

THE EUROPEAN UPPER CRETACEOUS CROCODILIAN FOSSIL RECORD

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Rezumat

Fosile de crocodilieni din Cretacicul Superior European

Date despre crocodilienii europeni se cunosc încă din 1860, totuși, până acum nu s-a făcut o sinteză a acestora.

Acesta este scopul lucrării noastre, alături de încadrarea crocodilienilor europeni într-un context filogenetic. Studiul asociațiilor de crocodilieni din Cretacicul superior din Europa este crucial pentru înțelegerea istoriei evolutive a crocodililor moderni, dat fiind că în această perioadă au originea majoritatea membrilor din grupul Eusuchia.

Localities of the crocodilian Upper Cretaceous European assemblage

The knowledge of the European Upper Cretaceous crocodilian fauna has undergone two crucial events. The first one was the discoveries carried out by MATHERON and NOPCSA between 1860 and 1920. The second one is the reactivation of the Upper Cretaceous research as a consequence of the publication on the extraterrestrial hypothesis on the Cretaceous - Tertiary extinction by Alvarez et al in 1980. The synthesis between the old collections and the recent discoveries is unachieved at present. A great amount of work has, nonetheless, been done, comparing small isolated fragments and relating them to more complete material (VASSE, 1993, 1995; BUSCALIONI et al., 1997; BUSCALIONI & ORTEGA in press; BUSCALIONI et al., in prep). Moreover, the final part of this research should contemplate the necessity to place the European Upper Cretaceous crocodiles into a phylogenetic context. The study of the Upper Cretaceous crocodilian assemblage is crucial to understand the evolutionary history of modern crocodiles, since it was in this period that most of the early members of the crown group of the Eusuchia originated.

All of the European Upper Cretaceous localities with crocodilian remains are Campanian or Maastrichtian in age, corresponding approximately to an interval of 18 million years. The biostratigraphic correlation of most of these localities needs a more detailed re-examination, and

there is currently a renewed interest in this issue (MULDER et al., 1998). Recently, the use of dinosaur eggshells has been suggested for biostratigraphical purposes in the southern France and Catalonia localities (VIANEY-LIAUD et al., 1994; VIANEY-LIAUD & LOPEZ MARTINEZ, 1997; GARCIA, 1998). LE LOEUFF (1991) listed the main group of localities that are representing sectors of the Campano-Maastrichtian outcrops in the Upper Cretaceous European archipelago. Among them, several areas have yielded crocodilian remains. The Ibero-Armorican area gathers localities from Portugal, Spain, and southern France. The faunal description of the Ibero-Armorican area at a global level has been carried out by BABINOT et al., 1983; BUFFETAUT, 1980, LE LOEUFF, 1992, and VASSE, 1993. Some partial revisions of the faunal Ibero-Armorican assemblages have also been carried out, for instance, references to crocodilian remains in the French localities of Fox-Amphoux by BROIN et al., (1980) and Champ Garimond (Sigé et al., 1997), and of Provence by Garcia (1998). Several revisions have been done for the Spanish localities of Villamitjana (BUSCALIONI et al., 1986), Armuña (BUSCALIONI & SANZ, 1987; ORTEGA & BUSCALIONI, 1992), Laño (ASTIBIA et al., 1990; BUSCALIONI & ORTEGA, in press) and Quintanilla del Coco (Pol et al., 1992). The Gosau beds at Muthmannsdorf, in Austria, represent the Apulian area (BUFFETAUT, 1979). The Vălioara fossil site mainly represents the Transylvanian area from the Hațeg Basin, in Romania. The Scandinavian area gathers localities from Sweden, Belgium and Netherlands.

The crocodilian Upper Cretaceous genera

A brief updated comment on the taxonomic status and on the phylogenetic position of the European Upper Cretaceous crocodiles is given below, including the distribution of their corresponding geographical areas:

Ischyrochampsia (VASSE, 1995) is known from a mandible and a fragment of premaxillae and maxillae. It is the only known locality of Saint-Estève-Janson (Bouches-du-Rhône, France), although isolated teeth attributed to this genus were found in Capens (Département de l'Ariège) also upholds its presence in southern France. *Ischyrochampsia* has been proposed as a member of the trematochampsids, although its phylogenetic position is not fully resolved. It is a monospecific genus (*I. meridionalis*).

Musturabalsuchus (BUSCALIONI et al., 1997) has been recorded in the Ibero-Armorican and Transylvanian areas. This genus has been proposed as the valid denomination of MATHERON's (1869) *Crocodylus affuvelensis*. *Musturabalsuchus* is known from abundant isolated cranial elements. The mandible and the rest of the skull have never been found associated, except in the specimen housed in the Natural History Museum of Marseilles (figure 4 in BUFFETAUT, 1980). *Musturabalsuchus* is regarded as an Alligatoroidea, being probably one of the closest sister taxa of the

clade Alligatoridae (BUSCALIONI et al., 1997; BUSCALIONI & ORTEGA, in prep.). Only one species has been proposed (*M. buffetautii*)

Allodaposuchus (NOPCSA, 1928; BUSCALIONI et al., in prep) has been discovered in Transylvania and in the Ibero-Armorican area. It is known from abundant isolated cranial fragments and an almost complete skull (although the mandible is unknown) from Spain. *Allodaposuchus* is a key genus for the understanding of the Eusuchia evolutionary history, since it has been discussed either as the closest sister taxon of the crown-group Crocodylia, or as the sister group of Brevirostres (using the clade denomination proposed by BROCHU, 1998 a and b). It is a monospecific taxon (*A. praecedens*), and maintains the denomination proposed by Nopcsa.

Acynodon (BUSCALIONI et al., 1997) is based on fragmentary isolated cranial bones, and on a complete skull from a private collection. It has been recorded in the Ibero-Armorican and Transylvanian areas. *Acynodon* is a member of Alligatoridae, closely related to the North American genera *Stangerochampsia* and *Brachychampsia*. Two species have been proposed (*A. iberoccitanus* and *A. lopezii*).

Doratodon carcharidens (SEELY, 1881; BUFFETAUT, 1979, 1980) is based on scarce cranial elements. The material has been found in the Apulian and in the Transylvanian areas. It is a neosuchian ziphiodont with uncertain phylogenetic relationships (ORTEGA, in prep.).

The other three genera of crocodiles from the Upper Cretaceous of Europe are long snouted, aquatic animals: *Aigialosuchus villandensis* (PERSSON, 1959) from Scania (Blacksudden, southern Sweden) is based on fragmentary remains of a rostral region and anterior part of lower jaw. The other taxon is *Thoracosaurus*; its domain being the northeastern European area (Scania, Netherlands, Belgium and Crimea) (MULDER, 1997; MULDER et al., 1998). Up to now, two species are accepted as valid: *T. macrorhynchus* and *T. neocesariensis*. *Aigialosuchus* does not have a clear phylogenetic position, and was initially referred to the family Crocodylidae. *Thoracosaurus* may be discussed as the sister taxon of Gavialoidea (BROCHU, 1997) or as a member of the Crocodyloidea. The third form is a long-snouted “mesosuchia”, probably belonging to the dyrosaurids (pers. Obs.), being probably the sole coastal non-eusuchian European crocodile. This undescribed material (a rostrum and several skull bones) was found at the locality of Averio (Portugal).

Isolated elements: teeth and postcranial remains

A number of isolated teeth is the most abundant component of the Upper Cretaceous European crocodilian record. Most of the isolated crowns are not taxonomically discernible, because they possess the common conical shape that is widespread in diverse crocodilian lineage. Particular morphologies such as serrated teeth assessed to *Doratodon*, have been collected in Transylvania (Vălioara, BUFFETAUT, 1980 and pers. obs.) and Apulia (Gosau Beds, BUFFETAUT, 1979). The species *A. lopezii*, from Quintanilla del Coco (Spain), is based on striking lanceolated to molariform teeth (POL

et al., 1992; BUSCALIONI et al., 1997). Many other localities distributed along the Ibero-Armorican, Apulian and Transylvanian areas also have yielded molariform acynodon-like teeth (BUFFETAUT, 1980; Sigé et al., 1997).

No articulate skeletons have been found in the Upper Cretaceous European crocodilian fossil record. The postcranial remains are mostly isolated osteoderms, vertebral centra, and appendicular fragments. Many of the old papers on Upper Cretaceous crocodilian fauna provide a shallow description and figures of postcranial elements (i.e. those coming from the Fuvelian lignites of Provence in France figured by MATHERON, 1869), and the Vălioara outcropping figured by NOPCSA, 1928). These isolated appendicular and axial elements can be just identified as eusuchian crocodiles.

The importance of the Upper Cretaceous European crocodilian record and the origin of modern crocodiles

The Upper Cretaceous European crocodilian assemblage is characterized by the prevalence of eusuchians crocodiles in comparison with the non-eusuchians. Europe and North America are the only continents characterized by a higher proportion of Eusuchia, their percentage being more than 60% of the total crocodilian fauna during the Upper Cretaceous. In the other continents (Asia, South America and Africa) the non-eusuchians constitute the preponderant faunas, more than 60% of the total crocodilian assemblage (BUSCALIONI & ORTEGA, in prep.). All of the Upper Cretaceous crocodilian fossil record is mainly concentrated in Campano-Maastrichtian localities. This is especially noticeable in the Cenomanian and Santonian record of North America and Europe, where the non-eusuchians are represented by two taxa (*Gilchristosuchus* and *Woodbinesuchus*), and the record of Eusuchia is represented by the Senonian-Lower Campanian European localities that have provided remains of the coastal crocodile *Thoracosaurus*. Therefore, the knowledge of the early history of modern crocodiles is biased, but we may assume that this bias shows the same trend as the entire continental tetrapod fossil record. The early Late Cretaceous record of tetrapods has relatively low values of metric completeness (Turonian: 21.6; Coniacian: 28.6; Santonian: 37.2) with respect to the latest two stages (Campanian: 84.7; Maastrichtian: 95.1) (BENTON, 1987).

Europe and North America reflect expansions of Eusuchia earlier than those reflected by Asia, Africa and South America. Modern crocodiles (known as Crocodylia) diversified in an expansive radiation during the Campano-Maastrichtian. This expansive radiation suggests that a global biotic replacement of primitive crocodiles by modern ones took place in Europe and North America, where there was no extinction of the non-eusuchia crocodiles but a drop in their number of genera (VASSE & HUA, 1998). The Euriamerican expansion was a large-scaled event apparently concentrated in the Uppermost Cretaceous (BUSCALIONI & ORTEGA, in prep.). The early history of modern

crocodiles started in the Euriamerica paleocontinent, the subsequent Tertiary history has modeled the recent circumtropical distribution of crocodilians.

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