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„ The effects of ecology and phylogeny on the skull shape of extinct crocodilians (Crocodyliformes, Archosauria) as indicated by morphometric analyses. "

verfasst von / submitted by

Patrick Abdalla, BSc

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Contents

Abstract

Crocodyliformes is a clade of Archosauria which in the past was considered morphologically conservative. Extant members do indeed appear to form a morphologically quite uniform group, but an incredible amount of diversity and morphologic disparity existed amongst fossil species. Throughout the Mesozoic and Early Cenozoic, a multitude of assemblages encompassing multiple taxa of Crocodyliformes occurred in limnic environments world-wide. While these reptiles also differed from each other in their sizes and proportions, the main feature setting them apart was the shape of their skulls. Morphometric analyses concerning the skull shape of extant crocodilian species and the factors influencing it were conducted on an increasing scale during the last two decades. Some scientists found the main factor to be the animals' ecological niche, others regarded phylogeny as more important and yet others suggested geographic distribution to be decisive regarding the influence on skull shape. The extensive diversity of fossil members of Crocodyliformes, however, has yet to be assessed in a similar fashion. Here, five fossil crocodyliform assemblages were analysed using two-dimensional morphometrics and Procrustes fit analytical approaches. They were compared to each other as well as to the extant Crocodylia diversity to assess the presence of trends in morphospace occupation and the amount of variance accounted for by various factors. The factors investigated were size, stratigraphic age, locality and phylogenetic affiliation on family level and above. Interestingly, the assemblages seem to show no real trend in morphospace occupation. Neither are limnic crocodiles developing broader or longer skulls throughout time nor are taxa from the same assemblages tending to move further apart. The only noticeable result is that the morphospace occupation of the assemblages is the largest during the Early Cretaceaous, when – according to previous research – the diversity of limnic crocodiles peaked before going through a prolonged extinction phase. The fact that the "metriorhynchid" skull shape, which is defined by a wide skull rapidly tapering towards a narrow but comparatively short snout, is most definitely related to this. Of all factors assessed, the phylogenetic affiliation of taxa has by far the most effect on total variance, consistently accounting for 41.604% of it. Skull shape therefore seems to be a mostly phylogenetic trait in limnic Crocodyliformes. The disappearance of certain skull shapes seems to be a consequence of the clades this condition was common in going extinct. Future research on Crocodyliformes phylogeny should incorporate skull shape as a factor, while ecological assessments might focus more on the teeth and lower jaw.

Keywords

Introduction

One of Biology's oldest standing principles is that the shape of anatomic features is determined by their respective functions (Cuvier, 1817). Consequently, selection favours individuals with anatomic traits better suited to the task they are meant to perform. It would thus seem logical that the shape of any anatomic structure was a clear indicator of its purpose, thereby making it not only possible but comparatively easy to determine an organism's ecological niche based on it. However, there are certain constraints that limit the evolvability of organisms. It has been known for multiple decades now that the expression of anatomic traits isn't solely decided by ecologic factors. One of the primary constraints of evolvability is phylogenetic affiliation. In some clades, the shape of certain anatomic features is so much a result of their evolutionary history that it is more indicative of phylogenetic relationships than functional purpose (McKitrick, 1993). One of the most distinctive parts of a vertebrate's body with a shape greatly influenced by both ecology and phylogeny is the skull.

A clade where the skull represents the feature regarded as most indicative of the species' identity is Crocodylomorpha. Crocodylomorpha is a group of reptiles with a fossil record dating back at least to the Middle Triassic (Tykoski et al., 2002). Firmly rooted within the larger group Archosauria they are the closest known relatives of both the pterosaurs and the dinosaurs including Aves. Their extensive fossil diversity is divided into three groups. The most basal taxa are placed into Protosuchia while most of the Mesozoic and all Cenozoic species form the Crocodyliformes. It is this group which includes the extreme diversity and disparity of Mesozoic crocodylomorphs as well as the more derived members of Eusuchia with their typical "crocodilian" appearance. All extant species of crocodiles and caimans, the two species of alligator and the peculiar gharial are members of Eusuchia (Benton & Clark, 1988). The extensive diversity of both extant and extinct Crocodyliformes has been a subject of scientific research before. One of the primary subjects of these studies was the skull shape of these animals, but the exact focus of these works varied considerably and a wide field of topics was tackled by a multitude of researchers. Among them were the preservation of embryonic skull shape throughout ontology (Morris et al., 2019), the effect of allometric cranial growth on analyses of crocodilian relationships (Piras et al.,

2010), the mechanical performance of extant crocodiles' skulls (Pierce et al., 2008), the general evolution of crocodylomorph skull shape (Godoy, 2019) and the morphologic diversity of crocodylomorph skulls throughout the Mesozoic and Cenozoic (Wilberg, 2016).

The aim of the work presented is to conduct a morphospace analysis of various Mesozoic and Cenozoic crocodyliform taxa. The primary intent is not to determine the position of individual species, but rather to look at the entirety of fossil crocodyliform assemblages and their morphospace occupation. The important questions addressed here are: Are there observable trends throughout time? If there are, what are they? Do the assemblages as a whole become more uniform (e.g. longirostrine – which could indicate a diet of fish – or broad-snouted – which could signify durophagy), or diverse? Is there a tendency of the individual datapoints to move further apart from each other? This would suggest that as crocodyliforms radiated and diversified, their members became more different from each other in a significant way. Such a trend would be indicative of minimising competition by maximising niche partitioning (Dobrev et al., 2001). Most importantly: Is skull shape even a trait primarily influenced by the animal's ecological niche? Or is it more indicative of phylogenetic relationships within Crocodyliformes? Answers to these questions – however partial – may have a significant positive effect on future research directions concerning the ecology and phylogeny of Crocodyliformes throughout the past 160 Million years.

Matherial and Methods

Morphometric Analysis

To assess the morphospace occupation of crocodyliforms through time the skulls of 36 individuals representing 20 extinct and 5 extant species were used to establish their morphospace occupation two-dimensionally. In two dimensions, the cranial shape of extant crocodiles is described using the length and width of the skull as the two axes of a coordinate system (Figure 1). This coordinate system can be divided into four quadrants based on the shape of the skull; short and narrow, short and wide, long and narrow and long and wide. Extant species with a short and narrow skull include *Crocodylus niloticus* and the two species of the genus *Alligator*. Short and wide skulls can be found within species such as *Caiman yacare* and *Osteolaemus tetraspis*. Examples for species with long and narrow skulls are *Tomistoma schlegelii* and *Crocodylus johnstoni*. The quadrant containing species with a long and wide skull is largely unoccupied. *Gavialis gangeticus* occupies the extreme outer fringe of this part

of the coordinate system. The skull of this species is considered wide because of its width at the jaw joint (Pierce et al., 2008). Regarding extinct crocodyliforms, the morphometric coordinate system works a bit differently, because a different range of cranial shapes is present (Figure 2). Length and width are still the defining factors, but the way the skull tapers towards the tip of the snout now plays a role as well. Three of the four extremes are largely identical to shapes present in extant crocodiles. The very wide and blunt skull shape corresponds to the short and wide morphotype, the triangular skull shape corresponds to the short and narrow morphotype and the
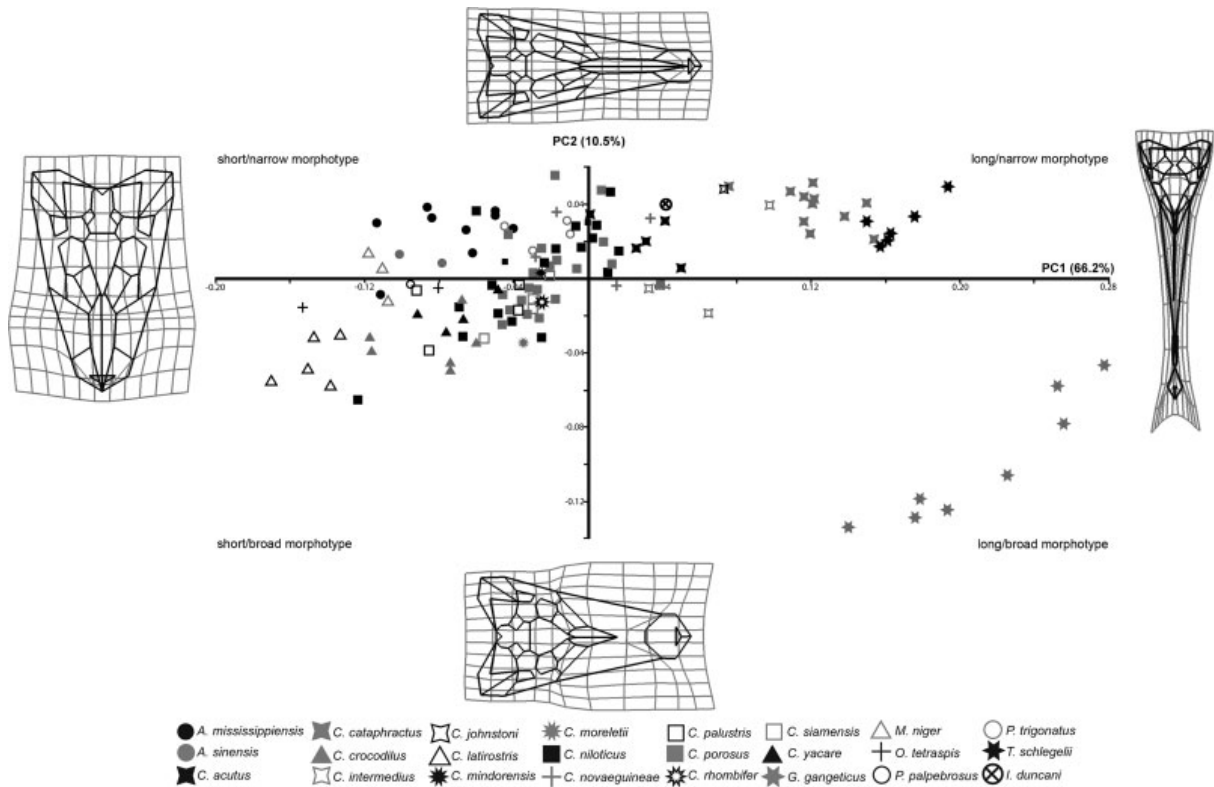
Figure 1; Cranial morphospace occupied by the extant members of Crocodylia as described by Pierce et al., 2008.

elongated skull shape combines the long and narrow and the long and wide morphotype. The fourth skull shape is the so called "metriorhynchid" condition, which is defined by a wide skull rapidly tapering towards a narrow but comparatively short snout. This last morphotype is absent from today's crocodile morphospace (Wilberg, 2016).

The fossil assemblages examined to analyse the morphological disparity of extinct Crocodyliformes are the Oxfordian Qigu and Shishugou formations of the Junggar Basin in the north of the People's Republic of China (Wings et al., 2010), the Berriasian Purbeck limestone group of Dorset on the southern coast of England (Salisbury, 2002), the Aptian to Albian sandstones of Gadoufaoua in Niger (Sereno et al., 2003), the

Maastrichtian molasse deposits of Romania's Hațeg Basin (Martin et al., 2006) and the German Lagerstätte Messel of the Lower Eocene (Franzen, 1985). At least four specimens from every locality were used in the analysis. For the Hațeg Basin, these represented various growth stages of two species rather than four different taxa. Previous research showed considerable variations in crocodilian skull shape related to ontogeny (Piras et al., 2010, Morris et al., 2019), so the analysed skulls were always
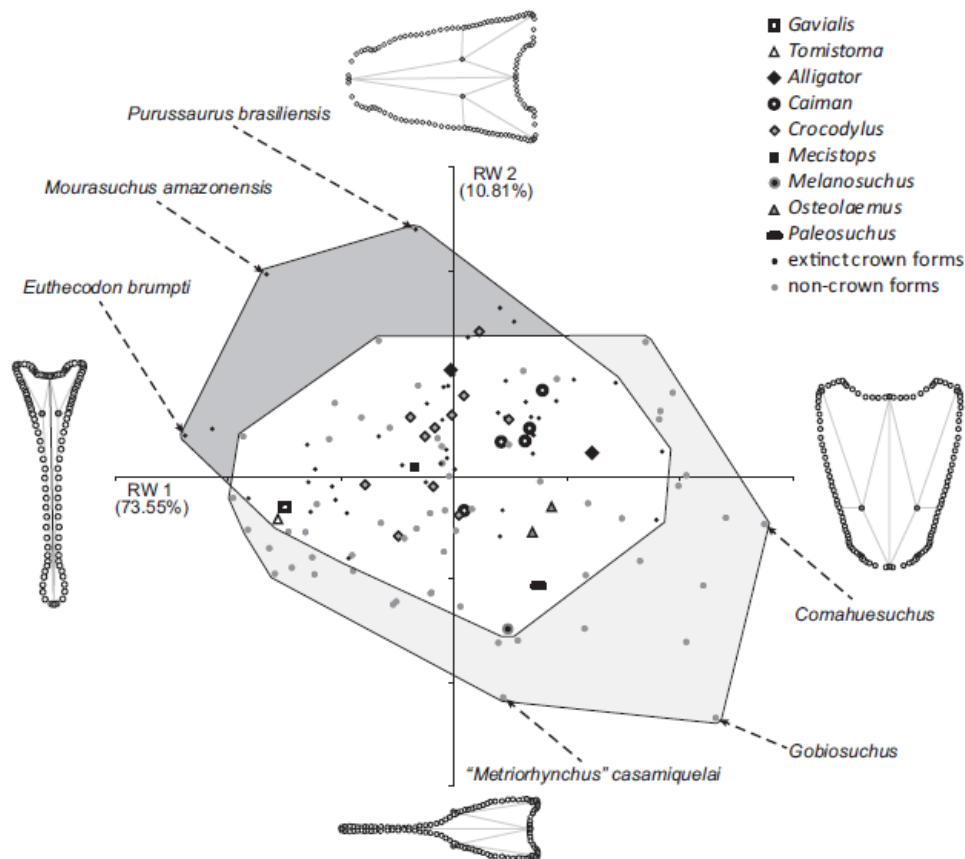
Figure 2; Cranial morphospace occupation of Mesozoic Crocodyliformes as described by Wilberg, 2016.

those of adult specimens. Nevertheless, whenever possible, multiple individuals of the same species representing various growth stages or different degrees of robustness were sampled. This was done to account for possible shifts of morphospace occupation a species might experience during ontogenetic development and to more accurately assess the total morphospace occupied by the members of the same crocodyliform assemblage throughout their respective lives.

A two-dimensional landmark analysis of the skull in dorsal view was conducted to determine the position of each taxon within a shared morphospace. There is a multitude of methods, which in the past were used to decide where to position corresponding landmarks. Some of the available skeletal material was expected to be fragmentary, so one complete side of the skull had to be sufficient for analysis in order

for a method to be chosen. Of the possible methods, two approaches emphasise the placement of landmarks along the sutures of the skull as well as the edges of various cranial elements (Pierce et al., 2008, Piras et al., 2010), whereas another one emphasises the placement of landmarks along the outer curve of the skull (Wilberg, 2016). The first two methods result in a more complete depiction of the skull's internal structure, which is important for conducting analyses of its mechanical properties and allows for a more detailed assessment of its function (Pierce et al., 2008). Analysing the shapes and ratios of cranial elements is highly useful for phylogenetic analyses as well (Piras et al., 2010). Both these methods, however, have been used almost exclusively for extant species of the clade Crocodylia and their immediate relatives in the past (Pierce et al., 2008, Piras et al., 2010). The focus of this study, conversely, was to determine whether the ecological adaptation of the respective species influenced the cranial shape of Crocodyliformes considerably. This therefore made accurately depicting the outer shape of the skull a primary concern. Additionally, the fragmentary nature and fossilisation-induced crushing of some of the used material would have made it highly difficult or even impossible to accurately place some of the important landmarks if such a method were

used. Choosing to place the landmarks primarily along the skull's edge mitigated these problems. This also allowed for a more exact depiction of the cranium's outer shape than the first two methods would have (Wilberg, 2016). A further contributing factor for the decision to use this method was the fact that it had already been used to conduct analyses concerning the skull shape of Mesozoic Crocodyliformes (Godoy, 2019).

The arrangement of the landmarks used in the morphometric analysis is comparatively simple (Figure 3). Four fixed landmarks were placed at important edge points of the skull representing; the most posterior point of the supraoccipital (fixed landmark 1), the most anterior point between the premaxilla (fixed landmark 2), the most anterior point of the orbit (fixed landmark 3) and the most posterior corner of the quadratojugal (fixed landmark 4). Along the outer edge of one of the cranial sides 100 sliding landmarks were placed at regular intervals, creating a curve stretching from fixed landmark 2 over fixed landmark 4 to fixed landmark 1. This was done using tpsUtil32, tpsdig232 and tpsRelw32 (Rohlf, 2010). After placing the landmarks, the curve was appended and a sliders file created using tpsUtil323. The skull images used for extinct taxa were two-dimensional reconstructions or high-quality photographs taken from published studies concerning the respective species. For the Qigu and Shishugou formations, these are *Junggarsuchus sloani* (Clark et al., 2004), *Nominosuchus arcanus* (Kurzanov et al., 2001), *Edentosuchus tienshanensis* (Li, 1985) and *Sunosuchus junggarensis* (Wu et al., 1996). The species of the Purbeck limestone are *Bernissartia fagesii* (Buscalioni et al., 1985, Buscalioni & Sanz, 1990, Norell & Clark, 1990), *Theriosuchus pusillus* (Martin et al, 2010), *Nannosuchus gracilidens* (Salisbury, 2002), *Pholidosaurus purbeckensis* (Martin et al., 2017) and *Goniopholis simus* (Salisbury et al., 1999) with *Bernissartia fagesii* including a robust and a slender adult as well as a juvenile. *Stolokrosuchus lapparenti* (Larsson & Gado, 2000), *Araripesuchus gomesii* (Ortega et al., 2000), *Sarcosuchus imperator* (Sereno et al, 2001) and *Anatosuchus minor* (Sereno et al., 2003) represent the crocodyliform assemblage of Gadoufaoua.

Figure 3; Landmark pattern used in the morphometric analysis. Numbered points indicate fixed landmarks.

The only species from the Haṭeg Basin are *Acynodon adriaticus* (Delfino et al., 2007) and *Allodaposuchus precedens* (Martin et al., 2015), but the latter is represented by a juvenile, a subadult and an adult specimen. The youngest fossil assemblage is that of Messel, which includes *Asiatosuchus germanicus* (Vasse, 1992), *Baryphracta deponiae* (Eberhard et al., 1987, Antunes, 2003), *Allognathosuchus woutersi* (Brochu, 2004), *Hassiacosuchus haupti* (Brochu, 2004) and *Diplocynodon darwini* (Piras &

Buscalioni, 2006, Martin et al., 2014). *Baryphracta deponiae* is represented by a robust and a slender adult, while *Allognathosuchus woutersi* includes an adult and a subadult specimen, respectively. The images depicting the skulls of a juvenile, a subadult and an adult of *Alligator mississippiensis* and a subadult, a slender adult and a robust adult of *Crocodylus niloticus* are photographs of material belonging to the osteological collection of the Palaeontological Department of the University of Vienna, which were prepared specifically for this paper. The images depicting the skulls of *Crocodylus johnstoni*, *Gavialis gangeticus* and *Osteolaemus tetraspis* are scans taken from the DigiMorph website (http://digimorph.org/listthumbs.phtml?grp=alligator&name=SpeciesName).

The data was subsequently read into a script of R (Ihaka & Gentleman, 1993). A Procrustes fit analysis was conducted and used as a base to determine the morphospace and the taxa's respective positions within it. Subsequently, the four extremes of the morphospace were calculated and displayed separately. In order to more accurately assess the morphospace occupation of each fossil assemblage and the extant crocodylian diversity, hull shapes were established encompassing all species of one locality. These hull shapes were then subjected to a number of analyses such as a pairwise comparison, an ANOVA analysis, a MANOVA analysis, a

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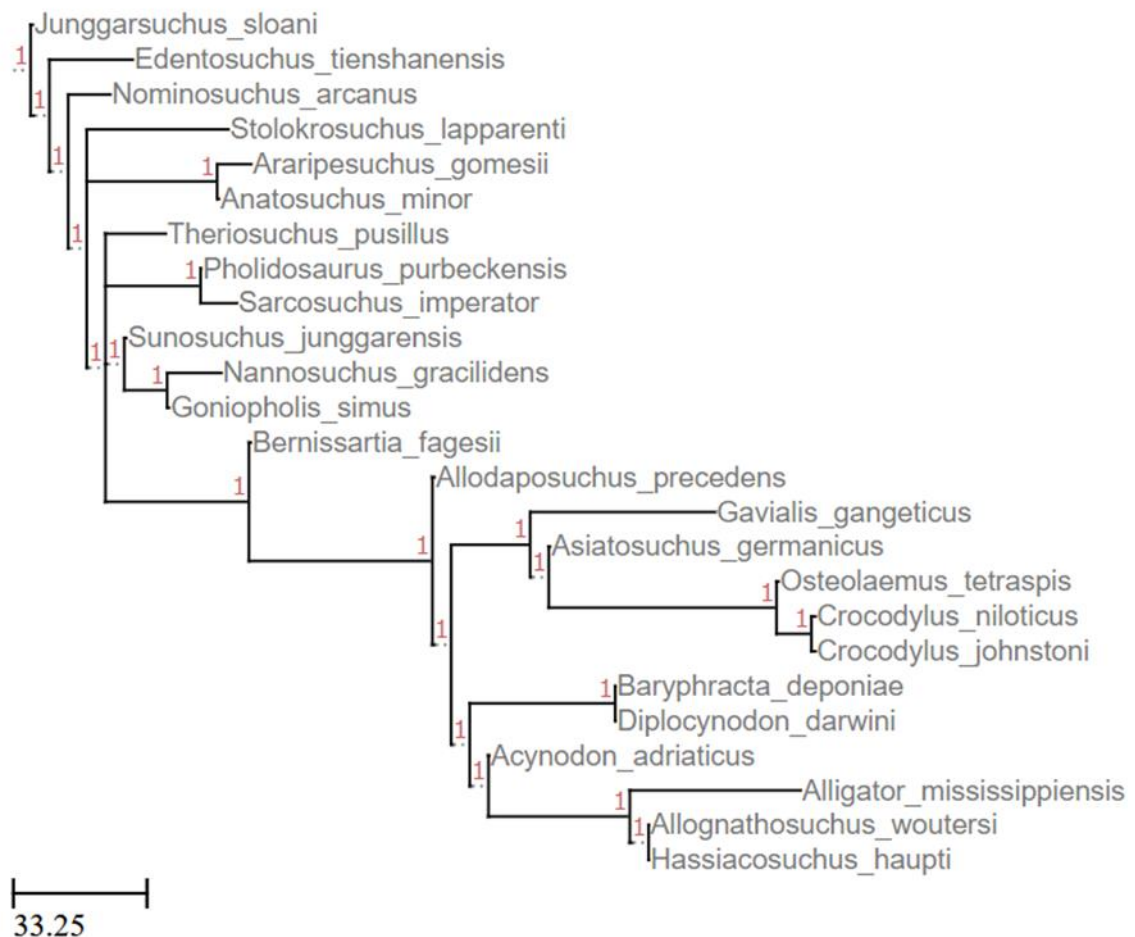
PERMANOVA analysis and an f-test. These were conducted to determine whether or not and to what extend significant overlap concerning the morphospace occupation of the various assemblages existed.

Procrustes Fit and Phylogenetic Analyses

A phylogenetic tree was generated by combining the results of previous research on the phylogeny of Crocodyliformes in general (Wilberg, 2015), extant Crocodylia (Oaks, 2011) and more basal Crocodyliformes and Notosuchia (Pol et al., 2014). The resulting phylogenetic tree was converted into Newick format and read into a script within R (Figure 4). The results of the Procrustes fit morphospace analysis were then converted into a two-dimensional data array. This data array was combined with the phylogenetic tree in order to create a phylomorphospace. Two versions were created, one using the families as grouping factor and one using larger clades. These larger clades are synonymous with the monophylum above family level the species belongs to. The taxa belonging to the families Alligatoridae and Diplocynodontidae for example form the clade "Alligatoroidea", while Allodaposuchia and Atoposauridae both belong to the clade "basal Eusuchia". Multiple Procrustes fit analyses were then conducted to calculate the percentage of variance explained by the factors size, locality (encompassing the assemblage and geological age) and clade (signifying position within the phylogenetic tree). Allometry was calculated as well, using the methods "size/shape", "RegScore", "PredLine" and "CAC".

Finally, all taxa were compared using discrete traits of the teeth and the lower jaw. In order to make the analysis more robust, the 25 species were represented by one individual each only instead of including all 36 of them. The individuals sampled were always the most robust adult specimens of their species. A total of 28 traits were used, of which 21 relate to the teeth and seven represent characteristics of the lower jaw's posterior section (Table 1). This was done to allow for a phylogenetic analysis using Winclada (Nixon, 1999 – 2002). The analysis was conducted as a response to the findings of the analyses conducted in R. The goal was to search for the differences between the phylogenetic tree obtained here and the one used for the phylomorphospace. The method used in the Winclada analysis was a Heuristics search with a maximum of 33000 trees kept. The number of replications was 1, there was a single starting tree per replication, no random seeds were employed and the trees were not submitted. The search strategy was "Multiple TBR + TBR (mult*max*)"

and the search was unconstrained. These settings are adhering to the customs of the institute.

Table 1. Matrix used for the phylogenetic analysis conducted in Winclada; 0 = trait not expressed, 1 = trait expressed, ? = expression of the trait not observable in the specimens used.

Junggarsuchus sloani	0110011000101000101101001 0??
Nominosuchus arcanus	1011101000100100010110111010
Edentosuchus tienshanensis	1011100110000100010011000110
Sunosuchus junggarensis	1010101010000101000100 1?1010
Bernissartia fagesii	1011100110000100100111000101
Theriosuchus pusillus	1010110110001000011110111010
Nannosuchus gracilidens	0110101000100111000100111001
Pholidosaurus purbeckensis	0110101010000101000100111 0??
Goniopholis simus	0110100110000101000110111001
Stolokrosuchus lapparenti	1010101000100101000100101010
Araripesuchus gomesii	1111100110000100011011010110
Sarcosuchus imperator	0110100100101000100100110110
Anatosuchus minor	1010101000100101000100101001
Acynodon adriaticus	10010101010010010010101 ?0110
Allodaposuchus precedens	1010100100101001001000110101
Asiatosuchus germanicus	1010100110000101000110110110
Baryphracta deponiae	1010101000100101000100111001
Allognathosuchus woutersi	1010100110000101000110100101
Hassiacosuchus haupti	1010100110000101000110100101
Diplocynodon darwini	0110101010000101000110101001
Alligator mississippiensis	1010100110000101000110110101
Crocodylus niloticus	1010100110000101000110110101
Crocodylus johnstoni	1110101010000100100100111001
Gavialis gangeticus	1110101000100100100100111010
Osteolaemus tetraspis	1010100110000100100011010101

Traits; 00. straight teeth, 01. curved teeth, 02. pointed teeth, 03. flat teeth, 04. conical teeth, 05. teeth latero-labially compressed, 06. slender teeth, 07. robust teeth, 08. ridges on the tooth surface, 09. humps on the tooth surface, 10. smooth tooth surface, 11. serrated edge, 12. smooth edge, 13. no edge, 14. lateral groove on the tooth, 15. homodont, 16. slightly

heterodont, 17. strongly heterodont, 18. teeth for cutting, 19. teeth for piercing, 20. teeth for crushing, 21. high surangular, 22. low surangular, 23. elongated surangular, 24. slender mandible, 25. robust mandible, 26. long symphysis, 27. short symphysis

Results

Phylogenetic Analysis

Conducting a phylogenetic analysis based on traits of the teeth and lower jaw of all 25 species using Winclada (Nixon, 1999 – 2002) resulted in a total of 13 fully resolved trees. They were combined into a strict consensus tree of 84 steps, with a consistency index of 32 and a retention index of 63 (Figure 5). Expectedly, the phylogenetic tree created through applying a strict consensus isn't fully resolved. The most basal position within this tree is node A, where *Junggarsuchus sloani* splits off. Going up the tree one encounters the three consecutive bifurcations designated node B, node C and node D. *Sarcosuchus imperator* splits off from the rest of the tee at node B, *Gavialis gangeticus* at node C and *Nominosuchus arcanus* at node D. Node E represents a bifurcation with node F on one branch and node G on the other. Node F includes the sister taxa *Sunosuchus junggarensis* and *Stolokrosuchus lapparenti*. *Anatosuchus minor* splits off the rest of the tree at node G, *Baryphracta deponiae* at node H, *Nannosuchus gracilidens* at node I, *Crocodylus johnstoni* at node J, *Pholidosaurus purbeckensis* at node K, *Diplocynodon darwini* at node L and *Goniopholis simus* at node M. Node N represents the largest node of the entire phylogenetic tree and is the least resolved. *Asiatosuchus germanicus*, *Allognathosuchus woutersi*, *Hassiacosuchus haupti*, *Alligator mississipiensis* and *Crocodylus niloticus* as well as the branches leading to nodes O and P all split off at node N. It is among the nodes with the highest number of defining characters, but all of them are homoplasies. Node O is a trifurcation encompassing *Theriosuchus pusillus*, *Acynodon adriaticus* and *Allodaposuchus precedens*. At node P we find *Bernissartia fagesii* and *Osteolaemus tetraspis* in addition to node Q. The bifurcation at node Q represents the final split in the phylogenetic tree, the one between *Edentosuchus tienshanensis* and *Araripesuchus gomesii*. This phylogenetic tree has hardly any resemblance to the one used as basis for the phylomorphospace. Even species considered closely related to each other such as *Araripesuchus gomesii* and *Anatosuchus minor* or *Pholidosaurus purbeckensis* and *Sarcosuchus imperator* are placed on branches far apart from each other. Highly derived taxa like *Gavialis gangeticus* or *Crocodylus johnstoni* are placed in a more basal position than basal

species such as *Theriosuchus pusillus* and *Edentosuchus tienshanensis*. The only part of the phylogenetic tree somewhat consistent with the established phylogeny of crocodilians is node N. The more derived members of Eusuchia such as *Asiatosuchus germanicus*, *Allognathosuchus woutersi*, *Hassiacosuchus haupti*, *Alligator mississipiensis* and *Crocodylus niloticus* all split off at this point, but their relationships with each other aren't resolved to any degree. Furthermore, basal taxa

Figure 5; Phylogenetic tree yielded by the Winclada-analysis conducted using traits of the teeth and lower jaw. White circles indicate homoplasies, black circles mark autapomorphies. For phylogenetic interrelationships see text.

like *Theriosuchus pusillus*, *Bernissartia fagesii*, *Edentosuchus tienshanensis* and the notosuchian *Araripesuchus gomesii* are considered more derived in this phylogenetic tree than the species splitting off at node N. As a result, there are essentially no similarities between this tree and the established phylogeny of Crocodyliformes.

Morphometric Analysis

The initial analysis including all taxa irrespective of their age or assemblage yielded a two-dimensional morphospace, in which Principal Component 1 (PC1) accounts for 41.4% of the variation and Principal Component 2 (PC2) accounts for 27.7% of it. Creating a tangent space divides the morphospace coordinate system into quadrants (Figure 6). The lower left quadrant (called "quadrant A" from here on) contains taxa with long slender snouts such as *Stolokrosuchus lapparenti* (Aptian/Albian) and *Gavialis gangeticus* (extant). The lower right quadrant ("quadrant B") contains taxa such as *Acynodon adriaticus* (Maastrichtian) and *Asiatosuchus germanicus* (Lower Eocene), which are characterised by their comparatively short, very robust skulls. In the upper left quadrant ("quadrant C") we find species with strongly triangular skulls that are quite wide at the jaw joint and rapidly taper towards a very acute snout such as *Edentosuchus tienshanensis* (Oxfordian) and *Nannosuchus gracilidens* (Berriasian), but also the peculiar *Anatosuchus minor* (Aptian/Albian). The upper right quadrant ("quadrant D") contains taxa with a broadly "alligatoroid" skull shape like *Nominosuchus arcanus* (Oxfordian) and *Theriosuchus pusillus* (Berriasian). Most of the extant Crocodylia are spread along the vertical axis of the coordinate system, with the various growth stages of *Alligator mississippiensis* (extant) clustering at the parting line of quadrants C and D and the four specimens of genus *Crocodylus* (all extant) lying within the extreme right section of quadrant A (Figure 6).

It is evident that most of the studied fossil assemblages are occupying quadrants A and C (Figure 7).

The hull shape of the Junggar Basin's assemblage is positioned predominantly within quadrant C, with the very acute-snouted *Edentosuchus tienshanensis* being positioned quite high up in this quadrant. The narrow skull of *Junggarsuchus sloani* and the more typical "crocodile head" of *Sunosuchus junggarensis* place these taxa in quadrant A. *Nominosuchus arcanus* is placed in quadrant D.

The Purbeck assemblage's hull shape encompasses the largest area of all analysed assemblages, including the extant crocodilian diversity. It contains the two most extreme forms concerning Principal Component 2, which are the triangle-headed *Nannosuchus gracilidens* in quadrant C and the extremely slender-snouted *Pholidosaurus purbeckensis* in quadrant A. The five remaining specimens from this locality all cluster far closer to the intersection of the PC-axes. The juvenile *Bernissartia fagesii* is positioned just within quadrant C, close to the parting line to quadrant D. The robust specimen of *Bernissartia fagesii* and *Theriosuchus pusillus* are occupying

quadrant D. The slender specimen of *Bernissartia fagesii* is positioned in quadrant B near the centre of the coordinate system. *Goniopholis simus* is situated within quadrant A as well, clustering in one group with the extant *Crocodylus niloticus* specimens (Figure 7).
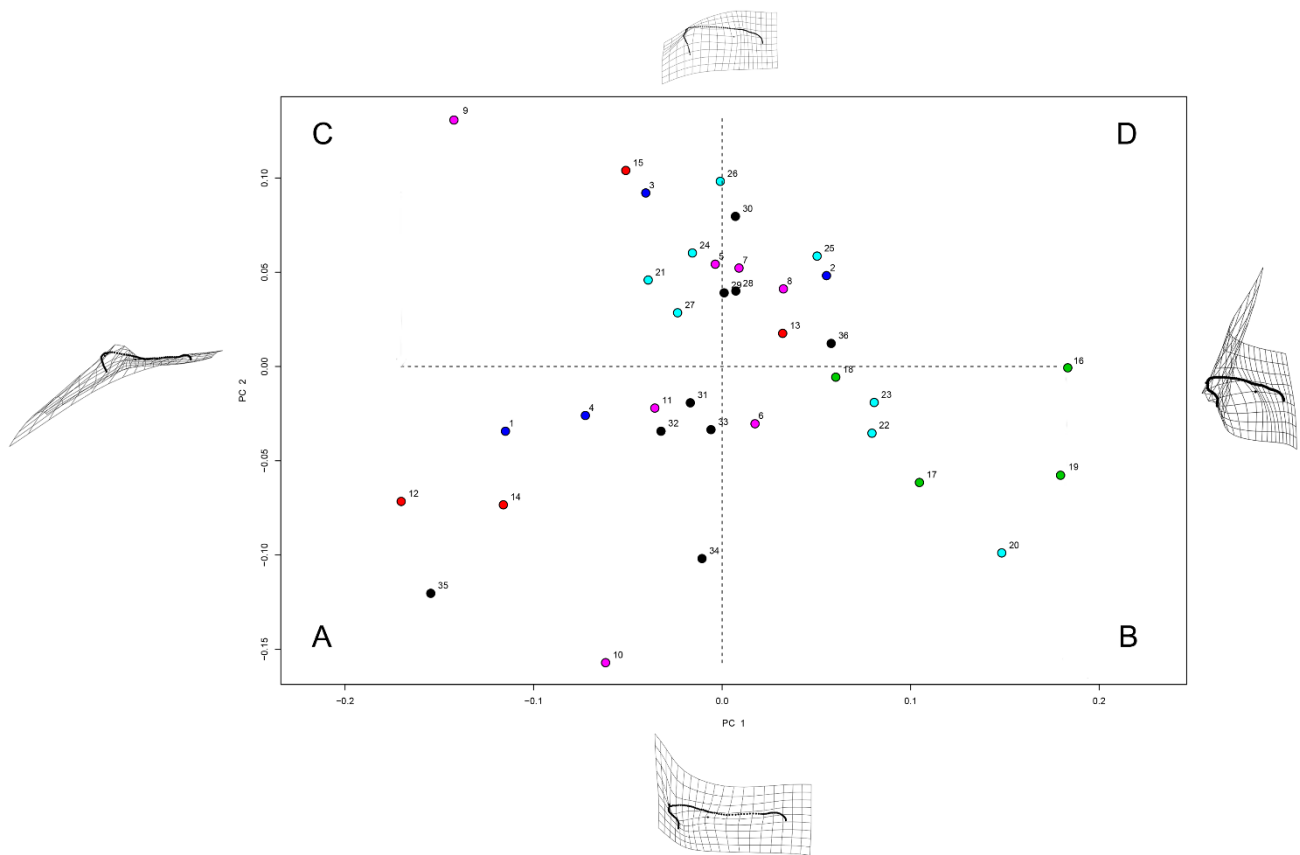

Figure 6; Results of the morphometric analysis. Numbers indicate specimens as follows; 1 *Junggarsuchus sloani*, 2 *Nominosuchus arcanus*, 3 *Edentosuchus tienshanensis*, 4 *Sunosuchus junggarensis*, 5 *Bernissartia fagesii* juvenile, 6 *Bernissartia fagesii* slender, 7 *Bernissartia fagesii* robust, 8 *Theriosuchus pusillus*, 9 *Nannosuchus gracilidens*, 10 *Pholidosaurus purbeckensis*, 11 *Goniopholis simus*, 12 *Stolokrosuchus lapparenti*, 13 *Araripesuchus gomesii*, 14 *Sarcosuchus imperator*, 15 *Anatosuchus minor*, 16 *Acynodon adriaticus*, 17 *Allodaposuchus precedens* juvenile, 18 *Allodaposuchus precedens* subadult, 19 *Allodaposuchus precedens* adult, 20 *Asiatosuchus germanicus*, 21 *Baryphracta deponiae* slender, 22 *Baryphracta deponiae* robust, 23 *Allognathosuchus woutersi* subadult, 24 *Allognathosuchus woutersi* adult, 25 *Hassiacosuchus haupti*, 26 *Diplocynodon darwini* juvenile, 27 *Diplocynodon darwini* adult, 28 *Alligator mississipiensis* juvenile, 29 *Alligator mississippiensis* subadult, 30 *Alligator mississippiensis* adult, 31 *Crocodylus niloticus* subadult, 32 *Crocodylus niloticus* slender, 33 *Crocodylus niloticus* robust, 34 *Crocodylus johnstoni*, 35 *Gavialis gangeticus*, 36 *Osteolaemus tetraspis*.
Specimens marked with the same colour are from the same assemblage.

The position of the hull shape of the crocodile assemblage of Gadoufaoua resembles that of the extant crocodilian diversity the most, but is shifted towards quadrant C

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somewhat. It isn't too different from that of the Junggar Basin's hull shape either. *Stolokrosuchus lapparenti* and *Sarcosuchus imperator* are positioned in quadrant A, as their gharial-like skulls would suggest. *Araripesuchus gomesii* occurs in the lower section of quadrant D, while *Anatosuchus minor* is positioned high up in quadrant C (Figure 7).
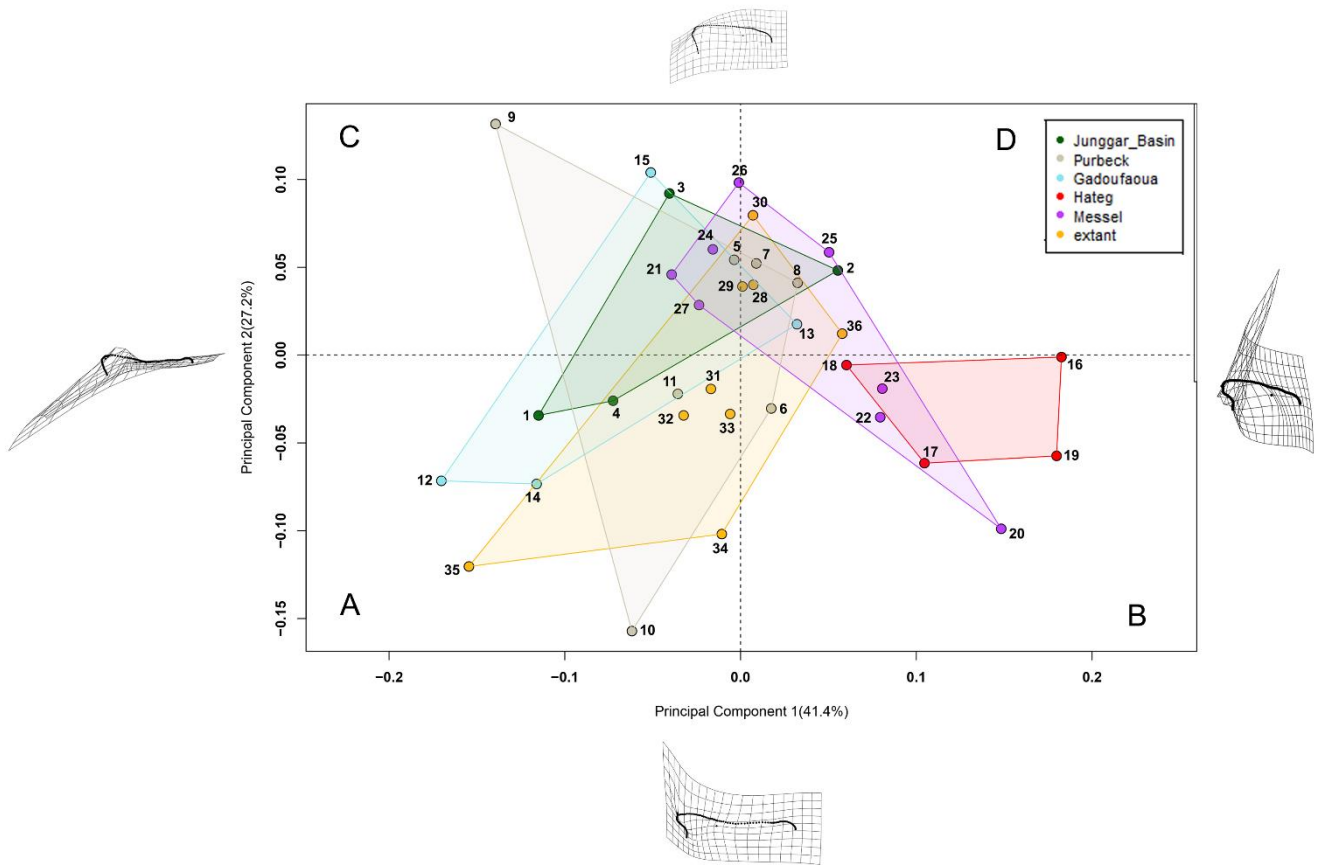
Figure 7; Results of the morphometric analysis, displaying the hull shapes of the vassemblages. Numbers indicate specimens as follows; 1 *Junggarsuchus sloani*, 2 *Nominosuchus arcanus*, 3 *Edentosuchus tienshanensis*, 4 *Sunosuchus junggarensis*, 5 *Bernissartia fagesii* juvenile, 6 *Bernissartia fagesii* slender, 7 *Bernissartia fagesii* robust, 8 *Theriosuchus pusillus*, 9 *Nannosuchus gracilidens*, 10 *Pholidosaurus purbeckensis*, 11 *Goniopholis simus*, 12 *Stolokrosuchus lapparenti*, 13 *Araripesuchus gomesii*, 14 *Sarcosuchus imperator*, 15 *Anatosuchus minor*, 16 *Acynodon adriaticus*, 17 *Allodaposuchus precedens* juvenile, 18 *Allodaposuchus precedens* subadult, 19 *Allodaposuchus precedens* adult, 20 *Asiatosuchus germanicus*, 21 *Baryphracta deponiae* slender, 22 *Baryphracta deponiae* robust, 23 *Allognathosuchus woutersi* subadult, 24 *Allognathosuchus woutersi* adult, 25 *Hassiacosuchus haupti*, 26 *Diplocynodon darwini* juvenile, 27 *Diplocynodon darwini* adult, 28 *Alligator mississipiensis* juvenile, 29 *Alligator mississippiensis* subadult, 30 *Alligator mississippiensis* adult, 31 *Crocodylus niloticus* subadult, 32 *Crocodylus niloticus* slender, 33 *Crocodylus niloticus* robust, 34 *Crocodylus johnstoni*, 35 *Gavialis gangeticus*, 36 *Osteolaemus tetraspis*.

According to theresults obtaines here, it is immediately apparent that the Maastrichtian Haţeg Basin assemblage differs vastly from that of all other assemblages, as it lies completely within quadrant B. There are only two described limnic crocodiles from this locality; *Acynodon adriaticus* and *Allodaposuchus precedens*, both of which are also known from the Late Cretaceous of Laño in Northern Spain (Buscalioni et al., 1999). *Allodaposuchus precedens*, however, exhibits quite an extensive phenotypical

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diversity throughout its ontogeny (Martin et al., 2015). Of all analysed taxa, *Acynodon adriaticus* is positioned the furthest to the right, directly on the axis of PC1. The juvenile of *Allodaposuchus precedens*, conversely, is positioned directly in the centre of quadrant B. The subadult individual is further up and slightly closer to the coordinate system's centre, in the upper section of quadrant B. The adult specimen of *Allodaposuchus precedens* is situated below and slightly to the left of *Acynodon adriaticus*, at the right fringe of quadrant B (Figure 7).

The Eocene Grube Messel's crocodyliform assemblage has a unique hull shape, running more or less perpendicular to all others within the coordinate system. The slender specimen of *Baryphracta deponiae*, the adult specimen of *Allognathosuchus woutersi* and the adult specimen of *Diplocynodon darwini* are all positioned in the right section of quadrant C, close to the extant *Alligator mississippiensis*. The juvenile *Diplocynodon darwini* is situated slightly further to the right on the PC2-axis. In quadrant D, *Hassiacosuchus haupti* is located. *Asiatosuchus germanicus*, the robust specimen of *Baryphracta deponiae* and the subadult *Allognathosuchus woutersi* lie within quadrant B. This gives the hull shape of the Messel assemblage a distinct spike reaching into this section of the morphospace coordinate system (Figure 7).

Extant crocodilians were added to the analysis to allow for a comparison of morphospace occupation between fossil assemblages and all possible crocodilian skull shapes known from the Holocene. This hull shape occupies an area close to the centre of the coordinate system. The specimens of *Alligator mississippiensis* cluster within quadrant D, close to the parting line between this section and quadrant C. The adult specimen lies further up along the PC2-axis than the subadult and the juvenile. *Osteolaemus tetraspis* is the extant crocodilian positioned the furthest to the right, in the lower section of quadrant D. The various morphotypes of *Crocodylus niloticus* are positioned closely together near the centre of the coordinate system, but clearly within quadrant A. *Crocodylus johnstoni* lies far down in quadrant A, closer to the PC2-axis. The major outlier of this group is *Gavialis gangeticus*. It is positioned near the left fringe of quadrant A, closest to *Stolokrosuchus lapparenti* from the Albian to Aptian Gadoufaoua (Niger) locality (Figure 7).

The analysis of variance of the morphospace hull shapes yielded a comparatively small F-value of 6.4683, which often indicates a lot of overlap between the groups in general. The factor size accounts for 15.984% of the total variance, thus leaving a lot of residuals to explain the majority of the variance (Table 2).

Table 2. Variance of morphospace hull shapes.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
size	1	0.09415	0.094149	0.15984	6.4683	2.9447	2e-04
Residuals	34	0.49489	0.014555	0.84016			
Total	35	0.58903					

The pairwise comparisons examining the distances between means (Table 3) and the pairwise 95% upper confidence limits between means (Table 4) yielded very similar results to each other regarding the pattern of differences. For instance, the distance between the means of the hull shapes of the "extant" assemblage and that of Gadoufaoua is the same as that between the means of the hull shapes of the "extant" assemblage and that of Hațeg in both analyses. The mean of Hațeg's hull shape is considered the most similar to that of Gadoufaoua's and the most distant to the mean of the Junggar Basin's hull shape in both analyses. The mean of the "extant" assemblage's hull shape is the least distant to that of all other assemblages' hull shapes on average in both analyses. These and other patterns are present to the same extent in the results of both analyses.

Table 3. Pairwise distances between means.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	0.000000e+00	1.240782e-16	1.240782e-16	1.512222e-16	2.785433e-16	2.337565e-16
Gadoufaoua	1.240782e-16	0.000000e+00	0.000000e+00	8.314297e-17	2.674319e-16	2.229160e-16
Hațeg	1.240782e-16	0.000000e+00	0.000000e+00	8.314297e-17	2.674319e-16	2.229160e-16
Junggar Basin	1.512222e-16	8.314297e-17	8.314297e-17	0.000000e+00	3.136984e-16	2.707409e-16
Messel	2.785433e-16	2.674319e-16	2.674319e-16	3.136984e-16	0.000000e+00	1.973450e-16
Purbeck	2.337565e-16	2.229160e-16	2.229160e-16	2.707409e-16	1.973450e-16	0.000000e+00

Table 4. Pairwise 95% upper confidence limits between means.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	0.000000e+00	1.702479e-16	1.702479e-16	2.092655e-16	2.825179e-16	2.635581e-16
Gadoufaoua	1.702479e-16	0.000000e+00	0.000000e+00	9.855232e-17	2.719288e-16	2.529683e-16
Hațeg	1.702479e-16	0.000000e+00	0.000000e+00	9.855232e-17	2.719288e-16	2.529683e-16
Junggar Basin	2.092655e-16	9.855232e-17	9.855232e-17	0.000000e+00	3.288739e-16	3.080466e-16
Messel	2.825179e-16	2.719288e-16	2.719288e-16	3.288739e-16	0.000000e+00	2.021671e-16
Purbeck	2.635581e-16	2.529683e-16	2.529683e-16	3.080466e-16	2.021671e-16	0.000000e+00

Two pairwise comparisons were conducted; one examining the effect sizes between means (Table 5) and the other one analysing the P-values between means (Table 6).

Table 5. Pairwise effect sizes (Z) between means.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	0.0000000	-2.28750581	-2.28750581	-2.26685392	1.379177	-0.2930043
Gadoufaoua	-2.2875058	0.00000000	NaN	-0.08949272	1.219661	-0.5666412
Hațeg	-2.2875058	NaN	0.00000000	-0.08949272	1.219661	-0.5666412
Junggar Basin	-2.2668539	-0.08949272	-0.08949272	0.00000000	0.742300	-0.6384776
Messel	1.3791771	1.21966091	1.21966091	0.74230003	0.000000	1.2855693
Purbeck	-0.2930043	-0.56664119	-0.56664119	-0.63847759	1.285569	0.0000000

Table 6. Pairwise P-values between means.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	1.0000	0.99020	0.99020	0.99120	0.0782	0.6108
Gadoufaoua	0.9902	1.00000	0.50005	0.54125	0.1111	0.7110
Hațeg	0.9902	0.50005	1.00000	0.54125	0.1111	0.7110
Junggar Basin	0.9912	0.54125	0.54125	1.00000	0.2236	0.7379
Messel	0.0782	0.11110	0.11110	0.22360	1.0000	0.1002
Purbeck	0.6108	0.71100	0.71100	0.73790	0.1002	1.0000

The ANOVA-analysis conducted with a focus on the effect of assemblage (in this work considered synonymous with age because every fossil assemblage was deposited at a different time in Earth's history) on the variance yielded a very small F-value of 2.3025. What assemblage a specimen comes from explains 27.733% of the total variance (Table 7).

Table 7. Results of the ANOVA-analysis.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
Assemblage	5	0.16336	0.032671	0.27733	2.3025	2.5007	0.0027
Residuals	30	0.42568	0.014189	0.72267			
Total	35	0.58903					

For the MANOVA-analysis, the inquired factors were size (the length of the skull when measured from the most posterior point of the supraoccipital to the most anterior point between the premaxilla) and assemblage (again synonymous with age). The F-value of size is distinctly higher than that of assemblage (7.8961 compared to 2.6339), but still very low. The joined F-value is extremely small with 0.37501. Size accounts for 15.984% of the variance, assemblage for 26.659% (Table 8).

Table 8. Results of the MANOVA-analysis.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
size	1	0.09415	0.094149	0.15984	7.8961	2.94466	0.0002
Assemblage	5	0.15703	0.031406	0.26659	2.6339	2.85400	0.0004
size:Assemblage	5	0.05169	0.010338	0.08776	0.8671	0.37501	0.3638
Residuals	24	0.28617	0.011924	0.48582			
Total	35	0.58903					

The results of the PERMANOVA are identical to those produced by the MANOVA (Table 8). The Procrustes variances of the different assemblages all lie between 0.0113 and 0.0256. The "extant" assemblage, Purbeck and Messel lie in the lower half of this range, Gadoufaoua, Hațeg and the Junggar Basin in the upper half (Table 9).

Table 9. Procrustes variances.

extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
0.01135383	0.02210840	0.02550266	0.01982086	0.01310292	0.01604276

The pairwise absolute differences between the assemblages' hull shapes' variances show a somewhat different pattern than the pairwise distances between means (Table 3, Table 4). The absolute differences are generally far smaller as well. A distinct pattern of similarities and differences seems to be hardly present, if at all (Table 10).

Table 10. Pairwise absolute differences between variances.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	0.000000000	0.010754572	0.014148826	0.008467029	0.001749092	0.004688931
Gadoufaoua	0.010754572	0.000000000	0.003394254	0.002287543	0.009005480	0.006065641
Hațeg	0.014148826	0.003394254	0.000000000	0.005681797	0.012399734	0.009459895
Junggar Basin	0.008467029	0.002287543	0.005681797	0.000000000	0.006717937	0.003778098
Messel	0.001749092	0.009005480	0.012399734	0.006717937	0.000000000	0.002939839
Purbeck	0.004688931	0.006065641	0.009459895	0.003778098	0.002939839	0.000000000

When the P-values between the various assemblages' hull shapes are examined, a more clearly resolved pattern is visible. The hull shape Hațeg is again the least similar to that of the "extant" assemblage, while that of Messel is the most similar. The pattern is different from that of previous analyses (Table 3, Table 4, Table 10), but quite well resolved (Table 11).

Table 11. P-values.

	extant	Gadoufaoua	Hațeg	Junggar Basin	Messel	Purbeck
extant	1.000	0.189	0.074	0.273	0.780	0.472
Gadoufaoua	0.189	1.000	0.742	0.811	0.282	0.462
Hațeg	0.074	0.742	1.000	0.537	0.127	0.251
Junggar Basin	0.273	0.811	0.537	1.000	0.417	0.652
Messel	0.780	0.282	0.127	0.417	1.000	0.666
Purbeck	0.472	0.462	0.251	0.652	0.666	1.000

Procrustes Fit Analysis

The five Procrustes fit analyses conducted produced various results depending on what factors were compared.

When the effects of size and clade affiliation were compared, the results showed that the latter accounted for 41.604 % of the total variance. This is not only an objectively high value, but clearly higher than that of any other factor in the previously conducted analyses (Table 12).

Table 12. Comparison of the effects of size and clade affiliation on variance.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
Clade	9	0.24506	0.027229	0.41604	2.0582	2.3528	0.003
Residuals	26	0.34397	0.013230	0.58396			
Total	35	0.58903					

Examining the percentage of variance caused by size, shape and age, size accounts for 15.984% of the variance and age for 22.992%. Size seems to consistently yield comparatively low percentages of explained variance regardless of the method of analysis employed (Table 13).

Table 13. Comparison of the effects of size, shape and age on variance.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
size	1	0.09415	0.094149	0.15984	7.6389	2.9125	0.001
Age	5	0.13543	0.027086	0.22992	2.1977	2.4187	0.002
size:Age	5	0.06366	0.012732	0.10807	1.0330	0.9255	0.184
Residuals	24	0.29580	0.012325	0.50217			
Total	35	0.58903					

Looking at the effect of size and shape while considering the phylogeny results in the lowest percentage of explained variance of all analyses. Size accounts for just 6.678% of the total variance in this case (Table 14).

Table 14. Comparison of the effects of size, shape and phylogeny on variance.

	Df	SS	MS	Rsq	F	Z	Pr (>F)
size	1	0.009638	0.0096380	0.06678	2.4328	1.7738	0.037
Residuals	34	0.134697	0.0039617	0.93322			
Total	35	0.144335					

Analysing the percentage of variance caused by size and age when factoring in phylogeny, the results are similar to those of previous analyses. The factor size again only accounts for 6.678% of the variance. Age explains 15.801% of the total variance, which is a bit lower than in the analysis factoring in shape (Table 15).

Table 15. Comparison of the effects of size, age and phylogeny on variance.

	Df	SS	MS	Rsq	F	Z	Pr (>F)
size	1	0.009638	0.0096380	0.06678	2.7515	1.95894	0.027
Age	5	0.022806	0.0045613	0.15801	1.3021	0.95893	0.179
size:Age	5	0.027821	0.0055642	0.19275	1.5885	1.52115	0.058
Residuals	24	0.084069	0.0035029	0.58246			
Total	35	0.144335					

The results of the analysis examining the effects of shape, clade and age on the total variance are again rather unambiguous. As in previous analyses, clade affiliation accounts for 41.604% of the variance. Age explains 9.821% of the total variance, which is the lowest percentage of this factor in all analyses (Table 16).

Table 16. Comparison of the effects of shape, clade and age on variance.

	Df	SS	MS	Rsq	F	Z	Pr (>SS)
Clade	9	0.24506	0.027229	0.41604	2.2143	2.3528	0.003
Age	4	0.05785	0.014463	0.09821	1.1761	1.3206	0.082
Clade:Age	1	0.02788	0.027880	0.04733	2.2672	1.8359	0.012
Residuals	21	0.25824	0.012297	0.43841			
Total	35	0.58903					

Plotting the observed allometry against the expected patterns produced no unexpected results. There are no significant outliers that indicate certain species would become disproportionately robust with increasing size or stay unexpectedly slender. Allometry therefore doesn't seem to be a major factor when it comes to the results of the morphometric analysis.

Discussion

Morphometric Analysis

It is obvious that most hull shapes of the crocodilian assemblages cluster within the same general area when considering the distribution of the hull shapes within the morphospace coordinate system and the area occupied by them. Using the extant crocodilian diversity as basis, the pairwise P-Values of the hull shapes' means show the same trend. Considering the fact that the "extant" assemblage doesn't represent a single locality but rather all skull shapes that can be found among Holocene crocodiles, this isn't too surprising. Skull shape within this clade seems to not evolve much further than to the extremes observable within its extant diversity. However, it is noteworthy that quadrant B isn't occupied by any extant crocodile. This section of the morphospace coordinate system represents forms such as *Edentosuchus tienshanensis*, which are characterised by a skull that is very wide at the jaw joint and tapers rapidly towards a

comparatively short snout. This is consistent with findings obtained by previous studies (Wilberg, 2016). This skull shape, sometimes referred to as "metriorhynchid", used to be quite common during the Jurassic and Early Cretaceous but then suddenly disappeared at the beginning of the Late Cretaceous (Wilberg, 2016). This peculiar skull shape isn't exclusive to a single clade of limnic crocodyliforms included in the analysis. The taxa exhibiting this trait are a single member of Goniopholididae and multiple taxa within Notosuchia. The former one is a typical family occurring in limnic deposits in the Upper Jurassic and Lower Cretaceous of Laurasia, but was already in decline since the Barremian (Buscalioni et al., 2013). The latter represents a highly diverse group in the Cretaceous that reached its diversity peak between the Turonian and the Santonian. During the early Campanian, the group experienced the sudden extinction of most of its taxa without any subsequent radiation, thus greatly reducing its overall diversity (Pol & Leardi, 2015). In limnic families of Crocodyliformes, the "metriorhynchid" skull shape therefore already was in decline during the latest part of the Cretaceous, which explains why this shape disappeared before the Late Cretaceous extinction. What exactly caused the Campanian drop in Notosuchia diversity, however, is so far unknown. The first studies conducted on the paleodiversity of the affected groups (especially Baurosuchidae and other highly derived taxa) concluded an actual extinction event had taken place, but couldn't determine the causes (Pol & Leardi, 2015). More recent research suggests that Lagerstätte effects are to blame for the extreme differences in diversity when comparing Santonian and Campanian fossil bearing formations (de Celis et al., 2020). The latter may very well be the more correct assertion, but nonetheless creates an explanatory problem concerning the disappearance of the "metriorhynchid" skull shape. If the families this trait was common in didn't suddenly go extinct, ecological changes unfavourable to taxa exhibiting it would have to be the cause. Conducting further research concerning the "metriorhynchid" condition and the clades it was common in would be a commendable course of action to fill in these blanks in our current knowledge.

Interestingly, the fossil assemblage showing the most similarity to all other assemblages is the one from the Berriasian Purbeck limestone. This is most likely a consequence of the area this locality's hull shape occupies within the morphospace coordinate system, which is the largest of all the sites sampled. The Early Cretaceous Gadoufaoua assemblage's hull shape shows considerable similarities to that of most other assemblages, with the notable exception of extant crocodilians. This result parallels the graphic analysis, which shows that the hull shape of the Gadoufaoua

assemblage is clearly shifted into quadrant C when compared to the "extant" hull shape (Figure 7). The Late Jurassic Junggar Basin assemblage's hull shape falls somewhere in the middle, possessing a means' pairwise P-value showing obvious similarity to the hull shapes of the Purbeck, Gadoufaoua and "extant" crocodyliform assemblages. The main outliers are the hull shapes of the assemblages from the Eocene of Messel and the Late Cretaceous of Hațeg, which when looking at their respective P-values show the least similarity to those of the other assemblages while being extremely different from each other as well (Table 10). The Messel assemblage's hull shape is unique in the sense that its main axis stretches between quadrants B and C rather than between A and D or along the main axes. Most taxa from this location cluster around the same area of the morphospace coordinate system as extant alligatoroids, but species like *Asiatosuchus germanicus* and the robust morphotype of *Baryphracta deponiae* cause the hull shape of this assemblage to stretch far into quadrant B. This quadrant contains the most robust crocodilian species sampled and isn't occupied by any extant taxon, with *Osteolaemus tetraspis* and the robust individual of *Crocodylus niloticus* coming the closest but still remaining clearly outside it. The hull shape of the crocodilian assemblage of the Hațeg Basin is positioned completely within quadrant B and includes the two species with the most robust skulls and shortest snouts; *Allodaposuchus precedens* and *Acynodon adriaticus*. The overlap with the Messel assemblage's hull shape is minimal and only present on the left margin of the Hațeg assemblage's hull shape. This explains why the pairwise P-value between their respective means is so close to 0.

It is remarkable that there is no clear trend regarding the position of their respective hull shapes within the morphospace coordinate system when considering all assemblages. The assemblages of the Junggar Basin and the Purbeck limestone are the most similar to the extant crocodilian morphospace when it comes to the morphospace occupation of their hull shapes. This is despite the fact that these are the oldest localities and their taxa are the most phylogenetically different from extant crocodilians. Interestingly, the assemblages the most different from the "extant" assemblage in terms of their hull shapes' position in the morphospace are the Hațeg and Messel associations, which are also the stratigraphically youngest ones. In fact, the pairwise P-value of the means of Messel and the extant crocodilian morphospace is the second lowest in the entire pairwise analysis. Quite unusually, when looking at pairwise P-values, the Purbeck assemblage is the least similar to the "extant" one. Comparing the exact position of all assemblages' hull shapes sorted by age the

position of their respective central points at first shifts from the right section of quadrant C downwards towards the central axis of PC1, then slightly upward and to the left back into quadrant C, rightward and down into quadrant B and finally to the centre towards the central axis of PC2 (Figure 7). The only apparent trend seems to be a general tendency for crocodilians to be more short-snouted and robust in their skulls during the Late Cretaceous and Early Palaeogene. More interesting is the area of the morphospace coordinate system occupied by each assemblage's hull shape. The "extant" assemblage is disregarded here as it is a representation of Holocene crocodilian morphospace resulting from various localities rather than representing a single association. There is no indication of any trend of the assemblages' hull shapes to enlarge the morphospace occupied by them throughout time. Enlarging the morphospace would indicate evolutionary pressure to make skulls more different from each other. This would indicate a major radiation if skull shape indeed is a phylogenetic trait, as an increased number of clades within Crocodyliformes would allow for a greater variety of cranial shapes. If it was a trait primarily influenced by ecological factors, an enlarged morphospace would suggest a trend to minimise competition, since skull shapes more different to each other are indicative of more differences regarding the respective taxas' diets in this case. The two fossil assemblages with the largest morphospace occupation are clearly those of Purbeck and Gadoufaoua. Incidentally, these are also the two assemblages with the highest number of preserved taxa. Whether or not there is a causal correlation between the area of morphospace occupied by the hull space of the assemblage and the number of taxa in it wasn't examined in this work. If an enlarged hull shape was found to consistently be caused by increased diversity, these results would support the findings of previous research, which suggested that the diversity of Crocodyliformes peaked during the Middle Cretaceous (Wilberg, 2016). Somewhat surprisingly, the K/Pg-boundary event doesn't seem to have had a long-term detrimental impact on the morphospace occupation of limnic crocodilian assemblages. The hull shape of the Late Cretaceous Hațeg Basin's assemblage is in fact considerably smaller than the one of the early Eocene assemblage of Grube Messel. Moreover, the hull shape of the Messel assemblage also is the only one besides the one of the Hațeg assemblage that shows a strong presence in quadrant B. According to the results of the analyses conducted within the scope of this work, this quadrant of the morphospace was therefore primarily occupied around the K/Pg-boundary. Furthermore, besides *Allodaposuchus precedens* (basal Eusuchia) from Hațeg and *Asiatosuchus germanicus* (Crocodyloidae) from Messel, all taxa from these two assemblages are members of Alligatoroidae. This clade seems to

have been favoured by selection during this period and is the only group exhibiting a heavy presence in quadrant B. There are two taxa of Crocodyliformes known from Haţeg compared to five from Messel, making the latter the one with the greater diversity. The Late Cretaceous mass extinction therefore seems to not have had a particularly strong or long-lasting effect on neither the prevalent skull shape of limnic Crocodyliformes nor the diversity of this group. This correlates with other researchers' findings which indicate that Crocodylia experienced its first major peak of diversity during the earliest Paleogene (de Celis et al., 2019). However, the Haţeg Basin represents an island biome which experienced a comparatively high degree of isolation during the Late Cretaceous (Csiki-Sava et al., 2015). This could have resulted in a reduced diversity of the assemblage or a decreased area of the morphospace occupied by its hull shape. Therefore, it may very well not be an ideal dataset to use as base for such a comparison.

While the P-values as well as the results of the ANOVA-, MANOVA- and PERMANOVA-analyses clearly support the similarities and differences between the assemblages that were described above, it has to be noted that they do not consistently reach the set significance value for any assemblage. This is especially true for the pairwise P-values between the hull shapes' means, which clearly show that some assemblages are vastly more similar to each other in morphospace occupation than others, but still never reach the chosen significance value of <0.05.

Procrustes Fit Analyses

The Procrustes fit analyses of the phylomorphospace were conducted to determine what percentage of the variance is caused by what factor when considering the position of a single specimen within the morphospace. Multiple possible factors were analysed for this in various combinations. It is immediately obvious that the factor size only has little effect. As explained previously, here, "size" signifies the length of the skull when measured from the most posterior point of the supraoccipital to the most anterior point between the premaxilla. These points correspond to the fixed landmarks 1 and 2 (Figure 3). When clade and/or shape are factored into the Procrustes fit analysis, only 6.678% of the variance are explained by differences in size. This result is quite impactful for the complete study, as it shows that species vastly different in size (e.g. *Sarcosuchus imperator* and *Bernissartia fagesii*) can still reasonably be compared using the method employed. The percentage of variance explained by size is higher when it is cross-compared with shape and age, at 15.984%. This, while somewhat significant, is still less than the average values of the other factors examined.

Of all factors analysed, age was the most variable in percentage of variance explained by it. In this work "age" signifies geological stage and is therefore synonymous with a specific locality. The Junggar Basin represents the Oxfordian, Purbeck the Berriasian, Gadoufaoua the Upper Aptian/Lower Albian, Hațeg the Maastrichtian and Messel the Lower Eocene. This factor was chosen to examine whether or not there was a significant trend in morphospace occupation throughout time (i.e. assemblages as a whole moving toward a more robust or more longirostrine shape of the skull on average). The exact percentage of variance explained by the factor age varies considerably depending on what other factors are co-analysed. When size and shape were included, age accounted for 22.992% of the total variance. When it was compared to the effect of size while factoring in phylogeny the percentage of variance explained by age dropped to 15.801%. The lowest percentage of variance explained by age is obtained when simultaneously analysing the effect of shape and clade affiliation. Age only accounts for 9.821% of total variance in this case.

The final factor examined in the Procrustes fit analysis was clade affiliation. In this work "clade" refers to the monophylum above family level the species belongs to. For instance, the taxa belonging to the families Alligatoridae and Diplocynodontidae form the clade "Alligatoroidae", Allodaposuchia and Atoposauridae both belong to the clade "basal Eusuchia", Goniopholididae and *Bernissartia fagesii* are assigned to "derived Neosuchia" and so forth. The results of these analyses were somewhat surprising. No matter what other factors are used alongside it in the analysis, "clade" always accounts for 41.604% of the total variance. This makes it not only the most crucial factor, but also the most robust one as it shows the most consistent percentage of explained variance. Based on these results, it has therefore to be concluded that skull shape in Crocodyliformes is a trait closely tied to their phylogenetic affiliation rather than ecological factors.

Bones of a larger size are typically more robust than corresponding bones from a smaller individual, because larger bones have to be thicker in comparison to their length simply to carry their own weight. To make sure this didn't impact the morphospace analysis a number of allometry analyses were conducted. These consistently showed that the allometry, while present, had minimal impact. All taxa clustered reasonably close to the predicted line of linear growth, with *Gavialis gangeticus*, *Allodaposuchus precedens* and *Acynodon adriaticus* being the furthest away from it. Since these represent one of the slenderest and the two most robust taxa of the sample, this isn't unexpected. Taking into account the fact that the Procrustes fit

analysis showed that of all factors size had the least effect on the taxa's position within the morphospace coordinate system, it can be concluded that any present allometry had a negligible impact on the study as a whole.

Phylogenetic Analysis

The phylogenetic analysis was conducted as a response to the findings of the analyses conducted with R. The Procrustes fit analyses made it apparent that the skull shape was mainly influenced by the clade affiliation, so it was decided to test the traits of the teeth as well. The main objective was to determine whether or not the tooth shape in general is tied to the skull shape and therefore the taxon's position within the phylogeny. If it wasn't, the teeth might represent a better indicator of the niche occupied by their owner than the skull shape does.

The phylogenetic tree produced by the Winclada analysis (Figure 5) is decidedly different from the one used for the phylomorphospace (Figure 4). Since the latter was obtained by combining the finds of three previous phylogenetic studies concerning the intra-relationships of Crocodyliformes (Oaks, 2011, Pol et al., 2014, Wilberg, 2015), it represents a more inclusive analysis of the relationships of the taxa involved. Therefore, the shape of the teeth most definitely doesn't represent a phylogenetic signal. This is further substantiated by the fact that closely related species such as *Araripesuchus gomesii* and *Anatosuchus minor* or *Pholidosaurus purbeckensis* and *Sarcosuchus imperator* are placed on branches far apart from each other in the phylogenetic tree derived from the Winclada analysis. As a result, it is concluded that while the skull shape in Crocodyliformes is mostly determined by phylogenetic affiliation, the shape and edge of the teeth might represent a trait correlated more with the ecological niche.

Conclusions

Examining all findings of the analyses concerning the skull shape of Mesozoic to Cenozoic members of Crocodyliformes and the factors influencing it conducted within this study, a number of conclusions can be drawn.

The morphospace coordinate system obtained through the analysis conducted in R is divided into four quadrants. Quadrant A includes all taxa with long and slender snouts such as *Gavialis gangeticus* and *Stolokrosuchus lapparenti*. Species with the most robust yet still broadly "crocodilian" skulls, e.g. *Allodaposuchus precedens* and *Asiatosuchus germanicus*, are placed within quadrant B. Quadrant C is where the most

unusual skull shape is located, which is a short skull rapidly tapering towards a narrow snout. It includes members of Notosuchia like *Edentosuchus tienshanensis* and *Anatosuchus minor*, but also *Nannosuchus gracilidens* of the family Goniopholididae. In quadrant D the taxa possessing the "alligatoroid" skull shape with a wide rounded intersection of the snout such as *Hassiacosuchus haupti* and *Alligator mississippiensis*, are located.

The hull shapes of the fossil assemblages of the Junggar Basin, Purbeck and Gadoufaoua localities as well as the extant diversity of Crocodylia within the morphospace coordinate system all mainly cluster close to the intersection of the two PC-axes. They all possess a main axis stretching between quadrants A and D with quadrant B being mostly unoccupied. Messel's hull shape is centred near the axis of Principal Component 2 but also stretches far into quadrant B. Its main axis therefore runs between quadrants B and C. Hațeg has the smallest hull shape of all sampled assemblages, which is entirely located in quadrant B. This quadrant thus was occupied by crocodiles mainly around the Cretaceous-Paleogene boundary.

One of the main findings of this work is the lack of effect the K/Pg-boundary had on limnic crocodyliform assemblages. The assemblage of Messel contains more taxa than the one of the Hațeg Basin and is similar in diversity to the Gadoufaoua assemblage. If the Late Cretaceous mass extinction indeed had a strong negative effect on limnic crocodyliform diversity, it had already recovered by the early Eocene. Neither is there a sudden shift regarding the morphospace occupation of the assemblages' hull shapes across the Cretaceous-Paleogene boundary. The hull shape of the Hațeg assemblage lies completely within quadrant B and as a result is the hull shape the most heavily centred on this section of the morphospace. The Messel assemblage's hull shape shows a distinct spike reaching into quadrant B, thus being the hull shape with the second largest presence in this area of the morphospace. It therefore can be assumed that the Late Cretaceous mass extinction didn't influence the prevalent skull shape of limnic members of Crocodyliformes.

There is no real trend regarding the position of the hull shapes through time. Neither do crocodyliform assemblages as a whole tend to become more slender-snouted nor do they become more robustly skulled. They also don't tend to maximise the morphologic distance between their extremes. There is, however, an observable trend of the hull shapes shifting away from quadrant C throughout the late Mesozoic. By the Late Cretaceous, taxa with wide skulls that rapidly taper towards a narrow but very

short snout, the "metriorhynchid" condition, are completely absent from the fossil record.

There is a minor trend concerning the size of the assemblages' hull shapes. They tend to occupy more area of the morphospace towards the Middle Cretaceous and become smaller again afterwards. This fits well with the findings of previous studies, which suggest that crocodyliforms reached a diversity peak during this time (Wilberg, 2016).

When analysing the various factors contributing to the taxa's position within the morphospace coordinate system, it becomes clear that skull shape isn't considerably influenced by the size of the animal. Together with the results of the allometry analyses this proves that the analysis method employed in this work is feasible even when comparing specimens of vastly different size such as the skulls of *Bernissartia fagesii* and *Sarcosuchus imperator*. Scientists conducting future research concerning the skull shape of Crocodyliformes can therefore employ the method outlined by Wilberg (Wilberg, 2016) without having to worry about specimen size influencing the results. An other tested variable with little influence on the total variance is "age", which signifies the stratigraphic age of specific localities of the crocodyliform assemblages analysed here.

The one factor with the single most effect on the total variance is the systematic placement of taxa. Accordingly, clade affiliation consistently accounts for over 41% of the variance, which far surpasses the effect of all other tested variables. Skull shape can therefore be considered a phylogenetic trait in limnic crocodyliforms. The results of the analyses conducted within this work thus confirm previous findings of some studies (Sadleir & Makovicky, 2008, Wilberg, 2016) while conflicting with those of others (Pierce et al., 2008, Godoy, 2019). Taxa seem to only be able to evolve within quite narrow constraints when it comes to this anatomic feature. In other words; what clade a limnic species of crocodyliform belongs to already severely restricts the evolvability of its skull shape. Changes in morphospace occupation of crocodyliform assemblages through time are most likely a result of macroevolutionary patterns rather than changes in the environment favouring different skull shapes. This also explains why the condition known as "metriorhynchid" skull shape suddenly disappeared during the Late Cretaceous. This condition is characterised by a skull that's very wide at the jaw joint and rapidly tapers towards a narrow but quite short snout. In the limnic environment, it was exhibited by taxa belonging to Goniopholididae and Notosuchia (Buscalioni et al., 2013, Pol & Leardi, 2015). Both of these groups were largely extinct by the Cenomanian, explaining why the "metriorhynchid" skull shape disappeared

before the Late Cretaceous mass extinction. It wasn't the consequence of environmental conditions no longer favouring this trait, but rather that of the clades it was common in going extinct.

Tooth shape and arrangement seems to be a far better indicator of the ecological niche of a crocodilian than its skull shape. A phylogenetic tree obtained by conducting an analysis based on traits of the teeth and lower jaw is vastly different from the established phylogenies. Even closely related species are vastly different from each other when it comes to the shape and arrangement of the teeth.

Future research on the phylogenetic relations of limnic crocodyliforms should incorporate skull shape amongst other traits. The results yielded by the morphometric and Procrustes fit analyses conducted within the scale of this work consistently show that cranial shape is far more indicative of phylogenetic relations than of ecological niche adaptation or geological age. It is already widely accepted that the cranium is one of the most important anatomical structures to examine when determining phylogenetic affiliations within Eusuchia. This sentiment could now be expanded at least partly to Mesoeucrocodylia, if not Crocodyliformes as a whole. When conducting research on the ecological niche of taxa belonging to Crocodyliformes on the other hand, traits of the teeth and the posterior section of the lower jaw might constitute good points of reference. These characters are vastly different even in closely related taxa and could therefore be indicative of their respective ecological niches, as they clearly aren't influenced by phylogeny. Further research on this subject would be recommendable. Additionally, taking into account the abundance of potential prey items and the faunal composition of the fossil assemblage may provide a good starting point for similar research concerning the ecology of extinct members of Crocodyliformes. Similarly, considering potential predators of limnic crocodilians in the form of terrestrial hunters such as Sebecosuchia or even Theropoda could result in interesting finds on the ecology of limnic crocodyliforms throughout the Mesozoic.

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Image Captions

Figure 1: Stephanie E. Pierce, Kenneth D. Angielczyk, Emily J. Rayfield; Patterns of Morphospace Occupation and Mechanical Performance in Extant Crocodilian Skulls: A Combined Geometric Morphometric and Finite Element Modeling Approach; 2008.

Figure 2: Eric W. Wilberg; Investigating patterns of crocodyliform cranial disparity through the Mesozoic and Cenozoic; 2016.

Figure 3: Patrick Abdalla; this work.

Figure 4: Patrick Abdalla; this work, after: Jamie R. Oaks; A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles; 2011., Diego Pol, Paulo M. Nascimento, Alberto B. Carvalho, Claudio Riccomini, Ricardo A. Pires-Domingues, Hussam Zaher; A New Notosuchian from the Late Cretaceous of Brazil and the Phylogeny of Advanced Notosuchians; 2014., Eric W. Wilberg; What's in an Outgroup? The Impact of Outgroup Choice on the Phylogenetic Position of Thalattosuchia (Crocodylomorpha) and the Origin of Crocodyliformes; 2015.

Figure 5: Patrick Abdalla; this work.

Figure 6: Patrick Abdalla; this work.

Figure 7: Patrick Abdalla; this work.

Anhang – deutsches Abstract

Bei Crocodyliformes handelt es sich um eine Clade von Archosauria die in der Vergangenheit als morphologisch konservativ angesehen wurde. Ihre heutigen Mitglieder scheinen tatsächlich eine morphologisch sehr einheitliche Gruppe zu bilden, doch bei ausgestorbenen Spezies findet sich ein beträchtliches Maß an Diversität und morphologischer Disparität. Während des Mesozoikums und frühen Känozoikums existierte auf der ganzen Welt eine große Anzahl von das Süßwasser bewohnenden Artgemeinschaften, aus denen mehrere Taxa von Crocodyliformes bekannt sind. Obwohl sich diese Reptilien auch in Größe und Proportionen teilweise sehr stark voneinander unterschieden wird als Hauptunterscheidungsmerkmal zumeist die Form ihres Schädels genutzt. In den vergangenen zwei Jahrzehnten wurden in zunehmendem Ausmaß morphometrische Analysen bezüglich der Schädelform heutiger Krokodile und der Faktoren die diese beeinflussen durchgeführt. Einige Forscher kamen zu dem Schluss, dass die ökologische Nische den wichtigsten Faktor darstellt, während andere Phylogenie als entscheidend ansahen und wieder andere in der geographischen Verbreitung den Hauptgrund für die Unterschiede in der Schädelform verschiedener Taxa sahen. Die umfangreiche Diversität ausgestorbener Vertreter von Crocodyliformes ist bis jetzt allerdings noch nicht in dieser Hinsicht untersucht worden. In dieser Arbeit wurden fünf fossile Gemeinschaften ausgestorbener Krokodilverwandter mittels zweidimensionaler Morphometrics und Procrustes-Fit-Analysemethoden untersucht. Besagte Gemeinschaften wurden anschließend miteinander und mit der heutigen Krokodil-Diversität verglichen, um nach Trends in ihrer Morphospace Occupation zu suchen und zu überprüfen, welcher Teil der vorhandenen Varianz durch verschiedene Faktoren erklärt wird. Die untersuchten Faktoren hierbei waren Größe, stratigraphisches Alter, Lokalität und phylogenetische Zugehörigkeit auf Familienniveau und darüber hinaus. Interessanter Weise scheinen die Gemeinschaften keinerlei Trend in ihrer Morphospace Occupation aufzuweisen. Weder setzen sich bei limnischen Crocodyliformes mit der Zeit zunehmend breitschädelige oder langschnäuzige Formen durch noch bewegen sich die verschiedenen Taxa innerhalb einer Gemeinschaft bezüglich ihrer Position im Morphospace weiter voneinander weg. Das einzige offensichtliche Ergebnis diesbezüglich ist, dass die Morphospace Occupation der Gemeinschaften in der Frühen Kreidezeit eindeutig am größten war. Während dieser Zeit erreichte die Diversität limnischer Crocodyliformes – laut den Ergebnissen früherer Forschung – ein Höchstmaß, bevor es zu einer längeren Phase des Aussterbens kam. Das

Verschwinden der "metriorhynchiden" Schädelform, bei der sich ein sehr breiter Schädel relativ abrupt zu einer schmalen aber vergleichsweise kurzen Schnauze verjüngt, hängt höchstwahrscheinlich hiermit zusammen. Von allen analysierten Faktoren hat die phylogenetische Zugehörigkeit eindeutig die größte Auswirkung, da sie unabhängig davon, mit welchen anderen Faktoren sie verglichen wurde, stets 41.604% der Varianz erklärt. Bei limnischen Crocodyliformes scheint die Schädelform daher ein vorrangig phylogenetisches Merkmal zu sein. Das Verschwinden gewisser Schädelformen scheint eine Folge des Aussterbens jener Clades zu sein, in denen diese häufig vorkamen. Zukünftige Forschung bezüglich der Phylogenie von Krokodilen und ihren unmittelbaren Verwandten sollte daher Schädelform als Faktor miteinbeziehen, während Untersuchungen zur ökologischen Rolle ausgestorbener Panzerechsen sich eher auf Merkmale der Zähne und des Kiefergelenks stützen könnte.