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A revision of the chimaeroid fishes (Holocephali, Chimaeroidei) from the British Cretaceous

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ABSTRACT:

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The preliminary results of a revision of the British Cretaceous chimaeroid fishes (Holocephali, Chimaeroidei) based on a study of museum collections are presented. The taxonomic composition (2 families, 9 genera, 20 species) and stratigraphic distribution of Cretaceous chimaeroid fishes are summarized. Some taxa, including *Callorhinchus, Elasmodus,* and *Lebediodon* are recorded from British Cretaceous for the first time.

Key words: Holocephali, Chimaeroidei, Cretaceous, British collections, Revision.

INTRODUCTION

Chimaeroid fishes of the suborder Chimaeroidei are a compact group of holocephalian cartilaginous fishes (Holocephali). In the Recent fauna, this suborder is represented by 3 families, 6 genera and about 30 species (DIDIER 1995), that inhabit mainly deep waters (rhinochimaerids, chimaerids) or near-shore environments (callorhynchids). In the fossil record Chimaeroidei is known from the early Mesozoic (Pliensbachian, Early Jurassic: WARD & DUFFIN 1989; and Norian, Late Triassic: unpublished material in the SSU collection). The principal fossil chimaeroid material collected are isolated dental plates (two pairs in the upper jaw – vomerine and palatine plates; one pair in the lower jaw – mandibular plates); rarer are fin spines and frontal claspers, extremely rare are egg case imprints and partial/complete skeletons (Late Jurassic, Germany; Late Cretaceous, Lebanon). The most commonly and best preserved material are dentitions, which are used for taxonomy and phylogenetic research.

HISTORY OF RESEARCH

"Fossil beaks" were firstly identified by William BUCKLAND in 1835 as dental plates of chimaeroid fishes (Holocephali, Chimaeroidei). After that, during the XIX century many British chimaeroid remains were collected and many new genera and species were erected by famous palaeontologists: AGASSIZ (1843), EGERTON (1843), NEWTON (1878) and WOODWARD (1891, 1911). As a result, 48 nominal chimaeroid species (33% of all known fossil chimaeroid species; see STAHL 1999) were described based on material from the Jurassic, Cretaceous and Palaeogene of the UK. Thus British chimaeroid collections are the most important ones among other "classical" collections of XIX century housed in France, Germany, Belgium and the USA. Research by NEWTON entitled "The chimaeroid fishes of the British Cretaceous rocks" and published in 1878 was the most significant work on chimaeroid fishes. It summarized all available chimaeroid material from different collections (public and private ones) and

recorded for British Cretaceous 3 genera (*Ischyodus, Edaphodon, Elasmodectes*) and 13 species (including 6 new ones) of chimaeroid fishes. Next and last summary of Cretaceous chimaeroid fishes was made by WOODWARD in his several publications (1891, 1911) including "Catalogue of Fossil Fishes in the British Museum (Natural History)". During the XXth century, little new Cretaceous chimaeroid material was collected in the UK, resulting in absence of any significant publications or revisions during last 100 years. Moreover, in the recently published "Fossils of the Chalk" field guides (OWEN & SMITH 1987; SMITH & BATTEN 2002) any data on chimaeroids were completely absent.

NEW MATERIAL FROM THE FORMER USSR

Meanwhile, during the two last decades, our knowledge about Mesozoic and Cenozoic chimaeroid

Age / formations			Taxa: C.	"Edaphodontidae"																				
			Callorhinchus cf. *borealis*	*Ischyodus townsendi*	*'Ischyodus' thurmanni*	*'Ischyodus' latus*	*'Ischyodus'* cf. *bifurcatus*	*'Ischyodus'* sp.	*Elasmodus planus*	*Elasmodus* spp.	*'Ischyodus' incisus* **(gen. nov.)**	Edaphodontidae **gen. et sp. nov.**	*Elasmodectes* sp.	*Elasmodectes willetti*	*Lebediodon oskolensis*	*Edaphodon sedgwicki*	*Edaphodon agassizi*	*Edaphodon crassus*	*Edaphodon reedi*	*Edaphodon mantelli*	*Edaphodon* **sp. nov.**	*Edaphodon* sp.	*'Edaphodon' laminosus* **(gen. nov.)**
K_2	Maa																							
	Cmp	U.Ch								?						?		?	?	?	?		
	San	U.Ch								?						?		?	?	?	?		
	Con	U.Ch								?						?		?	?	?	?		
	Tur	U.Ch								?						?		?	?	?	?		
	Tur	M.Ch								?						?	?	?	?	?			
	Cen	L.Ch	✕		?		✕			?	✕			✕		✕	✕		?	?			
K_1	Alb	U.Gr	✕		✕	✕	?		✕	?		✕			✕	✕		✕	✕				✕
	Alb	Glt	✕	✕	✕		?						✕		✕	✕		✕					✕
	Apt	L.Gr			✕											✕							
	Apt	A.b.b		✕				?														✕	
	Brm																						
	Hav																						
	Vlg																						
	Ber																						

✕ – 1
? – 2

Fig. 1. Taxonomic composition and stratigraphical distribution of the British Cretaceous chimaeroid fishes. Abbreviations: family: C. – Callorhynchidae; geological formations: U.Ch – Upper Chalk, M.Ch – Middle Chalk, L.Ch – Lower Chalk, U.Gr – Upper Greensand, Glt – Gault, L.Gr – Lower Greensand, A.b.b – "Aptian (Neocomian) bone bed" within the Lower Greensand. Other Cretaceous formations are not shown. Symbols: 1 – well dated records of taxa; 2 – questionable records

fishes has increased greatly due to new material from the former USSR (mainly Russia). Their remains (isolated dental plates mainly, many head claspers and fin spines, rare egg case imprints) were found from 115+ localities: in Russia (80+ localities, Norian to Oligocene), Ukraine (5: Albian to mid Eocene), Kazakhstan (20+: Albian to lower Oligocene), Uzbekistan (6: Albian to mid Eocene), Kyrgyzstan (1: Ypresian) and Lithuania (3: Albian). Some of these localities are very rich in chimaeroid material: 5000+ remains of 9 genera and 10 species were collected from the Albian-Cenomanian of Stoilenskii and Lebedinskii quarries in Belgorod Province, Russia (POPOV & AVERIANOV 2001).

During the study of this material, new methods and approaches (ontogenetic series, dentition reconstructions etc.) were applied to chimaeroid material resulting in better understanding of ontogeny and variability of chimaeroid dentitions and review of the systematics and phylogeny of the group (POPOV 2004). This new knowledge is a good basis for a re-examination of old collections.

MATERIAL STUDIED

During 2.5 months of research (February and mid-September to October, 2007) all available British collections with Cretaceous chimaeroid remains were studied: Natural History Museum in London (NHM; total 850+ specimens, British Cretaceous ones – 350+ specimens), British Geological Survey, Keyworth (BGS; 250+/200+), Sedgwick Museum of Earth Sciences, Cambridge University (SM; 480+/420+), Booth Museum of Natural History, Brighton (BM; 13/13), Yorkshire Museum, York (YM; 60+/50+) plus several private collections. All available chimaeroid material was recorded, measured and photographed, creating a database for future comparison and revision. It includes the type material of all new taxa previously described from the British Cretaceous (NHM – 6 species; BGS – 4; BM – 1; YM – 1).

RESULTS

The analysis of the collection data is still in progress, so this is a preliminary report. Nevertheless it is obvious that there is a more diverse Cretaceous chimaeroid assemblage (especially at genus level), than regarded earlier (Text-fig. 1). In central and southern England, about 50 Cretaceous chimaeroid localities were recorded. A large number of chimaeroid fish remains was re-determined in all collections studied. Some taxonomic and stratigraphical remarks are given below.

Chimaeroidei in the British Cretaceous consists of 2 families: Callorhynchidae GARMAN, 1901 and "Edaphodontidae" OWEN, 1846 (a combined family in need of revision, see discussion in POPOV & BEZNOSOV 2006). Callorhynchidae consists of one genus and species *Callorhinchus* cf. *borealis* NESSOV & AVERIANOV, 1996, recorded on a dozen mandibular and palatine plates (NHM, SM, YM, BGS) from the Gault, Upper Greensand and Lower Chalk formations. Some callorhynchid dental plates were determined earlier as "*Ischyodus thurmanni*" (e.g. NEWTON 1878, pl. 4, fig. 12) or "*Ischyodus latus*" (ibid, pl. 10, fig. 8).

The more diverse family "Edaphodontidae" consists of 8 genera including 2 new ones. *Ischyodus townsendi* BUCKLAND, 1835 differs from other "typical" Jurassic-Paleogene *Ischyodus* species by generic level characters (reported recently, POPOV 2007a) and being a type species of *Ischyodus* EGERTON, 1843 this species must be separated from all of other "*Ischyodus*" species.

The discovery of an *I. townsendi* mandibular plate (NHM P.28430) from the Gault extends stratigraphical distribution of this Tithonian species to the Early Cretaceous. A new genus can be erected for "*Ischyodus*" *incisus* NEWTON, 1878. Some mandibular plates of "*Ischyodus*" *thurmanni* PICTET & CAMPICHE, 1858, palatine and vomerine plates of "*Ischyodus*" *latus* NEWTON, 1878, both from the Upper Greensand can be described as a new species of the same new genus. A third new species of this genus (POPOV in prep.) occurs also from the Russian Albian-Cenomanian deposits (Belgorod and Saratov Provinces). Moreover, the distribution of "*Ischyodus*" *incisus* (new genus) can be restricted in Lower Chalk formation, older material (Gault, Upper Greensand) assigned to this taxon earlier (NEWTON 1878) are attributed to *Lebediodon oskolensis* NESSOV & AVERIANOV, 1996. The latter was discovered in the British Cretaceous for the first time (POPOV 2007b). This taxon was originally described from the late Albian of Belgorod Province, Russia (NESSOV & AVERIANOV 1996). Validity of "*Ischyodus*" *latus* NEWTON, 1878 is still unclear; palatine and vomerine plates attributed earlier to this species must be assigned to another species (see above), true palatine and vomerine plates of "*Ischyodus*" *latus* probably undistinguishable from that of "*Ischyodus*" *thurmanni*. Recorded earlier from the Cenomanian of Saratov Province (Russia) "*Ischyodus*" *latus* apparently is also a different species (POPOV & IVANOV 1996). *Ischyodus planus* NEWTON,

1878 (type NHM P.7226 plus several plates in BGS collection) from the Upper Greensand must be assigned to the genus *Elasmodus* EGERTON, 1843. Dental plates of another *Elasmodus* species (*E. rossicus* AVERIANOV, 1999 and/or *E. sinzovi* AVERIANOV, 1994) were recorded from the Upper Greensand and younger deposits (Chalk).

Dental plates of *Elasmodectes* sp. were discovered from the Gault. An unnumbered associated upper dentition of *Elasmodectes willetti* NEWTON, 1878 from the Lower Chalk, found in the storehouse of Sedgwick Museum finally solves the recently discussed problem (STAHL 1999, 2002) on the association of "*Ganodus*"-type palatine and vomerine plates and *Elasmodectes* mandibular plates in a single dentition. The genus *Edaphodon* BUCKLAND, 1835, is represented in the British Cretaceous by series of species, some of them have problematic validity and unclear distribution (especially within the Chalk). The validity of *Edaphodon sedgwicki* (AGASSIZ, 1843) and *Edaphodon crassus* NEWTON, 1878 can be confirmed but its distribution within Chalk is unclear. Interestingly, *E. crassus* has been determined from the Albian Kolbay locality in Kazakhstan (Mangyshlak Peninsula) and seems to be absent in boreal Albian deposits of the European Russia (pers. observation).

Edaphodon agassizi (BUCKLAND, 1835) (type NHM 28387, from the Lower Chalk) is probably the senior synonym of *E. sedgwicki* (AGASSIZ, 1843) (type BGS Gsa1524, Upper Greensand). The validity of *Edaphodon reedi* NEWTON, 1878 is evident, but the presence of this species in the Upper Chalk formation is uncertain. *Edaphodon mantelli* (BUCKLAND, 1835) may not be valid; some preparation of the syntype NHM 4280 is needed. *Edaphodon laminosus* NEWTON, 1878 based on mandibular, palatine and ?vomerine dental plates from the Gault and Upper Greensand can be separated from other *Edaphodon* species as a new genus. Record of reworked mandibular plate fragments of *Edaphodon* sp. from the "Aptian (Neocomian) bone beds" suggests a pre-Aptian origin of the genus, contrary to previous opinion (POPOV 2000). As a whole, poor dating of chimaeroid material from the Chalk (= Cenomanian-Campanian) obscures the sequence of *Edaphodon* species. The presence of more than 1-2 species of a single genus within a formation is unlikely, due to the concurrent exclusion rule. This is confirmed for fossil chimaeroids by Russian material. Several mandibular plates having two median tritors and figured as *Edaphodon sedgwicki* (WOODWARD 1911, pl. 40, fig. 4) from "Senonian zones" (Upper Chalk) of Norwich probably need to be described as a new species.

CONCLUSIONS

The taxonomic composition of the British Cretaceous chimaeroid fishes is more diverse (especially at the genus level) than previously regarded and includes new taxa. Callorhynchids (elephant fishes) and some "edaphodontid" genera (*Lebediodon*, *Elasmodus*) are recorded from the British Cretaceous for the first time. The rich and taxonomically diverse chimaeroid assemblage from the Cambridge Greensand is comparable to the late Albian – early Cenomanian chimaeroid complex from the Belgorod Province, Russia (POPOV & AVERIANOV 2001) but differs from the latter in being more diverse in 'edaphodontids' (*Edaphodon* species), more restricted in callorhynchids with the absence of *Brachymylus* and rhinochimaerids (*Belgorodon*). To resolve current taxonomic and stratigraphical questions, additional collecting with more precise stratigraphical data is needed, especially for the Chalk (most post-Cenomanian occurrences constitute at present questionable records) and Neocomian formations (e.g. Purbeck and Wealden, which currently lack of chimaeroid remains), with special attention to small-sized chimaeroid remains.

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