El Albani et al., 2004; Fig. 2). The basal unit (U1) is dominated by gypsum, with alternating thin beds of marl and clay, reflecting hypersaline conditions in a lagoon where occasional marine influx and low, but regular freshwater influx lead to the deposition of thick layers of evaporites. The second unit (U2) mainly includes more or less carbonate-rich marl beds with alternating clay horizons, overlain by lacustrine limestone deposits. This unit reflects deposition of continental material within the lagoon and there is a progressive increase of freshwater influence towards the top of the unit. The section has been dated by means of ostracods, charophytes and dinoflagellates, which all indicate a lower to middle Berriasian age of the Lower Cretaceous and suggest correlation with the lower part of the Middle Purbeck of southern England (Colin et al., 2004; El Albani et al., 2004).

The first occurrence of vertebrate fossils from these so-called "black marls" in the vicinity of Cognac was indicated by Coquand (1860), who reported isolated fish teeth and scales. After the opening of a large gypsum quarry, occasional vertebrate fossils were recorded from the succession in the 1980's and 1990's (Buffetaut et al., 1989; Hervat and Hervat, 1993; Le Loeuff et al., 1996; Vignaud et al., 1994). From 2001 to 2007, systematic excavations of these fossiliferous levels resulted in extensive collections of more than 1800 specimens of fossil vertebrates (Mazin et al., 2006, 2008), representing bony fishes, sharks and a wide variety of reptiles. Each of the 63 non-gypseous, marly horizons within the section was sampled and screen-washed in order to collect vertebrate microremains (Pouech et al., 2006; Pouech, 2008). All levels yielded microremain assemblages, revealing the presence of at least 28 vertebrate families, including amphibians and mammals. Selachian remains occur in 38 of the fossiliferous levels (Fig. 2), and the richest beds have yielded more than 1000 teeth per 100 kg of sediment.

3. Material and methods

Larger hybodont remains (cephalic spines and fin spines) were extracted during the excavations, whereas all selachian teeth were collected by means of screen-washing. For this purpose, 200 kg of sediment were sampled from each of the non-gypseous levels, with the exception of some very thin horizons. The samples were dissociated in water, combined with hydrogen peroxide and, for the more calcareous levels, diluted methanoic acid was used. The material was washed through sieves with mesh sizes of 1 mm, 0.500 mm and 0.315 mm. This process was repeated three times for each sample, in order to concentrate microvertebrates. Washing performance reached between 95% and 99.9% depending on the nature of the sediment. In two samples (beds 32 and 35), the fraction between 0.315 and 0.500 mm was treated with buffered acetic acid (see Jeppsson et al., 1999). Microvertebrate fossils were sorted under a stereomicroscope Leica MZ 7.5 and digital images of teeth and denticles were obtained through a Hitachi Scanning Electron Microscope.

The selachian material from Cherves-de-Cognac is housed in the public collections of Musée d'Angoulême (France), prefixed CHV, and a smaller part of the material is deposited in the collections of the Natural History Museum of Copenhagen (Denmark), GM-V-2008 and MGUH 30420.

4. Systematic palaeontology

Cohort Euselachii Hay, 1902
Superfamily Hybodontoidea Owen, 1846 *sensu* Zangerl, 1981
Family Lonchidiidae Herman, 1977 *sensu* Rees, 2008
Genus *Parvodus* Rees and Underwood, 2002

Type species. *Lissodus rugianus* Ansorge, 1990 from the Lower Cretaceous of Rügen, northern Germany.

Remarks. When this genus was first recognized and erected (Rees and Underwood, 2002), only three species were included; *Parvodus*