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Introducing the 'First European Symposium on the Evolution of Crocodylomorpha'

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Abstract:	The 1st European Symposium on the Evolution of Crocodylomorpha took place during the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP) organized by NOVA University of Lisbon (UNL) in Caparica, Portugal. Fourteen lectures and five posters were presented at the symposium in June-July 2018. This special issue showcases ten papers based on symposium contributions.

Editorial

Introducing the 'First European Symposium on the Evolution of Crocodylomorpha'

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Abstract. The 1st European Symposium on the Evolution of Crocodylomorpha took place during the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP) organized by NOVA University of Lisbon (UNL) in Caparica, Portugal. Fourteen lectures and five posters were presented at the symposium in June-July 2018. This special issue showcases ten papers based on symposium contributions.

More than a decade has passed since the First Symposium on the Evolution of Crocodyliformes. Taking place in Neuquén, Argentina during 2009, the results of that symposium were published as a special volume in this journal in 2011 (Pol & Larsson, 2011 and articles therein). Since then, the second symposium was held in 2011 in San Juan, Argentina, and a third was held in October 2019 in Uberlândia, Brazil. Following in the footsteps of these symposia, the 1st European Symposium on the evolution of Crocodylomorpha took place during the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP) organized by NOVA University of Lisbon (UNL) in Caparica, Portugal (Fig. 1).

The symposium was a success, featuring a fascinating keynote presentation by Dr Christopher Brochu, along with 13 oral presentations and five posters. This special volume was commissioned from these presentations, yielding ten published articles. It covers an array of crocodylomorph taxa ranging from the Jurassic to the present, including thalattosuchians, advanced neosuchians, basal eusuchians and crocodylians. Moreover, the included studies cover an array of topics (cladistics, systematics, functional anatomy and biodiversity) largely focused on European material, although global studies and those from other continents (such as South America) are also been included.

The 1st European Symposium on the evolution of Crocodylomorpha, and this special issue of the *Zoological Journal of the Linnean Society*, reflects the advances and new crocodylomorph discoveries made in Europe during the past decade. These ten years saw a renaissance of study into crocodylomorph evolution (Fig. 2) in Europe, spanning the discovery of new specimens, re-descriptions of historical specimens and advances in model-based macroevolutionary analyses.

One of the neosuchian clades reviewed over the last decade in Europe is Goniopholididae. This clade includes Jurassic/Cretaceous forms with a semi-aquatic lifestyle, a Laurasian distribution and a general gestalt reminiscent of extant crocodylians. One of the most common taxa in the fossil record of the Late Jurassic and Early Cretaceous of Europe is *Goniopholis*. Since the first *Goniopholis* was discovered and described, this genus has been used as a "wastebasket" taxon for a variety of fragmentary goniopholidids (Andrade *et al*., 2011), with as many as 19 species included within the genus (Salisbury & Naish, 2011). However, in the last few years, and thanks to new discoveries of several specimens, an exhaustive review of Eurasian goniopholidids has been undertaken (Andrade & Hornung, 2011; Andrade *et al*., 2011; Salisbury & Naish, 2011; Buscalioni *et al*., 2013; Puértolas-Pascual, Canudo & Sender, 2015a; Martin *et al*., 2016; Ristevski *et al*., 2018; Puértolas-Pascual & Mateus, 2020). As a consequence of these works, the genus *Goniopholis* is now restricted to three species and the remaining European species have been considered *nomina dubia*, junior synonyms or have been reassigned to the new genera *Hulkepholis* (Salisbury & Naish, 2011; Buscalioni *et al*., 2013; Arribas *et al*., 2019) and *Anteophthalmosuchus* (Salisbury & Naish, 2011; Buscalioni *et al*., 2013; Puértolas-Pascual, Canudo & Sender, 2015a; Martin, Delfino & Smith, 2016b; Ristevski *et al*., 2018).

There has been a revolution in our understanding of the small-bodied taxa spanning the transition from "advanced" neosuchians to basal eusuchians over the past decade. Indeed, the number of such forms has exploded since the turn of the millennium. But some of these forms are phylogenetically problematic. This is especially true of atoposaurids. These were diminutive crocodyliforms that were important components of Laurasian semi-aquatic and terrestrial ecosystems during the Jurassic and Cretaceous. Our sample of such forms has expanded greatly in the past decade (e.g., Martin *et al*., 2010, 2014a; Tennant & Mannion, 2014; Puértolas-Pascual *et al*., 2015b, 2016; Tennant *et al*., 2016; Young *et al*., 2016; Venczel & Codrea, 2019), but whether "Atoposauridae" as classically understood represents a clade is unclear, nor is it clear how many taxa these fossils represent. A recent review by Tennant *et al.* (2016) concluded that only three Late Jurassic genera from western Europe (*Alligatorellus*, *Alligatorium*, *Atoposaurus*) should be included in Atoposauridae, and that the putative atoposaurid genus *Theriosuchus* was polyphyletic, with none of its component species referable to Atoposauridae. Subsequent studies have reinforced the non-monophyly of *Theriosuchus*, but argued for an atoposaurid affinity for all such forms, with atoposaurids closely related to Paralligatoridae within Eusuchia (e.g., Schwarz *et al*., 2017). Further review of historical material is needed in parallel with the description of new taxa.

An endemic European clade important for our understanding of eusuchian origins is Bernissartiidae. This small-bodied clade is unique in having dentition adapted to a durophagous diet. Originally known only from *Bernissartia fagesii* Dollo, 1883 from the Early Cretaceous of Belgium, new material has been discovered and described from Spain (Puértolas-Pascual *et al*., 2015b and references therein). Recently, a new bernissartiid species based on a complete skull from the Early Cretaceous of England was named *Koumpiodontosuchus aprosdokiti* Sweetman, Pedreira-Segade & Vidovic, 2015.

Perhaps nothing has done more to advance our understanding of eusuchian and crocodylian origins than a series of studies exploring the systematics, phylogeny and palaeobiogeography of two endemic European radiations, Hylaeochampsidae (Martin, 2007; Delfino, Martin & Buffetaut, 2008b; Buscalioni *et al.*, 2011) and Allodaposuchidae (Martin & Buffetaut, 2008; Delfino *et al.*, 2008a; Puértolas, Canudo & Cruzado-Caballero, 2011; Blanco *et al.*, 2014; Puértolas-Pascual, Canudo & Moreno-Azanza, 2014; Narváez *et al.*, 2015; Blanco *et al.*, 2015; Martin *et al.*, 2016a; Narváez *et al.*, 2016; Blanco & Brochu, 2017; Narváez *et al.*, 2017) (Table 1). There has also been the discovery of a putative Middle Jurassic hylaeochampsid from the Isle of Skye, Scotland (Yi *et al.*, 2017).

The European fossil record of crown-group Crocodylia has been elucidated. These studies have ranged from the discovery of new taxa to reassessments of the morphology, phylogeny, taxonomy and palaeobiogeography of typical European taxa, such as the Palaeocene/Eocene crocodyloid *Asiatosuchus* (Delfino & Smith, 2009; Delfino *et al.*, 2017), the Eocene/Miocene alligatoroid *Diplocynodon* (Martin, 2010; Delfino & Smith, 2012; Martin *et al.*, 2014b; Díaz Aráez *et al.*, 2017; Rio *et al.*, 2019) and the Eocene tomistomine *Kentisuchus* (Jouve, 2016). In addition, the palaeobiodiversity (Mannion *et al.*, 2015; Puértolas-Pascual *et al.*, 2016; Wilberg, 2017) and phylogenetic relationships (Groh *et al.*, 2020) of Crocodylia through the Mesozoic and Cenozoic have been explored. Recently, the description of *Portugalosuchus* from the Late Cretaceous of Portugal hints that this new eusuchian could be the oldest known member of the crown-group, pushing back the origins of Crocodylia by 20 million years, and suggests that the European archipelago of the 'mid' Cretaceous could be the origin of this clade (Mateus, Puértolas-Pascual & Callapez, 2019).

Finally, there has been a renaissance in the study of European non-neosuchian crocodylomorphs, particularly for Thalattosuchia. These include re-study of historical specimens (e.g., Jouve, 2009; Young & Andrade, 2009; Johnson *et al.*, 2015, 2018; Sachs *et al.*, 2019a; Cau, 2019; Rio *et al.*, 2020) naming of new genera and/or species (e.g., Young *et al.*, 2010, 2013; Cau & Fanti, 2011; Parrilla-Bel *et al.*, 2013; Foffa *et al.*, 2018a; Sachs *et al.*, 2019b, Aiglstorfer, Havlik & Herrera, 2020), descriptions of isolated elements (Chiarenza *et al.*, 2015; Parrilla-Bel & Canudo, 2015) and how thalattosuchians ecologically interacted with other marine reptile groups (Foffa *et al.*, 2018b). There has also been renewed interest in the European notosuchians (e.g., Rabi & Sebok, 2015; Martin, 2016; Cubo, Köhler & Buffrénil, 2017), and non-mesoeucrocodylian crocodylomorphs related to Gobiosuchidae (Schwarz & Fechner, 2008; Buscalioni, 2017).

Following the call of the 1st European Symposium on the evolution of Crocodylomorpha and this special volume, ten new articles have been here included:

From the Jurassic-Early Cretaceous, there are three articles on the marine crocodylomorph clade Thalattosuchia. The first re-describes two historical species of teleosauroids, *Steneosaurus larteti* Eudes-Deslongchamps, 1869 and *S. boutilieri* Bronzati *et al.*, 2012, from the Bathonian (Middle Jurassic) of England (Johnson, Young

& Brusatte, 2020). This study confirmed the validity of these two species, but reassigned them to the new genera *Deslongchampsina* and *Yvridiosuchus*, respectively. Moreover, the re-description of these taxa hints that macrophagous / durophagous teleosauroids evolved prior to the Bathonian, and further elucidates the early evolution of the subclade Machimosaurini. The second article is about the other great clade within Thalattosuchia: Metriorhynchoidea. Here, Young *et al.* (2020a) described isolated tooth crowns, and the occipital region of a large *Torvoneustes* specimen from the Late Jurassic of England. They showed that at least some species of *Torvoneustes* could rival the giant metriorhynchid *Plesiosuchus* in body size. The third article related to Thalattosuchia investigates posterodorsal retraction of the external nares in metriorhynchids. They found that this adaptation to a sustained swimming ecology evolved independently several times, but curiously, unlike in other groups of Mesozoic marine reptiles metriorhynchids evolved from taxa with a single naris at the tip of the snout (Young *et al.*, 2020b).

Two articles on continental crocodylomorphs from the Jurassic of Portugal are also included. The first, focusing on the Late Jurassic of the Lourinhã Formation (Portugal), describes a three-dimensionally preserved articulated partial skeleton of a small goniopholidid. Comparative microCT datasets, comprising this specimen and other neosuchians yielded new inferences about the evolution and functionality of the dermal armour in goniopholidids (Puértolas-Pascual & Mateus, 2020). The second article focuses on crocodylomorph teeth from the same Formation. Over 120 teeth were studied and assigned to ten different morphotypes, which were then attributed to five different clades: Atoposauridae, Goniopholididae, Bernissartiidae, *Lusitanisuchus* and an undetermined crocodylomorph. This study not only addresses the palaeobiodiversity of the Lourinhã crocodylomorph fauna, but also explores their ecological relationships. Based on the different dental morphologies, four distinct feeding behaviours (durophagous, “insectivorous”, hypercarnivorous and generalist) are hypothesized (Guillaume *et al.*, 2020).

We include another tooth-based study, this time based on material from the Maastrichtian of Spain. In this study, several isolated tooth crowns, maxillary and mandibular remains recovered in the Tremp Formation (southern Pyrenees) are described and analysed. Based on the tooth morphological variation and taphonomy of each site, the crocodylomorph assemblage is found to be highly diverse, in terms of species richness, inferred feeding habits and environmental preferences (Blanco *et al.*, 2020).

This volume also includes a paper on the systematics and phylogeny of Allodaposuchidae. The study provides a detailed review of the historic material from the Maastrichtian of Romania assigned to *Allodaposuchus precedens* Nopcsa, 1928. From this, a new diagnosis for this taxon and comparisons with other allodaposuchids are presented and discussed (Narváez *et al.*, 2020).

Two papers focus on eusuchian evolution. The first is an analysis of the spatiotemporal distribution of Eusuchia (De Celis, Narváez & Ortega, 2020). This paper finds several peaks in eusuchian palaeodiversity, with the largest in the Palaeocene and the middle-late Miocene. The study also suggests that eusuchian palaeodiversity could be linked to the palaeotemperature among other abiotic and/or biotic factors. The second study (Cidade, Fortier & Hsiou, 2020) looks into the taxonomy and phylogeny of the alligatoroid

Necrosuchus ionensis Simpson, 1937. This study recovers *Necrosuchus* as a derived caimanine, as it lived during the Palaeocene eusuchian palaeodiversity maximum in South America, suggesting new perspectives on the early evolution and radiation of caimanines.

The final study in this special issue investigates the robustness and homoplasy of morphological characters used in crown crocodylian phylogenies (Sookias, 2020). The impetus for this study is the discordance between morphological and DNA-based phylogenies of extant crocodylians, primarily in the position of the Indian gharial. This study provides some indications as to how morphology may be able to be used in a more effective way for crocodylians, but also for other crocodylomorphs.

Ten major crocodylomorph clades — Metriorhynchidae, Teleosauroidea, Ziphosuchia, Goniopholididae, Atoposauridae, Bernissartiidae, Hylaeochampsidae, Allodaposuchidae, Eusuchia and Crocodylia — are approached in this volume from systematic, phylogenetic, palaeobiodiversity, palaeobiogeographical and palaeoecological points of view. All these contributions will impact crocodyliform research and shall serve to expand the knowledge of all these clades in particular, and Crocodylomorpha in general.

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Figure 1. Group photograph of the participants in the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP).

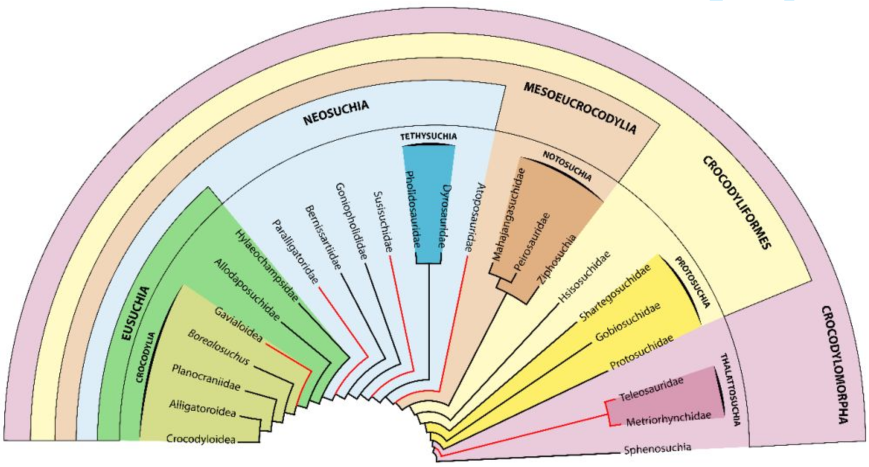

Figure 2. Morphology phylogeny of the main lineages within Crocodylomorpha based on recent studies such as Wilberg (2015), Pol & Leardi (2015), Buscalioni (2017), Dal Sasso *et al.* (2017), Barrios *et al.*

(2018), Mateus *et al.* (2019), Wilberg *et al.* (2019). Clades with red lines indicate taxa whose phylogenetic position is still under strong debate.

Basal eusuchians from Europe					
Before 2007			**After 2007**		
Clade	**Taxon**	**Age/Country**	**Clade**	**Taxon**	**Age/Country**
Hylaeochampsidae	*Hylaeochampsa vectiana* Owen, 1874	Barremian/ England	**Hylaeochampsidae**	*Iharkutosuchus makadii* Ősi *et al.*, 2007	Santonian/ Hungary
	Acynodon iberoccitanus Buscalioni *et al.*, 1997	Campanian–Maastrichtian/Spain and France		*Acynodon adriaticus* Delfino *et al.*, 2008	Campanian–Maastrichtian/ Italy
	**Acynodon lopezi* Buscalioni *et al.*, 1997	Maastrichtian/Spain			
Allodaposuchidae	**Massaliasuchus affuvelensis* (Matheron, 1898)	Campanian–Maastrichtian/France	**Allodaposuchidae**	*Arenysuchus gascabadiolorum* Puértolas *et al.*, 2011	Maastrichtian/ Spain
	Allodaposuchus precedens Nopcsa, 1928	Maastrichtian/Romania		*Agaresuchus subjuniperus* (Puértolas-Pascual *et al.*, 2014)	Maastrichtian/ Spain
	**Ischyrochampsa meridionalis* Vasse, 1995	Campanian–Maastrichtian/ France		*Allodaposuchus palustris* Blanco *et al.*, 2014	Maastrichtian/ Spain
	**Musturzabalsuchus buffetauti* Buscalioni *et al.*, 1997	Campanian–Maastrichtian/Spain		*Allodaposuchus hulki* Blanco *et al.*, 2015	Maastrichtian/ Spain
				Lohuecosuchus megadontos Narváez *et al.*, 2015	Campanian–Maastrichtian/ Spain
				Lohuecosuchus mechinorum Narváez *et al.*, 2015	Campanian–Maastrichtian/ France
				Agaresuchus fontisensis Narváez *et al.*, 2016	Campanian–Maastrichtian/ Spain
Other basal eusuchians	*Unasuchus reginae* Brinkmann, 1992	Barremian/ Spain	**Other basal eusuchians**	*Pietraroiasuchus ormezzanoi* Buscalioni *et al.*, 2011	Albian/Italy

Table 1. List of basal Eusuchians species discovered and described in Europe before and after 2007. Asterisks (*) indicate taxa with doubtful phylogeny or taxonomic validity.

Figure 1. Group photograph of the participants in the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP).

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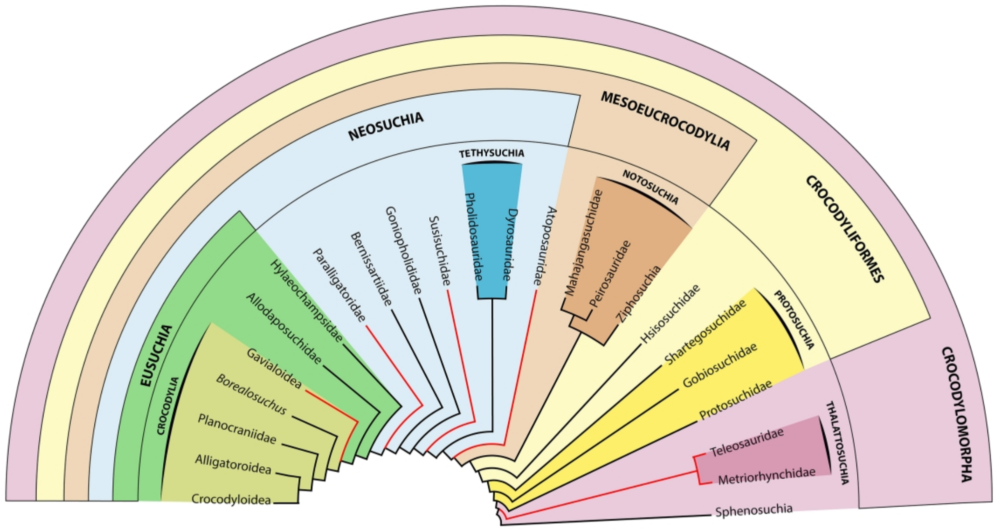

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Basal eusuchians from Europe					
Before 2007			**After 2007**		
Clade	**Taxon**	**Age/Country**	**Clade**	**Taxon**	**Age/Country**
Hylaeochampsidae	*Hylaeochampsa vectiana* Owen, 1874	Barremian/ England	**Hylaeochampsidae**	*Iharkutosuchus makadii* Ősi *et al*., 2007	Santonian/ Hungary
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Allodaposuchidae	**Massaliasuchus affuvelensis* (Matheron, 1898)	Campanian–Maastrichtian/France	**Allodaposuchidae**	*Arenysuchus gascabadiolorum* Puértolas *et al*., 2011	Maastrichtian/ Spain
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