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Research Article

The Late Cretaceous chondrichthyan fauna of the Elbtal Group (Saxony, Germany)

Jan Fischer[1,*], Ilja Kogan[2,3], Evgeny Popov[3,4], Nadine Janetschke[5] and Martin Licht[6]

[1]Urweltmuseum GEOSKOP, Thallichtenberg, Germany
[2]TU Bergakademie Freiberg, Freiberg, Germany
[3]Kazan Federal University, Kazan, Russia
[4]Saratov State University, Saratov, Russia
[5]Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany
[6]deceased

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Abstract - Upper Cretaceous (upper Cenomanian–lower Coniacian) marine strata of Saxony, eastern Germany, are mainly known for their rich invertebrate fauna, but have also yielded various vertebrate remains. The Saxonian Cretaceous marine strata, predominantly sand- and calcareous siltstones, marls and marly limestones, are mainly restricted to the clastic units of the so-called Elbtal Group, exposed in the area between Meißen and the Czech border in eastern Saxony. The ichthyofauna of the Elbtal Group is quite diverse. Currently, 19 species of cartilaginous fishes have been distinguished. The fauna was clearly dominated by mid- to large-sized lamniform sharks.

Keywords: Chondrichthyan, Late Cretaceous, Elbtal Group

1. Introduction

Upper Cretaceous (upperCenomanian–lower Coniacian) marine strata of Saxony, eastern Germany, are mainly known for their rich invertebrate fauna (e.g., Niebuhr and Wilmsen, 2014), but have also yielded various vertebrate remains. Fish fossils are most common among them and have been collected and described by different workers since the early 19th century (e.g., Fischer, 1856; Wanderer, 1909; Meier, 2005). The first and most influential author was the German geologist, mineralogist and palaeontologist, as well as former director of the Dresden Museum of Mineralogy and Geology, Hanns Bruno Geinitz (1814–1900) (e.g., Geinitz, 1839, 1875a, b). However, the fragmentary preservation of most of the recovered fish remains and the fact that all results were published in German left the Saxonian Cretaceous fish fauna nearly unnoticed in international literature, both then and today. Moreover, no systematic study on the chondrichthyan fauna has been compiled for more than one hundred years, wherefore the whole fauna is in need of revision (Licht *et al.,* in press). A current review, performed within the framework of a new inventory of Saxonian Cretaceous fossils, reveals a remarkably diverse marine ichthyofauna, composed of numerous cartilaginous and bony fish taxa (Kogan *et al.,* 2016). Here, we present a brief overview of the documented chondrichthyan fauna from the Saxonian Cretaceous deposits according to the current state of knowledge.

2. Geological Setting

The Saxonian Cretaceous marine strata, predominantly sand- and calcareous siltstones, marls and marly limestones (Wilmsen and Niebuhr, 2014), are mainly restricted to the clastic units of the so-called Elbtal Group, exposed in the area between Meißen and the Czech border in eastern Saxony. Sedimentation took place during late Cenomanian to early Coniacian times (95 – 89 my) in a neritic environment. Clastics accumulated on a hydrodynamically graded shelf, which can be divided into three main facies zones (Janetschke and Wilmsen, 2014): the coarse-grained nearshore sandy zone ("Küstensandsteinfazies" = inner shelf), the transitional zone ("Faziesübergangszone" = middle shelf), and the fine-grained marly offshore zone ("Plänerfazies" = outer shelf). Palaeogeographically, the Elbtal Group strata were deposited in a narrow sea strait between the Mid-European Island in the southwest and the Westsudetic or Lusatian Island in the northeast (Wilmsen and Niebuhr, 2014; Fig. 1). Here, the Saxonian Cretaceous sediments occupy an important intermediate position between the Tethyan warm water areas of the Bohemian Cretaceous Basin in the south and the temperate Boreal water of the Northwest European shelf in the north (Horna and Wilmsen, 2015; Fig. 1).

Vertebrate remains occur at several levels within the Upper Cretaceous succession, but are best known from the upper Cenomanian Dölzschen Formation and the mid-upper Turonian Strehlen Formation. Both intervals

*Author for correspondence: j.fischer1@yahoo.de

are reconstructed as times of sea-level high stand following major transgression phases (Janetschke *et al*., 2015).

3. Chondrichthyan ichthyofauna

The ichthyofauna of the Elbtal Group is quite diverse. Among osteichthyans, ten actinopterygian species have been ascertained to date, belonging to Pycnodontiformes (*Anomoedus*, *Pycnodus*) and several groups of Teleostei (Ichthyodectiformes [*Ichthyodectes*], Elopiformes [*Osmeroides*], Aulopiformes [*Cimolichthys*, *Rhynchodercetis*, *Enchodus*], Pachyrhizodontoidei [*Pachyrhizodus*], Beryciformes [*Hoplopteryx*]) based on teeth, cranial and postcranial fragments and some more complete individuals (Licht *et al*., in press). Older descriptions of material that was probably destroyed during World War II further suggest that coelacanths were present as well.

Nevertheless, chondrichthyans form the majority of vertebrate remains both in species number and numerically (>1600 teeth). The latter is due to the lifelong tooth replacement in sharks producing thousands of hard parts (teeth, scales) for the fossil record during their life time. Thus, sharks did not necessarily occur more frequent in the Cretaceous environments than osteichthyans, but left more preservable material behind in the clastic strata. The fossil record of the Elbtal Group mostly comprises disarticulated teeth and tooth crowns but also rare tooth plates, fin spines, vertebrae, cartilaginous tesserae fragments of the endoskeleton, and even spiral coprolites (Fig. 2). Altogether, 19 species within 17 genera, 14 families, and eight orders of cartilaginous fishes have been identified in the Cenomanian–Turonian fish assemblage of Saxony (Fig. 2):

The Holocephali are represented by a dozen tooth plates and a few fin spine fragments referable to two chimaeriform genera and species (*Edaphodon* cf. *sedgwicki*, *Elasmodus* sp.). Euselachian sharks form a minority with one preserved hybodontiform species (*Polyacrodus polyptychus*). In contrast, the neoselachians were highly diverse with 16 species and 14 genera dominating the chondrichthyan assemblage (Neoselachii incerdae sedis sensu Hoffman *et al*., 2016 – *Ptychodus decurrens*, *P. mammillaris*, *P. latissimus*; Hexanchiformes – *Hexanchus microdon*; Squaliformes – ?*Squalus* sp.; Heterodontiformes – *Heterodontus polydictyos*; Orectolobiformes – *Cantioscyllium decipiens*; Carcharhiniformes – *Pseudoscyliorhinus schwarzhansi*; Lamniformes – *Squalicorax falcatus*, *Cretolamna appendiculata*, *Cretodus semiplicatus*, *Cretoxhyrina mantelli*, *Paranomotodon angustidens*, *Scapanorhynchus raphiodon*, *Protolamna acuta*, *Carcharias* sp.). Thereby, the lamniform sharks seem to have been the most common group in the Saxonian Cretaceous marine environment, providing about 90% of all collected cartilaginous fish remains.

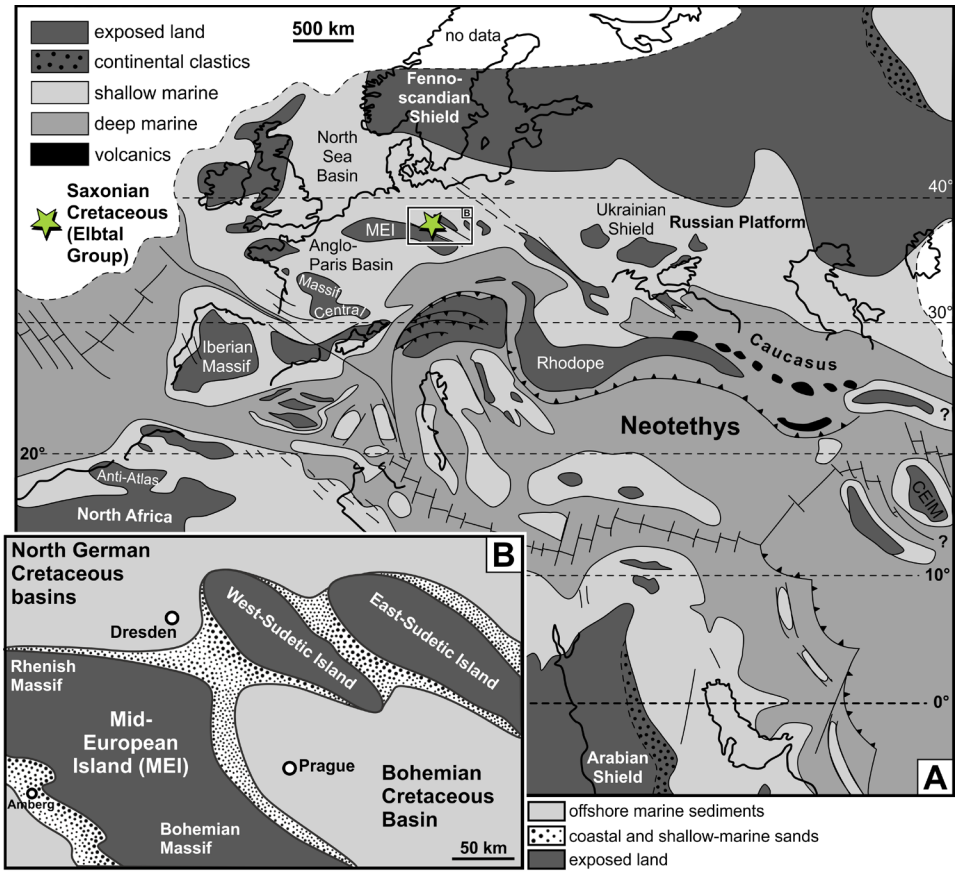

Figure 1. Palaeogeography and depositional setting of the Saxonian Cretaceous (Elbtal Group) with (A) the palaeogeography of the early Late Cretaceous (Cenomanian) in Europe and northern Africa (the map area of B is indicated), and (B) a detailed overview of the Elbtal Group setting, mediating between southern Tethyan waters and the Boreal realm of northern Europe (modified from Wilmsen and Niebuhr, 2014)

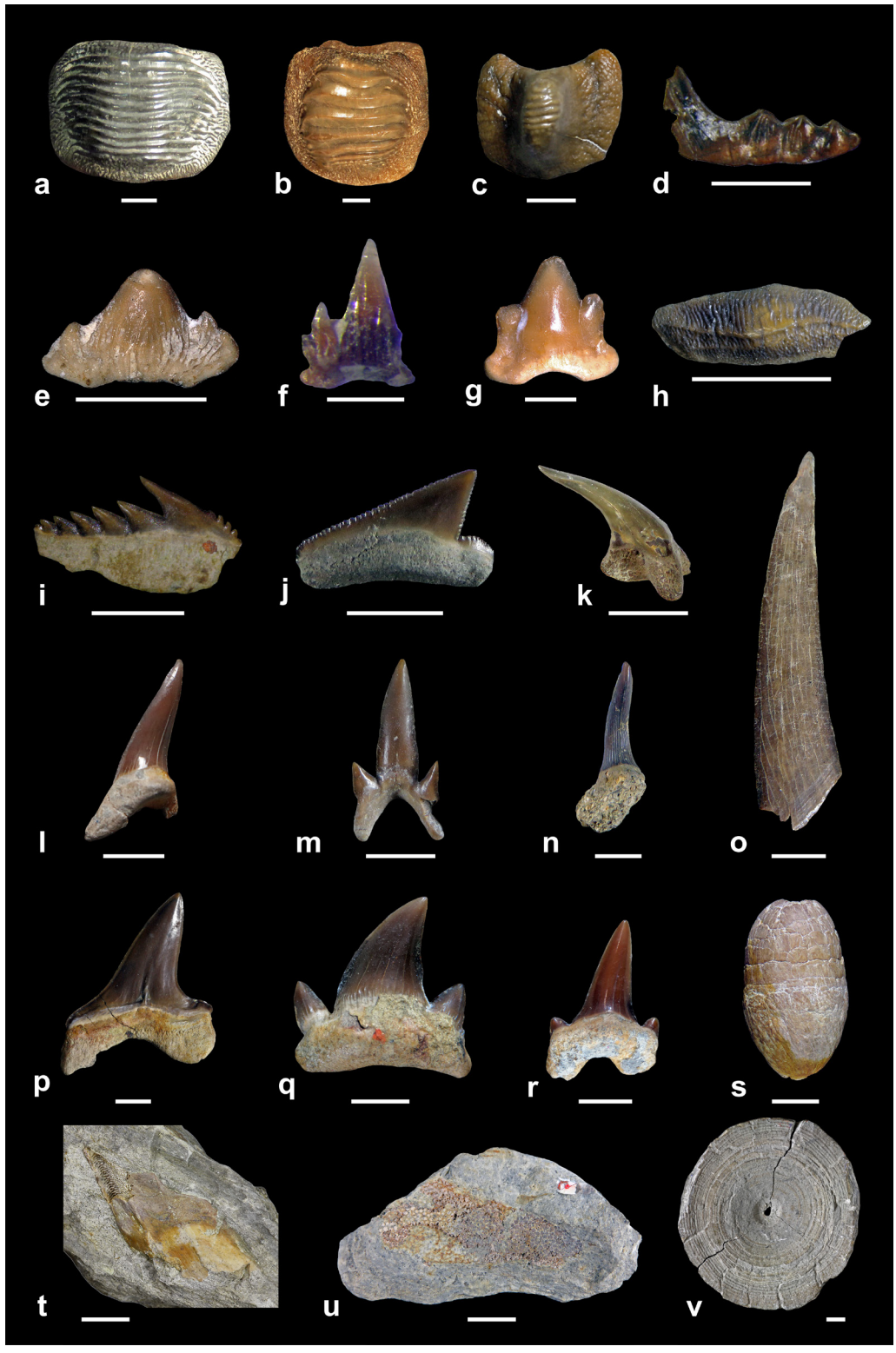

Figure 2. Chondrichtyan fauna from the Saxonian Cretaceous Elbtal Group. a – *Ptychodus decurrens*, occlusal view; b – *Ptychodus latissimus*, occlusal view; c – *Ptychodus mammillaris*, occlusal view; d – *Polyacrodus polyptychus*, lingual view; e – *Cantioscyllium decipiens*, labial view; f – *Pseudoscyliorhinus schwarzhansi*, labial view; g – *Heterodontus polydictyos*, anterior tooth, labial view; h – *Heterodontus polydictyos*, lateral tooth, occlusal view; i – *Hexanchus microdon*, labial view; j – *Squalicorax falcatus*, labial view; k – *Carcharias* sp., lateral view; l – *Paranomotodon angustidens*; oblique lingual view; m – *Protolamna acuta*, labial view; n – *Scapanorhynchus raphiodon*, oblique lingual view; o – squaliform anterior fin spine fragment, lateral view; p – *Cretoxyhrina mantelli*, lingual view; q – *Cretodus semiplicatus*, labial view; r – *Cretolamna appendiculata*, lingual view; s – spiral coprolite „*Koprolithes mantelli*“ (Geinitz, 1839); t – *Edaphodon* sp., left mandibular tooth plate, basal view; u – cartilaginous tissue fragment built up by tesserae; v – lamniform vertebra, rostral view. Scale bars for a–d, h–r equal 5 mm, for e–g equal 2 mm and for s–v equal 10 mm.

4. Comparison and discussion

Several of the Saxonian chondrichthyan taxa are true cosmopolitans (e.g., *Ptychodus*, *Hexanchus*, *Squalicorax*, *Cretoxyrhina*) showing a global distribution during the Late Cretaceous from Russia through Europe to North America (e.g., Müller and Diedrich, 1991; Welton and Farish, 1993; Cappetta, 2012). However, it is notable that in total the chondrichthyan assemblage seems to be depleted with respect to the available species diversity compared to other Cenomanian–Turonian localities (e.g., Reuss, 1846; Gonzáles-Barba and Espinosa-Chavez, 2005; Cook *et al*., 2013). Hybodontiforms are represented by only three tooth fragments of a single species, while in the southward adjacent Bohemian Cretaceous Basin they are clearly more abundant. Moreover, the characteristic chainsaw-tooth-like teeth of Squaliformes are lacking, and the absence of any batomorph remnant is also conspicuous. Nevertheless, it remains unclear how much of this perceived diversity pattern was biased by inadequate collecting rather than other causes.

Comparing the occurrence of single species through time in the Saxonian Cretaceous, it appears that, except for the lamniforms, the other chondrichthyan orders have not continuously existed there (Tab. 1). The fish assemblage was not rigid in its composition, probably due to repeated eustatic sea-level changes during Cenomanian–Turonian times (Janetschke and Wilmsen, 2014; Wilmsen and Niebuhr, 2014), and, associated therewith, distinct habitat shifts. For example, the durophagous *Polyacrodus* as well as *Heterodontus* vanished from the fossil record with the end of the Cenomanian, while on the other hand a further durophagous *Ptychodus* species entered the local faunal stage and the abundance of *P. mammillaris* increased. The disappearance of some durophagous chondrichthyans after the Cenomanian coincides with a decrease in diversity of the similarly durophagous pycnodontiform actinopterygians (three species in the Cenomanian vs. only one in the Turonian; Licht and Kogan, 2011). However, a possible bias in sample collection again may distort the perceived occurrence pattern.

Table 1. Occurrence and frequency of the Saxonian Cretaceous chondrichthyan taxa from late Cenomanian and middle Turonoian strata of the Elbtal Group (x – rare, xx – average, xxx – frequent).

Order	Taxa	Late Cenomanian	Late Turonian
Chimaeriformes	*Edaphodon* cf. *sedgwicki*		x
Chimaeriformes	*Elasmodus* sp.		x
Hybodontiformes	*Polyacrodus polyptychus*	x	
Neoselachii incerta sedis	*Ptychodus decurrens*	x	x
Neoselachii incerta sedis	*Ptychodus mammillaris*	x	xx
Neoselachii incerta sedis	*Ptychodus latissimus*		x
Hexanchiformes	*Hexanchus microdon*		x
Squaliformes	?*Squalus* sp.		x
Heterodontiformes	*Heterodontus polydictyos*	xx	
Orectolobiformes	*Cantioscyllium decipiens*	x	
Carcharhiniformes	*Pseudoscyliorhinus schwarzhansi*	x	
Lamniformes	*Squalicorax falcatus*	x	xxx
Lamniformes	*Cretolamna appendiculata*	x	xx
Lamniformes	*Cretodus semiplicatus*	xxx	x
Lamniformes	*Cretoxhyrina mantelli*	x	xxx
Lamniformes	*Paranomotodon angustidens*	xxx	xx
Lamniformes	*Scapanorhynchus raphiodon*	xxx	x
Lamniformes	*Protolamna acuta*		xx
Lamniformes	*Carcharias* sp.	x	

In terms of ecological diversity, these chondrichthyans occupied varied trophic niches from durophagous (Chimaeriformes, *Polyacrodus*, *Ptychodus*, *Heterodontus*), small- and mid-sized piscivorous (*Hexanchus*, *Pseudoscyliorhinus*, *Cantioscyllium*, ?*Squalus, Protolamna, Scapanorhynchus*) up to five to eight meter-long predators of the pelagic realm (*Squalicorax*, *Paranomotodon*, *Cretoxyrhina*, *Cretolamna, Cretodus*). The latter represented the apex predators of the Cretaceous seas, their only competition being the large marine reptiles whose teeth were also sporadically found in the Elbtal Group (Geinitz, 1875a; Sachs *et al*., in press).

5. Conclusions

The chondrichthyan assemblage from the Saxonian Elbtal Group, eastern Germany, is Cenomanian to Turonian in age. During the Late Cretaceous, this fish fauna flourished in the temperate waters of a shallow sea strait. Currently, 19 species of cartilaginous fishes have been distinguished. The fauna was clearly dominated by mid- to large-sized lamniform sharks.

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