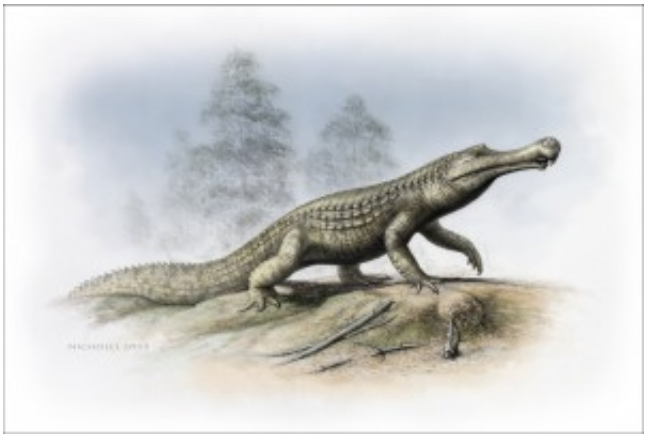
New fossil croc on the block

November 10 2015, by Jon Tennant



The giant croc Sarcosuchus. Credit: Bob Nicholls

Crocodiles are freakin' amazing animals. They've been around for about 250 million years, and throughout this time have survived two mass extinctions, and at least twice decided to hitch up and take to the seas. Their historical diversity, and general weirdness, was vast compared to what we see in modern crocs, which are on the face of it all fairly similar. Extinct forms included those that looked like armadillos and even ate plants, as well as some that became gigantic and streamlined for swimming out to sea. Others were up to 12 metres long, and snacked on dinosaurs!

All modern crocs, alligators, caimans, and gharials belong to a group known as Crocodylia. The origins of this group can be traced back to the Cretaceous, when many of these bizarre croc-cousins, known

collectively as crocodyliforms, where still around. Trying to work out the evolutionary origins of modern crocs though has proven to be a bit confusing for palaeontologists. Part of this is simply due to the fact that the fossil record preserves incomplete remnants of the lineage leading to modern crocs, which in turn creates issues in our understanding the relationships and anatomical changes that led to the origin of Crocodylia.

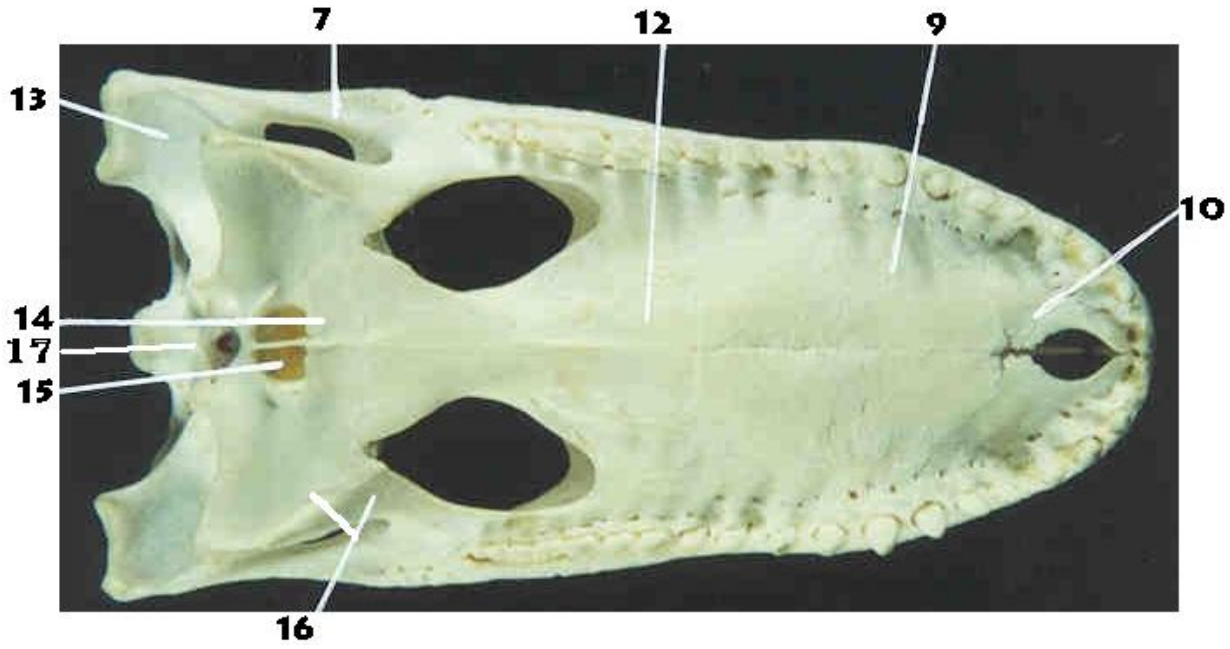
One thing we do know is that a group known as Eusuchia are the direct ancestors of modern crocs – Crocodylia belongs to Eusuchia, but not all eusuchians are crocodylians, if that makes sense. That's because some eusuchians went extinct during the Cretaceous, leaving just crocodylians (and a couple of other non-eusuchian groups like the now extinct marine dyrosaurids) around to take charge. One of the problems which croc workers have been trying to figure out is what defines Eusuchia, and therefore what croc species can be assigned to this group. If we know this, then we can look at the evolutionary changes that led to the origins of modern crocodilians, and why these chappies became so successful.

Eusuchians have been traditionally recognised based on a couple of really important modifications to the 'standard' crocodyliform skeleton that reflect major changes in their lifestyle. One of these involves the movement of the choanae, an opening in the top of the mouth that helped crocs to breathe more efficiently, from a position closer to the nostrils to a position further back in the skull. This was due to the development of what's called the secondary palate, the bony surface in the roof the mouth which grew as the overall skull lengthened in crocs to form the snout. Another important development of eusuchians was to do with the vertebrae. Until eusuchians, crocodyliforms (remember, the ancestors of modern crocs) had vertebrae in which the articular surfaces were either flat or concave, which limited mobility of the vertebral column. In Eusuchia, the articular surface facing towards the tail became progressively more hemispherical-shaped, or convex outwards, to what we call a 'procoelous condition', forming a sort of ball and socket

articulation. This would have allowed greater flexibility of the vertebral column, which is a pretty useful adaptation to have.

So why the confusion about what the origins of Eusuchia? Well, for starters, a lot of fossils that look like they could be a eusuchian are often preserved in a way that we can't tell what the choanae and vertebral columns looked like, or these bits are just missing. This leads to quite a lot of uncertainty about what constitutes a 'true' eusuchian, and has complicated both the species that can be assigned to Eusuchia, and the pattern of acquisition of these important anatomical features. Recently, a couple of papers by Alan Turner overhauled Eusuchia, and he suggested that other groups, including Paralligatoridae and Atoposauridae could both be included within Eusuchia too. However, I don't think this is 100% correct, as few if any of the species from these groups can be conclusively shown to have the features that define Eusuchia as mentioned above, and it is possible that atoposaurids and paralligatorids lie outside of Eusuchia (disclosure: I have a paper in review discussing this a bit at the moment). So that's a nice additional layer of confusion to add in!

So that's a whole lot of background, and I think important to wrap our heads around for a couple of reasons. Firstly, it shows that trying to figure out the taxonomy and evolutionary relationships of extinct animals is complicated, and pretty dynamic as far as what constitutes science (evidence-based inference) goes. Secondly, it shows how complicated our current understanding of the origins of modern crocs is, and the reasons for this complexity. Thirdly, it highlights how important new fossil finds might be in helping to unravel some of this evolutionary mess, which provides us with a nice segue into new croc species klaxon.



Those holes towards the back, labelled by I7, are the choanae.

Well, actually, two new crocs! A new study in PLOS ONE has identified two new species of crocodyliform from the same genus, Loheucosuchus (Low-hay-kwo-soo-kus). The first of these new crocs comes from near the village of Fuentes, Cuenco, in Spain, from a fossil locality known as Lo Hueco. The fossils here come from a time right towards the end of the Cretaceous, in time intervals known as the Campanian and Maastrichtian. This new species was called Lohuecosuchus megadontos, and it's probably pretty obvious where the genus name comes from. The species name means 'big tooth', and refers to the well, uniquely big teeth this new croc has! 'suchus' is Latinized from the Greek word souchos, and refers to an Egyptian crocodile-headed god!

As well as this new genus and species, they named a second new species referred to the new genus, Lohuecosuchus mechinorum, from the Fox-Amphoux site from Department of Var in France, and based on

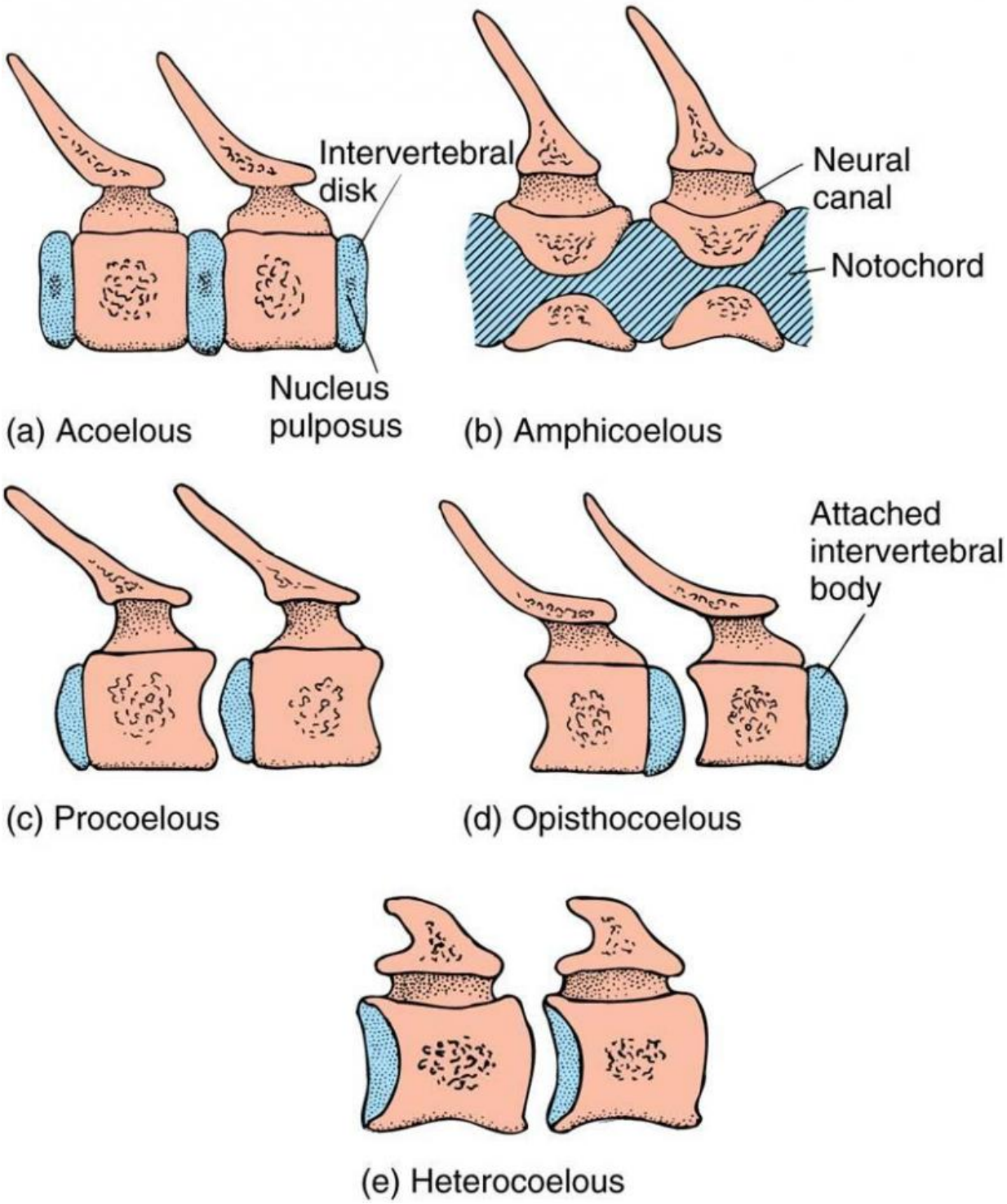
extensive comparisons with previously known material referred to a different species. The species name 'mechinorum' in this case is from the Mechin Collection (in honour of Patrick and Annie Mechin) at the Muséee des Dinosaures in Espéraza, France, which houses the specimens.

These new findings seem to provide a bit of insight into how Late Cretaceous crocs from Europe are related. They all fit within a newly resolved group known as Allodaposuchidae, named after Allodaposuchus as is common when naming these types of group. Allodaposuchus has been known for quite a while from multiple localities referred to several species from the Late Cretaceous of Europe. It's what we like to call in palaeontology a 'taxonomic nightmare'.

Allodaposuchidae seems to be related to another group of fairly unusual crocs known as Hylaeochampsidae, named after (you guessed it) Hylaeochampsa, another croc known from the Early Cretaceous of the Isle of White in Europe. Now Hylaeochampsidae is a bit of a taxonomic mess. Previously, species from the Cretaceous of North America (known as Pachycheilosuchus) and another from Italy called Pietraroiasuchus (I can't say it either..), where assigned to this group, along with others from Europe like Acynodon and Iharkutosuchus. But membership has always been in a bit of a state of flux, depending on which researchers you ask. This is important as historically, hylaeochampsids have been regarded as the earliest, or most basal, eusuchians. Solve Hylaeochampsidae, solve Eusuchia. Oh yeah, it's all coming together now.

Importantly, this new study finds both Allodaposuchidae and Hylaeochampsidae together to be the sister group to Crocodylia. In non-phylogenetics speak, this means that these groups are the closest relatives to the group that includes all modern crocodiles, alligators, and gharials, with the three of them together sharing a common ancestor (i.e., common origin). Hylaeochampsidae is found to comprise just

Hylaeochampsa, Acynodon, and Iharkutosuchus – three exclusively European crocs. This is important, as it pretty much cements the idea that Crocodylia originated in Europe from an exclusively European stock of eusuchian crocs. Or so it would seem..

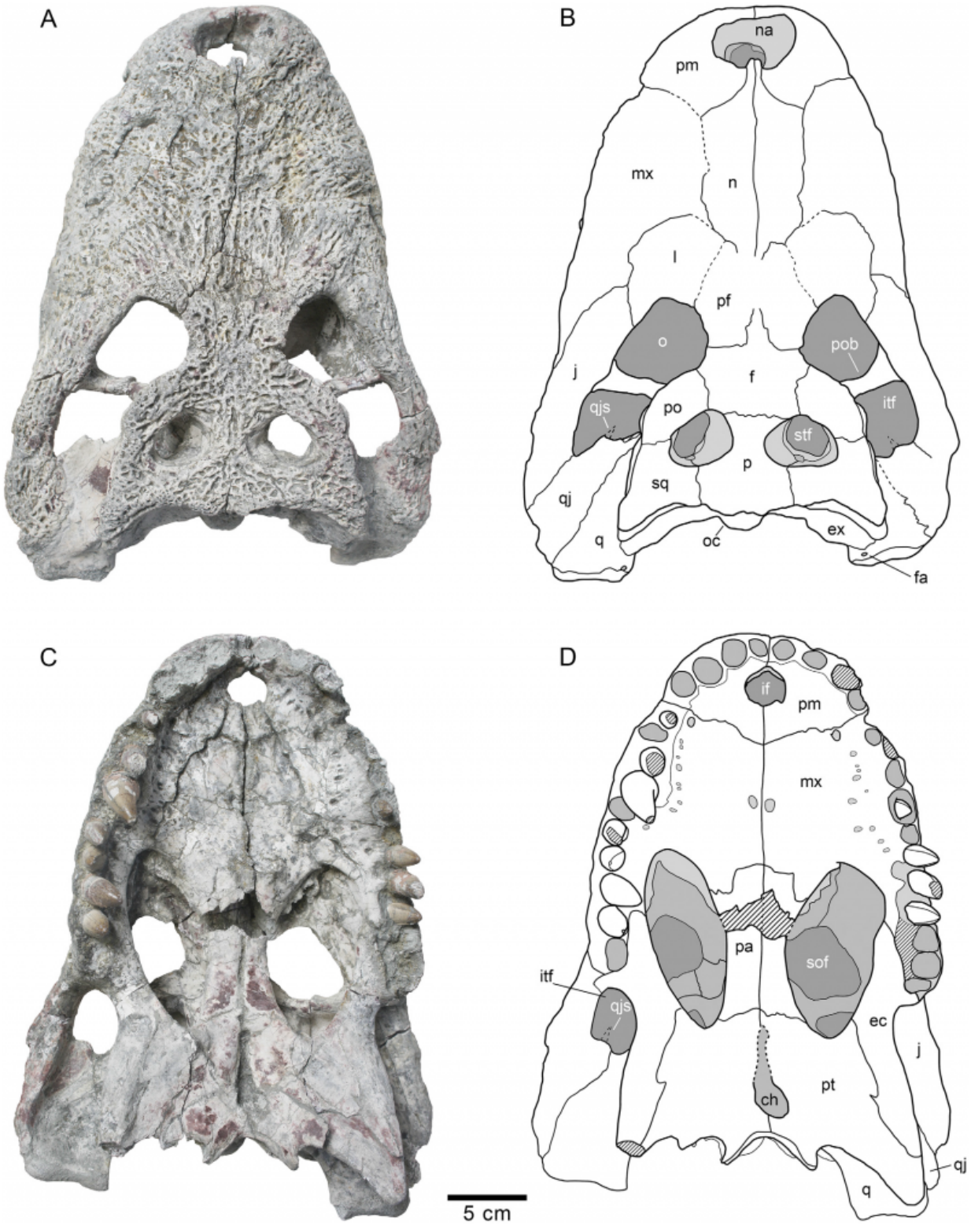


The different types of joint between vertebrae.

However, I wouldn't be a croc palaeontologist if I didn't raise a few potential issues. Or at least, things that spring to mind. The way in which palaeontologists analyse the relationships of organisms is though what we call phylogenetic analysis. These produce 'phylogenies', commonly depicted as trees, which illustrate the hierarchical relationships of organisms. These analyses are based on data matrices that comprise the morphology of organisms reduced to numerical codes that describe different aspects of their anatomy, and the different conditions these can take across all animals considered. What this means is that often when designed, these character matrices are created to test very explicit hypotheses about organismal relationships, based on whatever it is you want at the time, such as the relationships of a group or the position of a particular animal (taxon). But what a lot of researchers do, I imagine mostly for convenience, is to take data matrices used to test previous hypotheses, and simply add a new species into that matrix to test what is by default a very different hypothesis. And that's what happened here. The new study uses a matrix by Chris Brochu and Glenn Storrs, published back in 2012, designed to test the relationships of a new crocodylian species from the Pliocene-Pleistocene (the last few million years) of Kenya. So the question is, is that matrix adequate to test the relationships of a 'basal eusuchian' from the Late Cretaceous of Europe? By using a matrix designed to test the relationships of more advanced crocodylians, the character matrix will contain a lot more characters (anatomical features) that are found in more advanced crocodylians in order to resolve their relationships. By extension, this means that fewer of these characters will be appropriate to test 'deeper' crocodylian relationships back in the Cretaceous, and might explain why several species previously regarded as eusuchians are falling outside of this group in their analyses. If you think about the logic behind this, it's like looking just at modern birds, and trying to figure out what the relationships of Archaeopteryx are from it. You have to sample much deeper from down in the tree at older forms more closely related to the target animal in order to adequately test its relationships. While I don't

think this is a major issue with the results and placement of Lohuecosuchus, and the resolution of the new group Allodaposuchidae, I think it would have been really good to test alternative relationships for it by using different and possibly more appropriate matrices.

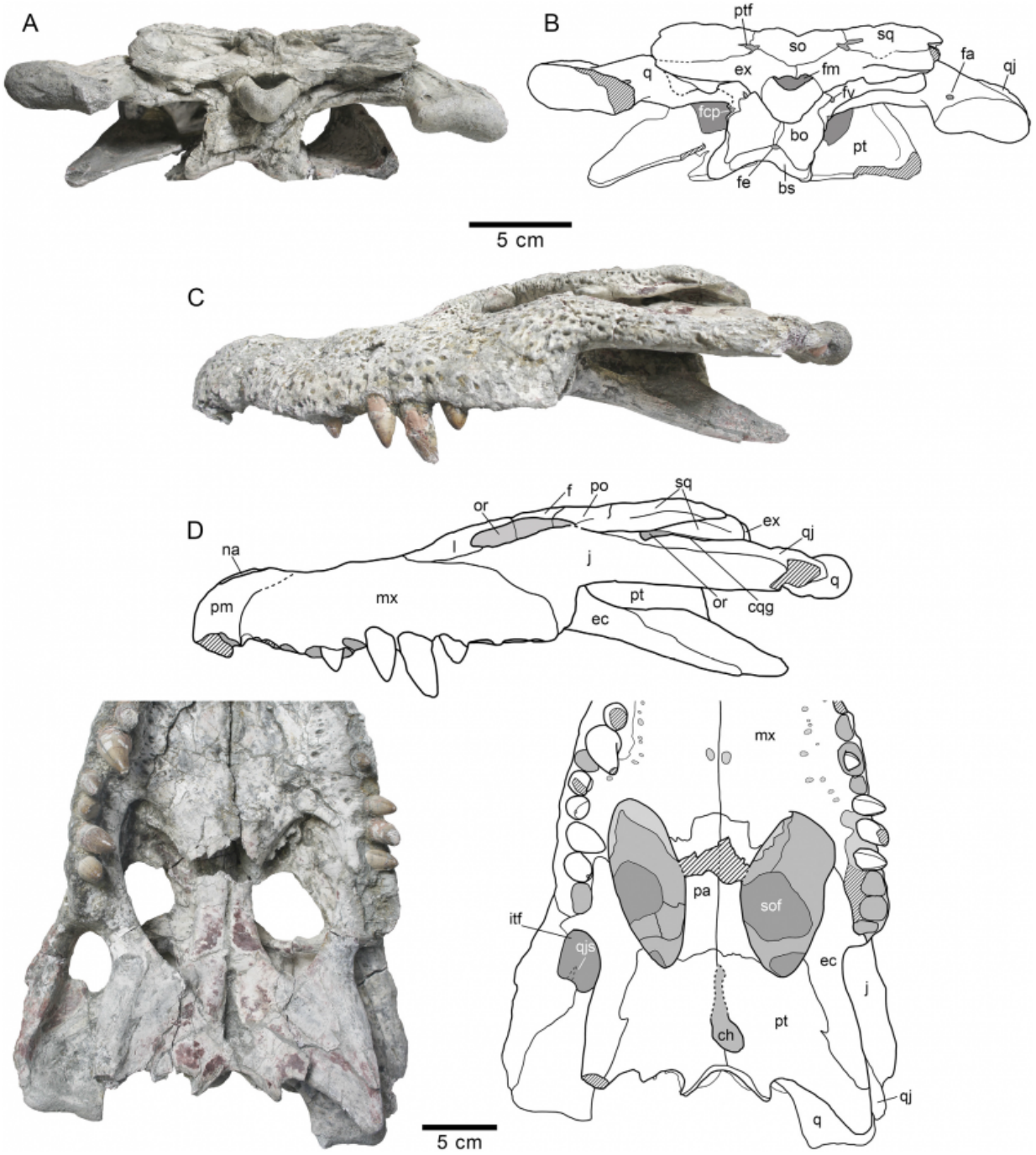
As well as this, such potential inadequacy might help to explain a few of the oddities in their results. As well as just using the matrix of Brochu and Storrs, they added several taxa mentioned above to this matrix and 'coded' them for their morphology. These included Shamosuchus, Pietraroiasuchus, and Pachycheilosuchus, and which the new analysis found all to be outside of Eusuchia. Weird that. While perhaps not unexpected for anyone familiar with these crocs, it is probably due to the issues mentioned above, and not sampling other crocs from deeper down in the tree related to these. In addition, the use of the closely related Bernissartia as what we call an outgroup (the taxon used to define the sequence of morphological evolution by being the most 'basal' in the analyses) is probably not appropriate, as typically more distantly related taxa are needed in order to understand what the actual 'basal' features of a group are. This issue has been raised recently with crocs, which found a completely different placement for a major marine radiation known as Thalattosuchia to be in a different phylogenetic placement depending on what is used as an outgroup.



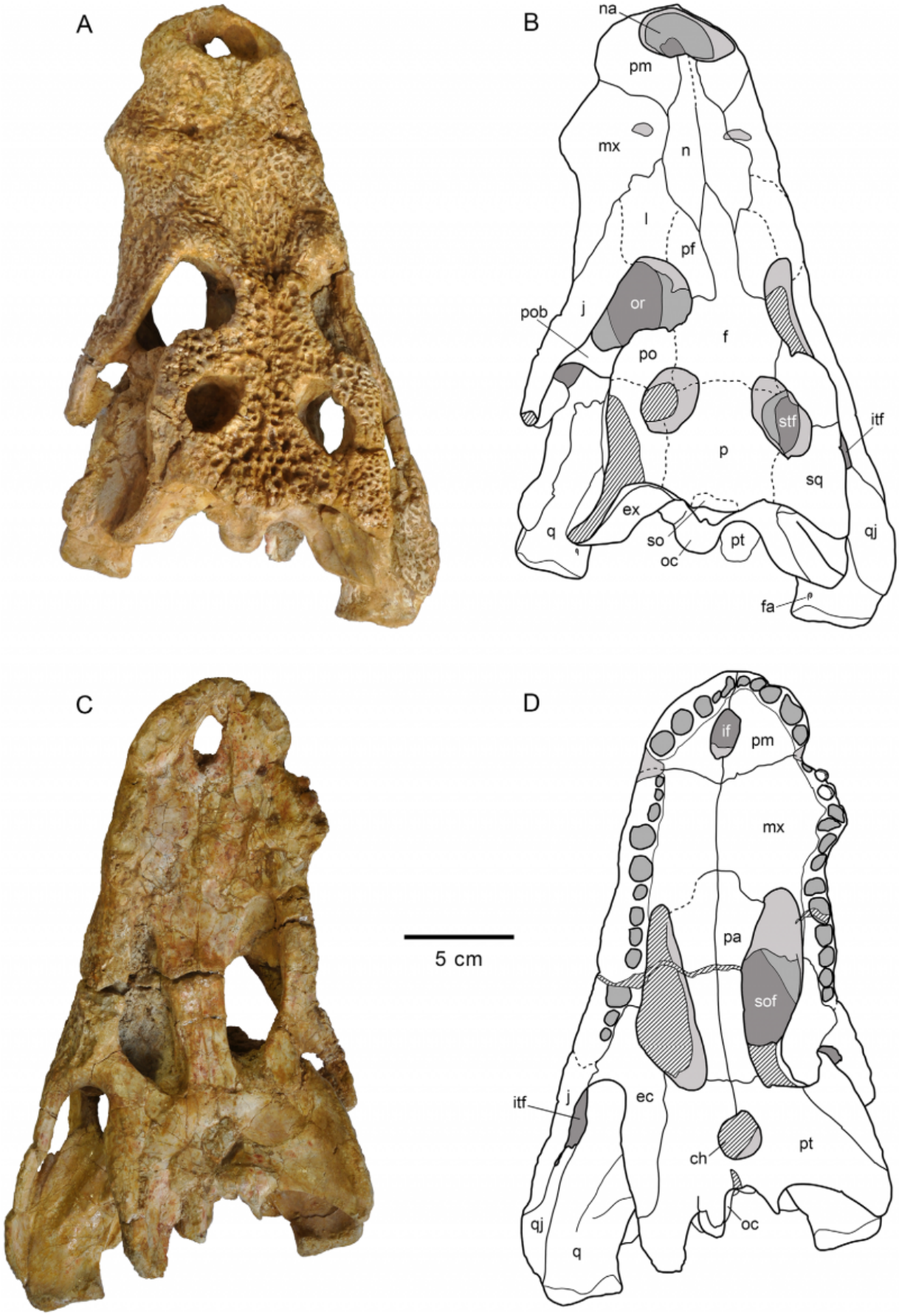
The holotype (specimen upon which a name is founded) of Lohuecosuchus megadontus in above (dorsal) and below (ventral) views

But, if the resolution of an allodaposuchid-hylaeochampsid only Eusuchia is true (along with Crocodylia), then it has some pretty important implications. Both of these groups went extinct at the end of the Cretaceous, in the mass extinction that also took out the pterosaurs, marine reptiles, and the non-avian dinosaurs. Could it be that this removed competition with early crocodylians, and allowed them to radiate in their absence? This supports recent studies which showed that crocs actually seemed to do pretty well after the end-Cretaceous mass extinction, and shows that while we might think of extinction as generally bad, it really depends on whether you're one of the survivors or not..

So for now, I'd still say we still haven't fully resolved Eusuchia, and the results of this new study should be taken with a pinch of salt. Still, a cool new croc, and I look forward to seeing future analyses including it to see where it fits within the broader scheme of croc evolution.



Another couple of views of Lohuecosuchus megadontus specimens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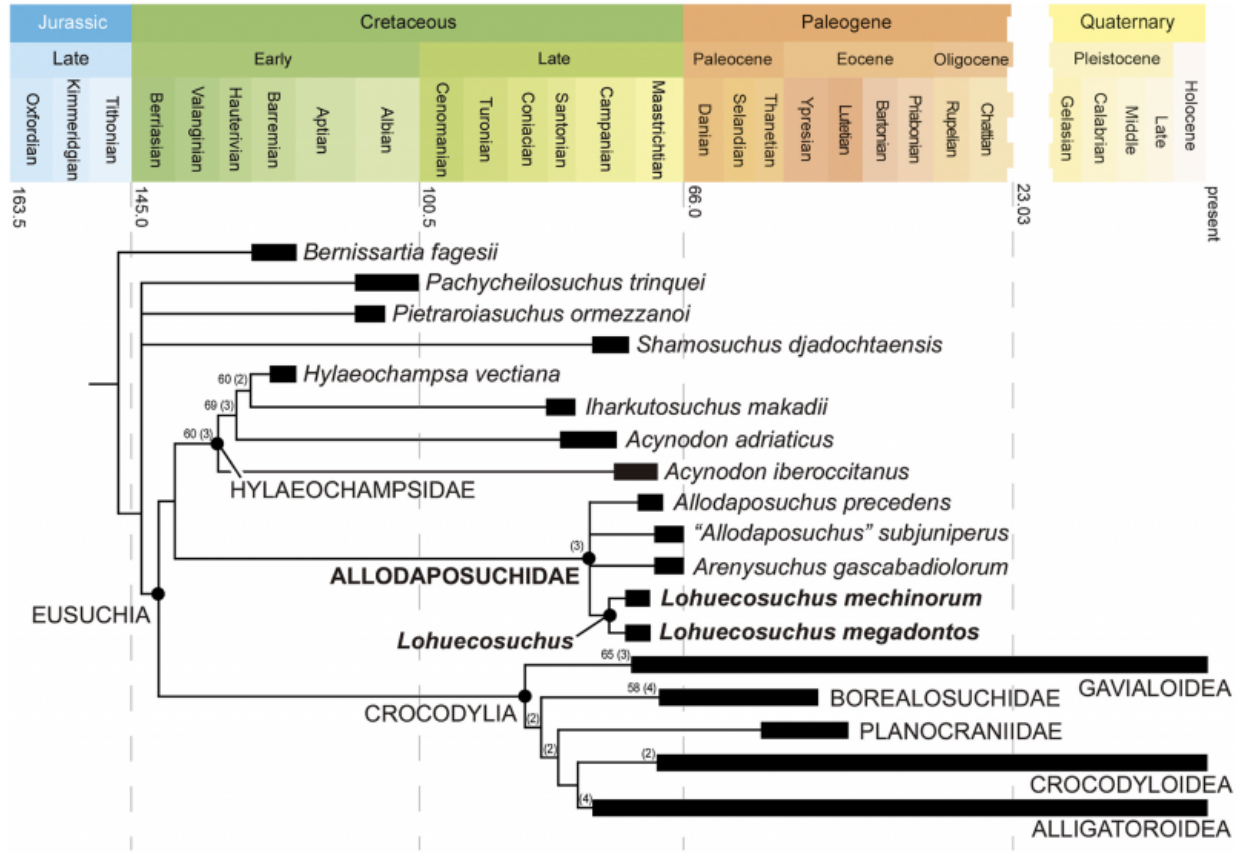
Holotype specimen of Lohuecosuchus mechinorum



Time-calibrated phylogeny based on the new analyses

More information: Iván Narváez et al. New Crocodyliforms from Southwestern Europe and Definition of a Diverse Clade of European Late Cretaceous Basal Eusuchians, *PLOS ONE* (2015). DOI:

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Christopher A. Brochu et al. A giant crocodile from the Plio-Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of in Africa , *Journal of Vertebrate Paleontology* (2012). DOI: 10.1080/02724634.2012.652324

Alan H. Turner et al. The monophyly of Susisuchidae (Crocodyliformes) and its phylogenetic placement in Neosuchia, *PeerJ* (2015). DOI: 10.7717/peerj.759