

Comments on the manuscript “A new species of *Allodaposuchus* (Eusuchia, Crocodylia) from the late Maastrichtian (Late Cretaceous) of Spain: Phylogenetic and paleobiologic implications.”.

As I wrote it in my first review, the paper is good, but I still disagree with the erection of a new species. In my opinion, the material is too poor, and numerous characters could be related to intraspecific variability... (see below). In particular the differences with *A. palustris* are unclear (this species is also formed with fragmentary remains....). So, I am not convinced by this new species.

If it is not possible (in my opinion) to determine if the new material is a new species or not, this does not reduce the interest of the paper (on the contrary !), and I agree with Massimo, I recommend the authors to focus the paper on the description of the inner structures of the skull and the sections about the forelimb miology and functional morphology.

That's why I recommend a major/minor revision (most of the work has been done by the authors).

I also would like to annotate that the authors seem to consider my comments as personal attacks, suggesting possible conflict of interest (“*Stéphane Jouve disputes our scientific objectivity being in our opinion excessively critical and severe underestimating our codings of morphological characters*”). I NEVER objected the scientific objectivity of the authors ! I consider all my reviews seriously, as an important part of my job, and I spend a lot of time in all my reviews, trying to provide as much comments as possible to improve the papers, and I did not provide more comments for this paper than for the others....

I am not “*excessively critical and do not severe underestimating their codings of morphological characters...*” as I proposed exactly the same conclusion as reviewer 1 !! (M. Delfino: “... *it seems very likely (I didn't see the material) that all the characters described are just intraspecific variation or related to the preservation of the material...*”).

Did Massimo “*severe underestimating their codings of morphological characters*”...? I have just spent much more of my time to detail and develop my comments and arguments (it is not a critic of the review of Massimo !), but I disagree in many points (yes, I consider that reconstruct the shape of the orbit only with its medial margin is.....daring...). This is also Science. I justified all my comments with arguments, and sometimes with figures. I do not think I am right each time. But could the authors consider that if I question some characters, it could be because the descriptions or comparisons are not perfect ?

Is this sentence of my review the problem : *“As often when the material is fragmentary, the authors try to find diagnostic characters, and often, in my opinion, use poor characters (intraspecific variability, weak differences...)”* ?

Did the authors not try to find diagnostic characters ? When the material is fragmentary, it is difficult to compare morphological characters (particularly when some of the other species are also based on fragmentary remains). No ?

I also NEVER claimed comparison with unpublished material (it would be particularly stupid to do this!)! And I have absolutely no conflict of interest with the present paper....(What kind of interest ???) ! The present paper having no consequences on the publication of my paper (on the contrary !!) (I recommended major modifications (mainly do to the disagreement on the new species and characters coding (as Massimo !)) and not the rejection of the paper).

Moreover I did not contradict published papers. The authors cited all along their letter portions of papers describing characters. Separate descriptions are strongly related to author perceptions (a crest described as weak in a species, could be described as strong in another by another author while both crests are of nearly same shape in the reality...), and only comparison can be used to determine if a character observed in a new specimen can be considered as different from the same structure observed in another specimen, comparison with the anatomical structure itself, not with its description provided by another author.

I strongly recommend to the authors to accept critics (and to avoid disrespectful comments...!!). Discussions and disagreements are Science !

I did not try to hurt the authors. If they were, they misinterpreted my work, and they should note that their next paper I will review, I would probably do as many comments as for this one... I hope my next review will be better appreciated ... I do not want (and never had) any conflict with colleagues, and I hope our future contacts will be more cordials and professionals....

In my following comments, I answer to the authors with the same ton than their answers..... often kindly and more abruptly when their answers were....

My answers are in red.

Best regards

Stéphane.

Validity of the findings

The paper describes new material of *Allodaposuchus* from Spain. This taxon is particularly important to resolve the phylogenetic relationships of Crocodylia. Many characters are provided to justify the erection of the new species, but as the material is poor (as for many species of the genus), the comparisons are difficult. As often when the material is fragmentary, the authors try to find diagnostic characters, and often, in my opinion, use poor characters (intraspecific variability, weak differences...) (see below). So, I am not convinced by this new species.

A: We concur with the reviewer that the understanding of the genus *Allodoposuchus* is very important to resolve the croc phylogeny. As in the previous reviewer, we are glad to see that both reviewers agree in the *Allodoposuchus* nature of the specimen reported. However, we are very sorry to read that the reviewer disputes our scientific objectivity in the description of the reported specimen. Surely we don't dispute the impartiality of the reviewer and we would like to remark that most of the characters herein presented were (and are) considered as taxonomically and phylogenetically valid and diagnostic for most of the croc experts. As stated in the methods section, we adapted our cladistic matrix from Brochu (2011). As above mentioned (reviewer #1), different authors discussed the possibility that the differences between the remains previously reported could represent different *Allodoposuchus* species (Martin and Buffetaut, 2005; Martin, 2010; Narváez and Ortega, 2011; Buscalioni et al., 2011; Puértolas-Pascual et al., 2013).

“However, we are very sorry to read that the reviewer disputes our scientific objectivity in the description of the reported specimen.” :

I disputed nothing ! Sorry to read it.... Maybe I wrote something that hurt the authors, but it was absolutely not my intention....

“we would like to remark that most of the characters herein presented were (and are) considered as taxonomically and phylogenetically valid and diagnostic for most of the croc experts.” :

I've never said the contrary. I used these characters probably long time before the authors read them for the first time.... As I published several papers on the subject, I think, modestly, that I am one of these specialists.... Moreover, in my last paper on crocodylians, I added more than 60 characters, and Brochu (2013) also added characters, not considered herein. If most of the characters used herein are considered as taxonomically and phylogenetically valid and diagnostic, I (and Massimo) discussed their interpretation and their use herein... I would like to remark that it is possible that Massimo and me (both reviewers suggested that the species seems to be supported by poor characters...), are lesser experts than the authors of the present paper.....

See references below:

-Jouve S, Bouya B, Amaghazaz M, Meslouh S. 2014. *Maroccosuchus zennaroi* (Crocodylia: Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical implications of the basalmost tomistomine. *Journal of Systematic Palaeontology* 12: 1-25.

-Brochu CA. 2013. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103: 521-550.

In our opinion, the new reported specimen present several cranial and postcranial character polarities that cannot be assumed only as intraspecific variability (although unfortunately to date there is no published study shedding light on the intraspecific variability of this genus) and we consider these differences as clear interspecific variability forcing us to erect this new taxon.

At least, the presentation of the characters should be revised, and a comparative diagnosis would be clearer when the character differs from only one other *Allodaposuchus* species (differs with ... in having...).

A: We agree with the reviewer that the previous version required an improvement about the diagnosis of the new taxon and for this reason and following the reviewer, all the characters were carefully checked again in the revised version. Moreover, according to both reviewers's suggestions, we provide a 'Differential Diagnosis' section to clarify the differences between our specimen and the other species in the revised version.

The phylogenetic analysis is well conducted, but I strongly disagree with the phylogenetic results obtained by the authors, and with some of the coding, but it is beyond the scope of this review, and that will be discussed in a paper in preparation. Nevertheless, the results should be more extensively discussed (see below), and the matrix in a nexus format should be provided.

A: We are glad that the reviewer agrees that the cladistic analysis was well conducted. As explained in the methods section we used the most complete phylogenetical matrix (regarding both number of genera and characters) up to date. The results are in agreement with those recovered by Brochu (2011) and Blanco et al. (2014). We really acknowledge the update that the reviewer is also working on this genus and that a new study will be out soon, with a new phylogenetical framework. Surely, different matrix could be used and most probably new ones will appear in the future and herein we used the most important one to date. The codings are according to those papers which describe each specimen (Delfino et al., 2008; Puértolas-Pascual, 2013). Now, we provide the matrix in the Supplementary Information 2.

I disagree with the phylogenetic relationship of *Allodaposuchus* with Crocodylia (and this result is not in agreement with Brochu 2011 and others...), but I did not contest the importance of the present result... On the contrary !

I think some grammatical mistakes are present in the text, but I am not a native English speaker. So, the English should be reviewed.

A: We apologize for the grammar problems in the previous version and we carefully checked the revised version and we hope that this new version fulfils all the grammar and stylistic requirements.

Comments for the author

Detailed comments

L23: Crocodylomorphs: Crocodylomorphes

A: solved in the revised version.

L149: Diagnosis:

Allodaposuchus hulki shows the following autapomorphies:

Quadratojugal does not extend along the infratemporal fenestra. : known only in *A. subjuniperus*, unknown in other species. It is not possible to know if it is an autapomorphy.

A:The quadratojugal spine is missing in *A. precedens* but the quadratojugals are partially preserved, and extends along the infratemporal fenestra. We checked in first hand this character in *A. precedens* as well in *A. subjuniperus*. Moreover, in the literature is it possible to read these descriptions from this character: Buscalioni et al., 2001: “The quadratojugal forms the posterior margin of the infratemporal fenestra”; Delfino et al., 2008: “The anterior development of the quadratojugal along the dorsal rim of the lower temporal fenestra prevents the quadrate to contact the fenestra”). Thus, this character should be considered an autapomorphy of the new taxon.

See references at the end of the response letter.

I thought that this character meant that the quadratojugal does not extend along the **ventral margin** of the infratemporal fenestra as in character 142 (Brochu, 2013).... This is not clear here and I misinterpreted your description. Sorry. Should it be better to precise that the quadrate participates to the dorsal margin of the ITF?

Spine of quadratojugal significantly reduced: known only in *A. subjuniperus*. Is its preservation allow a clear observation in present specimen?

A: Yes, it is complete.

Should be excluded from the diagnosis. The QJ spine is unknown in *A. precedens* (“*There is no indication of a quadratojugal spine owing to preservation.*” Buscalioni et al., 2001; “*The development of the quadratojugal spine ... cannot be evaluated due to its incompleteness*”, Delfino et al., 2008; “*The occurrence of a spine is impossible to establish because the bone is broken at this level.*”, Martin et al., 2010), and both species are described as sister taxa. This reduced spine could be a *A. precedens/A. hulki* synapomorphy. Moreover, as the shape of the spine is unknown in other *Allodaposuchus* (except in *A. subjuniperus*), it is not

possible to know if, on the contrary, the long QJ spine is a *A. subjuniperus* autapomorphy, and the short spine a plesiomorphy.

Absence of fossa at anteromedial corner of the supratemporal fenestra.

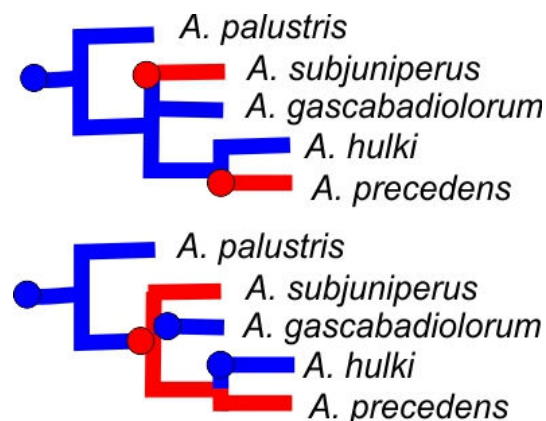
L448: Additionally, *A. hulki* and *A. palustris* are the two species that do not show a fossa around the supratemporal fenestrae. As it is present only in *A. subjuniperus* and *precedens*, its absence is a plesiomorphy. Moreover, its presence or absence cannot be observed in the present specimen, as the fossa is within the supratemporal fenestra, this one being obscured by sediments.

A: this character was actually explored using the CTscan. It is also visible in Fig. 7A, In addition, it is not a plesiomorphy. If it were a plesiomorphy, its presence in *A. subjuniperus* and *A. precedens* would be two independent autapomorphies. Therefore it is more parsimonious to assume that is an autapomorphy of *A. hulki*.

The fossa is absent in all crocodylians. The primitive condition for “*Allodaposuchia*” is thus “absence of fossa”, the derived condition is its presence in *A. subjuniperus* (Puértolas et al., 2013) and *precedens* (character 153, Brochu 2013) (absent in *A. palustris* (Blanco et al., 2014), *hulki*, and *Arenysuchus*). This is more parsimonious. The fossa is absent in *A. gascabadiolorum* (Puértolas et al., 2011).

But this depends on the coding of the character in the authors’ matrix, but the coding below follows the description and coding provided by authors that described the species used.

See references below



-Puértolas E, Canudo JI, Cruzado-Caballero P. 2011. A new crocodylian from the Late Maastrichtian of Spain: implications for the initial radiation of crocodyloids. *Plos One*: e20011. doi:10.1371/journal.pone.0020011.

-Brochu CA. 2013. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103: 521-550.

- Puértolas-Pascual E, Canudo JI, Moreno-Azanza M. 2013. The eusuchian crocodylomorph *Allodaposuchus subjuniperus* sp. nov., a new species from the latest Cretaceous (upper Maastrichtian) of Spain. *Historical Biology* 26:91-109.

-Blanco A, Puértolas-Pascual E, Marmi J, Vila B, Sellés AG. 2014. *Allodaposuchus palustris* sp. nov. from the upper Cretaceous of Fumanya (south-eastern Pyrenees, Iberian Peninsula): systematics, palaeoecology and palaeobiogeography of the enigmatic allodaposuchian crocodylians. *PLoS ONE* 12:e115837.

No ridge surrounds the foramen aërum.

L455: in *A. hulki* no ridge surrounds the foramen aërum, unlike the other three species of *Allodaposuchus*: No ridge in *A. precedens*. And not sure that the difference was such significant to be considered as anything else than individual variation.

A: We would like to remark that previous authors noted the presence of a ridge surrounding the foramen aërum of *A. precedens* “The location of the foramen aereum is indicated more than by the foramen itself, which is rather small and surrounded by other foramina, by the presence of a dorsal ridge developed anteriorly to the foramen” (Delfino et al. 2008). Moreover, the first author also examined the material of *A. precedens* and corroborates its presence. Thus, we don’t understand the criticism of the reviewer at this point. Nevertheless, and following the reviewer in the revised version we decided to exclude the absence of the ridge of foramen from the diagnosis due to the variability of this character. However, since any other species of *Allodaposuchus* lacks this character, we prefer retain it in the ‘ambiguous autapomorphies’ section.

See references at the end of the response letter.

I also examined the holotype and the material described by Martin (2010), and the ridge is absent in the Martin’s specimen, and very very weak in the holotype (but it is my interpretation). I think here we have a different perception of the character. Moreover, if the authors cite the description provided by Massimo Delfino, they should also refer to his review : “*the ridge corresponding to the foramen aërum is a too variable character to be included in a specific diagnosis*”.

This character is probably intraspecific variation.

No elevation rounds the rim of external naris: also absent in *A. precedens* and it is weak in *A. subjuniperus* (slightly elevated). So if this character is diagnostic (I doubt...) it is its presence in *A. subjuniperus*, not its absence in other *Allodaposuchus*.

A: This character is present *A. precedens*, as noted by Delfino and colleagues (2008) “ the dorsal surface is slightly elevated along the posterolateral sector of the choana” whereas in *A. subjuniperus* “The dorsal surface is slightly elevated along the lateral rim of the naris” (Puértolas-Pascual et al., 2013). Nonetheless both were considered as lacking this elevation (Ch. 85 (0)), so no difference affects to the topology. We agree to remove this sentence from the ‘Diagnosis’, but we prefer maintain it in the ‘Comparison’ section.

It is the problem of comparison and perception of characters.... Some authors can consider the elevation as weak, when other does not see it.... I do not see it in *A. precedens*. Can the absence of a slightly elevated rim be considered as diagnostic.....? or could it be considered as possibly related to intraspecific variation...?

OK. I agree with you, it is better in the comparison section.

Incisive foramen abuts first and second premaxillary teeth. The distance 1st tooth-FI is equal to the 1st tooth diameter in *A. subjuniperus* and *A. precedens*, and slightly lesser in the new specimen. The difference is weak, and it strongly depends on the angle of the photo in *A. subjuniperus*, and *A. precedens*.

A: After checking in first hand the type material of *A. precedens* and *A. subjuniperus* we can assess with confidence that it largely differs between the two species. Moreover, as previously also stated, in *A. precedens* “it is almond shaped and rather small (its maximum width is about 15 mm) and its anterior tip nearly reaches the premaxillary tooth row.” (Delfino et al. 2008), whereas in *A. subjuniperus* “its anterior rim at the level of the third premaxillary alveolus.” (Puértolas-Pascual et al., 2013). Our personal observations as well as those from the above mentioned descriptions from other teams shows that the angle is not depending of the picture and that these differences are real and objective.

OK.

Teeth bear smooth enamel, low-developed mesial and posterior carinae, and absence of longitudinal grooves in lingual side. Related to intraspecific variability, and insignificant differences with *A. subjuniperus* (see below). The lingual groove is present only in Premaxillary teeth in *A. precedens*. So, the tooth ornamentation varies along the tooth row, and the difference (if there is) is only with *A. precedens*....



A: We would like to remark that *A. subjuniperus* shows smooth enamel with two lingual grooves. These grooves are not present in *A. hulki*. In the case of *A. precedens*, this taxon shows longitudinal ridges in lingual and labial sides, absent in *A. hulki* and *A. subjuniperus*. Regarding *A. palustris*, this is the only one with false-zipodont ornamentation. Moreover, teeth inserted on the skulls of *A. precedens* and *A. subjuniperus* are scarce. And, due to the number of teeth present in *A. palustris*, ornamentation remains nearly constant along the tooth row, is the shape of the teeth that varies. Nonetheless, the first author additionally studied isolated teeth (paratype of *A. precedens*) housed in the the Hungarian Geological Institute (Budapest), supporting the former assertion.

I also observed isolated teeth (paratype of *A. precedens*), some teeth are smooth on both sides, and some bear a false-zipodontie (see below). I agree with the authors that we cannot be sure that these teeth can be reported to *A. precedens* with confidence, but I am agree with Massimo, and I am not sure that characters observed on 2 dentary teeth should be included in a diagnosis, while variation in shape and ornamentation is known along the tooth row in many crocodilian species.

Exclusive combination of the following synapomorphies: External naris opens in anterodorsal direction: as in all *Allodaposuchus*, except in *A. subjuniperus*.... It should a *A. subjuniperus* autapomorphy, but must not be included in the present diagnosis.

A: The external naris morphology is only known, besides in the new specimen, in *A. precedens* and *A. subjuniperus*. The naris is dorsally opened in *A. subjuniperus*, but it is anterodorsally opened in *A. precedens* and in the new specimen. The naris opened in dorsal direction characterizes the clade Crocodylia and this character is phylogenetically informative (Brochu, 2011; Ch. 81). After our phylogenetical results, since the genus is included within Crocodylia, this character is a *A. subjuniperus* plesiomorphy, and is a sinapomorphy of the clade (*A. hulki* + *A. precedens*).

Of course..... I considered the “classic” relationships.... The authors are right.

Premaxilla is wider than long: as posterior process of the premaxilla is not preserved this cannot be evaluated. But I think that the authors mean that the premaxilla is wide laterally to the external nares. This is mainly du to the size of the external nare, large in *A. precedens* (Delfino, 2008 and Martin, 2010), but it is comparable here to this is observed in *A. subjuniperus*, and *Acynodon*.... So, this is more probably a plesiomorphy. If the authors mean that the premaxilla is wider than the length from tip of snout to lateral premaxillary-maxillary suture, this is also the case in all other *Allodaposuchus*. Moreover, the posterior margin of the premaxilla seems to be strongly damaged. Is the premaxillo-maxillo suture preserved ? I am not sure on the figures.

A: The premaxilla is wider than the legth from tip of snout to lateral premaxillary-maxillary sutures, but it is not the case in all other *Allodaposuchus* (see Defino et al., 2008 and Puértolas-Pascual et al., 2013 for descriptions and comparisons). The premaxilla is wider than long in *A. subjuniperus*, and longer than wide in *A. precedens*. The premaxilla-maxilla suture is preserved in the new specimen, so comparisons could be performed and are discussed in the manuscript.

OK, but in the specimen described by Martin the Pmx is wider than long, and the premaxilla is also wider than long in *A. precedens* (Delfino, 2008) (slightly), but the authors are right, the Pmx seems to be wider in *A. subjuniperis* and new specimen.

Four premaxillary alveoli, being the third the largest. As in *A. subjuniperus*.

A: As previously commented (See reviewer #1), *A. subjuniperus* and *A. hulki* shares this character, in contrast with *A. precedens*

Premaxillary-maxillary suture does not reach the posterior margin of the incisive foramen. As in all *Allodaposuchus* ! Even if the distance between the suture and posterior margin of the foramen incisivum is longer in *A. subjuniperus* and present form compared to *A. precedens*, it is also large in *Acynodon*. This character (if you don't retain the possible intraspecific variability), could be a *A. subjuniperus* autapomorphy.

A: It is not the case in all other *Allodaposuchus* species. In the case of *A. subjuniperus*, Puértolas-Pascual et al. (2013) noted that "Another difference refers to the shape and position of the incisive foramen in relation to the premaxillary-maxillary suture. On the palatal surface of *Allodaposuchus subjuniperus*, the incisive foramen is large, subcircular and posteriorly placed, and it almost abuts the premaxillary- maxillary suture. By contrast, in (*A. precedens*) the incisive foramen is smaller, slightly anteroposteriorly elongated and located in the middle of the premaxillae further away from the premaxillary-maxillary suture)." There is no evidence of possible intraspecific variability. After our phylogenetical results, it should be considered a sinapomorphy of the clade (*A. hulki* + *A. precedens*).

No. As it is written in Puértolas-Pascual et al. (2013), and above, the premaxillary-maxillary suture DOES NOT abut the foramen incisivum. It ALMOST abuts. So, premaxillary-maxillary suture does not reach the posterior margin of the incisive foramen, as in all *Allodaposuchus* (in which it is known).

The character 88 (Brochu et al., 2013) should be scored as 1 (not 2. I did not look how it is scored in the matrice) in *A. subjuniperus*, or the character definition should be changed.

But the authors are right, the distance between the posterior margin of the foramen incisivum and the Pmx-Mx suture is longer in *A. precedens* (as I wrote it in my review !).

L430: In palatal view, the incisive foramen is located more anteriorly than *A. precedens* and *A. subjuniperus*. No, the FI is not more anterior than in *A. precedens* .

A: We are sorry to disagree but, yes, it is. See figures in Delfino et al. (2008) for comparisons. However, according to descriptions by Delfino et al., both were considered as 'abutting tooth row' (Brochu 2011, Ch. 89 (1)), so no difference affects to the topology. The different position is only described in the 'Comparison' section.

OK.

Wide and short orbits, without interorbital ridge in the frontal. How can you evaluate the size of the orbits, when they are not preserved ?? To evaluate the orbital width, its lateral margin is required! Moreover, comparing the authors

reconstruction with *A. subjuniperus* and *A. precedens*.... the difference is weak or absent. Not sure that it is possible to exclude the presence of a frontal crest. The anterior portion is absent herein, and it cannot be excluded that it was present anterior to the preserved portion (see *A. subjuniperus*).

A: The orbits were evaluated because their dorsal margin is well preserved, as in *A. palustris* (Blanco et al., 2014). The difference is not weak (Puértolas-Pascual et al., 2013: “The orbits are relatively wide and short...”; Blanco et al., 2014: “The orbits are relatively large, rounded and slightly elongated rostrocaudally”), however this character is merely a comparative description and not a diagnosis. Finally, according to the morphology of *A. subjuniperus*, the preserved portion of the frontal of the new specimen is enough to assess the absence of this crest.

See references at the end of the response letter.

“The orbits were evaluated because their dorsal margin is well preserved”:
So, again, how can the authors evaluate the width (and length) of the orbit with its medial margin only ...??

I still don't understand how the authors can evaluate the width and the general shape of the orbits without at least its anterior margin.... At least, I suggest the authors to consider this shape more cautiously, and not in the diagnosis. It is not possible to reconstruct with confidence the shape of the orbit just with its medial margin, even comparatively with the shape of medial margin found in other species.

Moreover, the difference between *A. subjuniperus* and *A. precedens* is weak, the orbit being nearly as wide as long in both species (the skull is dorsoventrally flattened in Delfino (2008)). (it is proportionally smaller in *A. subjuniperus* compared to the skull size).

The descriptions provided by Puértolas-Pascual et al., 2013 and Blanco et al., 2014 cannot really help, depending of personal perception. They are two independent descriptions. Comparison and relative sizes are important. Moreover, the reconstruction of the orbital shape of *A. palustris* is doubtful, as only its medial margin is preserved.

I still disagree with the authors. Compared with the frontal crest of other *Allodaposuchus*, it cannot be excluded that the frontal crest was present anterior to the preserved part... But at least a more prudent description should be used, considering that the crest is probably absent?

Quadrates bears two crests in ventral surface for muscle attachment. As in many eusuchians.... Its absence should be a *A. palustris* autapomorphy.

A: We would to remark that these crests are completely absent in *A. palustris* and different to *A. precedens* as described by other authors: Delfino et al., 2008: “The ventral surface of quadrates is characterized by a strong, nearly blade-like, quadrate crest that abruptly ends forming (best preserved on the right) a small tubercle.”, showing the importance of this character in this genus.

OK.

Capitate process of the laterosphenoid is anteroposteriorly oriented.
L463: In ventral view, the capitate process of the laterosphenoid is anteroposteriorly oriented in *A. hulki* and *A. subjuniperus*, but is laterally oriented in *A. precedens*. This character is not clear. See Buscalioni et al. (2001) Fig. 2, where the capitate process is anteroporteriorly oriented....

A: Buscalioni et al. (2001) made their revision of *Allodaposuchus* before the discovery of *A. subjuniperus* (2013) and we recommend the reviewer to check and update the references about these taxa. Many of the material described by Buscalioni et al. has unclear affinities, and the authors may mixed material from different species. Moreover, according to Buscalioni et al. this material could represent different taxa to the Romanian material. According to Delfino et al. (2008) and Puértolas-Pascual et al. (2013), the difference is clear, and this character is phylogenetically informative (Brochu 2011, Ch. 166).

“Buscalioni et al. (2001) made their revision of Allodaposuchus before the discovery of A. subjuniperus (2013)” :

and ? (immaterial to the subject)

“... and we recommend the reviewer to check and update the references about these taxa.” :

And I recommend the authors to avoid stupid comments Yes I update the references (don't understand why this comment....), but I invite the authors to **READ CAREFULLY** the comments provided by the reviewers and to see the **HOLOTYPE** of *Allodaposuchus* . Fig. 2 of Buscalioni et al. (2001) (cited in my comment!) is the holotype of *Allodaposuchus precedens* ! The capitate process is anteroposteriorly oriented in this holotype, as coded by Brochu for this species (he also based his coding on the holotype.... But he probably also didn't “*check and update his references*”.... no ??).

Here the holotype of *Allodaposuchus precedens*....



Here the description provided in Brochu's thesis for this character :

"The laterosphenoid-frontal contact in the Glen Rose form and most eusuchians is oriented anteroposteriorly such that the olfactory nerve exits anterior to the capitate process. In a few taxa (*Gavialis*, *Gryposuchus*, *Eogavialis*, *Thoracosaurus*), this contact is oriented mediolaterally, the capitate processes and olfactory foramen are in the same coronal plane, and the suture between the laterosphenoids and frontal is linear."

Aside of the previous characters, *A. hulki* has the following ambiguous autapomorphies: Anterolateral, anteromedial and olecranon processes of the ulna well developed. Ulnar shaft lateromedially compressed with lateral and medial grooves. Distal condyles of the ulna turned lateroposteriorly, causing a lateral crest in the shaft. We prefer coding all these autapomorphies as ambiguous, due to the absence of postcranial remains in other species of *Allodaposuchus*. New discoveries may reveal if they are autapomorphies of the genus.

As they cannot be compared with other *Allodaposuchus* (as many other Eusuchians), these characters should not be included in the diagnosis.

A: We agree with the reviewer that they cannot be compared with other *Allodaposuchus*, but largely differ with other compared taxa. For this reason these characters were excluded from the diagnosis of *A. hulki*, but mentioned as 'ambiguous autapomorphies', probably of the genus, pending new discoveries.

Ok, but as it is not possible to know if these characters are autapomorphies for the species or genus (or part of the species), they should also be excluded from the ambiguous autapomorphies.

L180: quatdrates: quadrates

L181: quatdratojugal: quadratojugal

A: We solved these issues in the revised version.

L217: In lingual view, an uncommon large medial jugal foramen: equivalent to the jugal foramen observed and coded as large in *A. precedens* (cf Brochu, 2011; char. 102)?

A: Is slightly bigger than *A. precedens*, but this sentence is merely a comparative description and not a diagnosis. Yes, both species were coded as 'large' (Brochu, 2011; Ch. 102 (1)).

L224: Quadratojugal spine is nearly absent and low in position: preservational artifact ?

A: The quadratojugal spine is well preserved and fortunately doesn't correspond to any preservational artifact.

OK

L234: Both articular hemicondyles are similar in size, although the medial hemicondyle is slightly smaller and ventrally deflected: in Fig. 2C-D, the quadrate condyle is figured as damaged.... How their shapes can be evaluated ?

A: Fortunately, the surface is slightly eroded, but it is complete allowing to assess with confidence the shape.

OK

L276: lateral margin of the supraorbital fenestra: supratemporal fenestra ?

L330: In the same side, but in a most ventrally position : In the same side, but in a more ventral position ?

L331: and immediately superior to supraglenoid: and immediately dorsal to supraglenoid ?

L346: the humeral head seem to have the same high: the humeral head seem to have the same height.

L351: several rugous areas around itself : not clear..... what does that mean?

L370: In proximal view is triangular-shaped: In proximal view it is triangular-shaped

L405: decrease in high respect the centrum: decrease in height respect the centrum... ? not clear.

A: We solved all the above mentioned punctual comments in the revised version.

L430: In *A. hulki* the anterior rim of incisive foramen is located between the first and second alveoli, whereas in *A. precedens* and *A. subjuniperus*, reaches the third premaxillary alveolus.

It depends on the orientation of the fragment. If the ventral view is oriented as the dorsal view, the anterior margin is located at the same level as the 3rd tooth (see below).

A: We refer to the previous question of the reviewer about this issue, as we explained and solved this issue (See answers in pages 11 and 12)

OK

L435: Moreover, *A. hulki* shows a pattern of occlusal pits different to *A. precedens* and *A. subjuniperus*. How ? Does not seem so different...

A: As explained in the manuscript, there are one occlusal pit between the first and second alveoli, other between the second and third, and no pit between the third and fourth alveoli. In turn, *A. precedens* shows one occlusal pit between the third

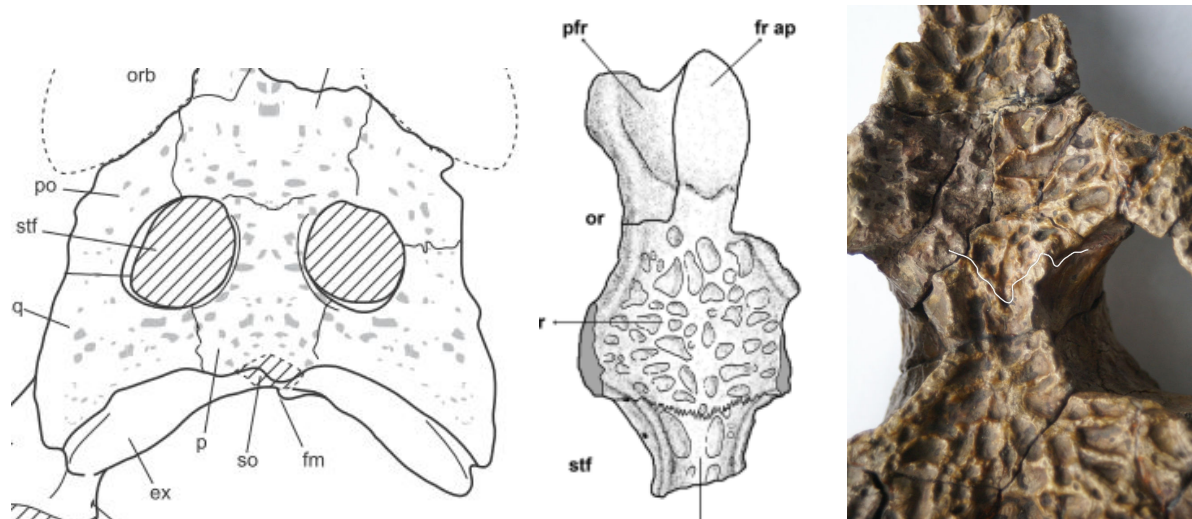
and the fourth, and other between the fourth and the fifth alveoli, whereas *A. subjuniperus* shows only a large diastema between the first and second alveoli.

OK. But the presence and size of occlusal pits could also be related to the age/size of the specimen.

L446: The frontoparietal suture of *A. hulki* is nearly linear, like *A. subjuniperus* and *A. precedens*. *Allodaposuchus palustris* is the only 'allodaposuchian' that shows a concavo-convex frontoparietal suture. The suture is not really concavoconvex in *A. palustris* (compare with *Crocodylus*), and no more than the specimen described herein (see below).

A: This suture is concavoconvex in *A. palustris* (coded in Blanco et al., 2014), and it clearly differs with those of *A. subjuniperus*, *A. precedens* and the new specimen. Moreover, the codification of others species exceeds the aim of this paper.

No.... The authors are wrong. It does not **clearly differ** from the new specimen.... The suture is also concavo convex, or equally linear. see below. (new specimen, *A. palustris*, *A. precedens* (holotype)). The suture is more concavoconvex in *A. precedens* (holotype) than in *A. palustris*, even if the suture seems to be more linear in the specimen described by Massimo (Delfino, 2008). This is important in your paper, as you study the relationships of *Allodaposuchus*.... Clearly, considering the figures below, the coding for this character is erroneous, and the inclusion of several *Allodaposuchus* species in phylogenetic analyses, implies to review the character coding at least for all *Allodaposuchus*. And this does not exceed the aim of your paper as this could consistently biase your result.....



L450: Like *A. precedens*, both articular hemicondyles of the quadrate of *A. hulki* are similar in size, although the medial hemicondyle is slightly smaller and ventrally deflected. In turn, *A. subjuniperus* shows a ventral expansion in the medial hemicondyle. in Fig. 2C-D, the quadrate condyle is figured as damaged.... How their shape can be evaluated ? The medial hemicondyle does not seem to differ between *A. subjuniperus* and described form.

A: We would like to remark that this question is very similar to another above one (L. 234) and as previously commented, the surface is slightly eroded, but it is complete, allowing to assess with confidence the shape. We also would like to remark that the medial hemicondyle differs between the new specimen, *A. precedens*, and *A. subjuniperus* (Delfino et al., 2008: “the area between the hemicondyles is nearly rectilinear dorsally and slightly concave ventrally; (...) small ventrally reflected hemicondyle.”; Puértolas-Pascual et al., 2013: “The articular hemicondyles are rather flat, with only a slight ventral expansion in the medial articular hemicondyle”), thus rejecting the criticism of the reviewer and showing the differences in this character between the different *Allodaposuchus* species..

I don't think so... Here also, two independent descriptions, not comparisons. Moreover, the difference between a “(...) small ventrally reflected hemicondyle” and “a slight ventral expansion in the medial articular hemicondyle”..... is not clear...

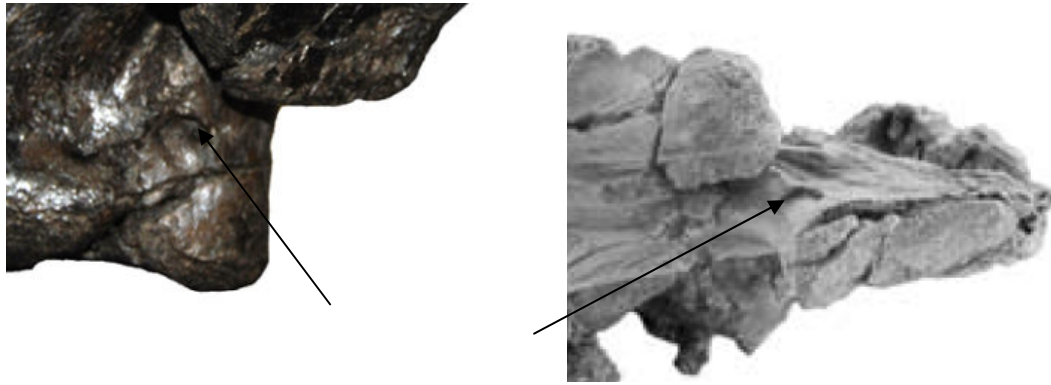
The difference is not clear in the figures. Are the authors sure that the difference is not too weak to suggest intraspecific variability.... ?

L452: The foramen aërum of *A. hulki* is small, like *A. precedens* and *A. subjuniperus*, but large in *A. palustris*. Not significantly larger in *A. palustris* (evident compared with *A. subjuniperus* below). More probably individual variations.

A: There is a large foramen in *A. palustris* (Blanco et al., 2014: “Medially to the foramen and boss, there is a large foramen aërum on the dorsal surface of the quadrate”). Moreover, the codification of other *Allodaposuchus* species exceeds the aim of this paper. This character was found as phylogenetically informative (Brochu, 2011; Ch. 178) and there is not evidence to date for an individual variation of this character in the literature. If yes, we would acknowledge that the reviewer could provide literature demonstrating this variability.

I would acknowledge that the authors could demonstrate a **clear** difference between the foramen aereum of *A. palustris* and *A. subjuniperus* below..... (maybe it exists, but it is not clear for me...).

Again, the authors answer with a description. Here it is a comparison. One author can describe a foramen as large, when another would describe a foramen of same size in another specimen as small, if they do not compare the foramens between both species.



Do the authors need literature to consider weak differences as possibly intraspecific variabilities ? Literature on this specific character does not exist, of course, but I recommend the authors to improve their knowledge on extant species.... I saw several specimen with absent foramen aereum on one side, and a small one on the other... To be considered as possibly diagnostic, the difference must be clear. It is not the case here. It is possible that it exists, but the authors have to demonstrate it.

“This character was found as phylogenetically informative”:

I did not contest this. Just how it is coded in some species (I don’t know how it is coded in the present specimen and *A. palustris*). It is huge in *Eosuchus*, and difference with other crocodylians is clear. It is much larger than in *A. palustris*, and I think, that it would not be coded as huge in *A. palustris*. The important thing to know is : how it is large compared to the foramen aereum of other species ? and compared to *Eosuchus* ? I think its size is closer to this observed in other *Allodaposuchus* than to this observed in *Eosuchus*.... And is the difference in size between *Allodaposuchus* species can allow to exclude variability.

“Moreover, the codification of other Allodaposuchus species exceeds the aim of this paper.”:

On the contrary, it is particularly important as you propose a phylogenetic relationships of the *Allodaposuchus*, and codification of other *Allodaposuchus* species could have consequences on the relationships of the discussed species.

L465: Unlike *A. precedens* and *A. subjuniperus*, quadratojugal does not extend to superior angle of infratemporal fenestra. Due to poor preservation, the participation of the quadratojugal is not larger in *A. subjuniperus* than in the present form, and in *A. precedens* is not so longer.

A: Please, see above answer for a similar question of the reviewer (L149).

OK

L469: The dentition of *A. hulki* also shows several characters that distinguish itself from the other species of the genus. In *A. hulki*, the enamel lacks ornamentation, both anterior and posterior carinae are poorly developed, and

there are not longitudinal grooves in lingual side. In contrast, *A. palustris* and *A. precedens* show ornamented enamel with well-developed carinae, whereas *A. subjuniperus* and *A. palustris* bear well-marked longitudinal grooves in lingual side. First, the size of the carinae can vary according to the position of the tooth in the tooth row (as the ornamentation of the enamel). The tooth enamel of *A. subjuniperus* is described as smooth. Moreover, the ornamentation is weak, smooth in *A. palustris*, and micrometric in the apex, and the difference with the specimen described herein is probably not significant (micrometric ornamentation also ?). Differs only with those of *A. precedens* (considering the differences between the premaxillary and maxillary teeth...).

A: Please, see above answer for a similar question of the reviewer (Page 11).

Discussion

Phylogeny

L547: The most parsimonious hypothesis obtained in our analyses suggests that the clade ‘Allodaposuchia’ belongs to Crocodylia.....L567: would be a reverted state in the other members of the clade ‘Allodaposuchia’ (Blanco et al., 2014) : All this paragraph is nearly identical to paragraph from the discussion in Blanco et al., 2014.....! This paragraph is not clear ! It would be more useful to discuss the character distributions in the results obtained by the authors, according to the different position of the *Allodaposuchus* in the trees (unresolved position of *Allodaposuchus* in the consensus tree, but what are their distributions in the various trees obtained??? Which consequences on the character distributions and history ??). I do not understand if the characters listed in the paragraph are those that support the presence of *Allodaposuchus* within Crocodylia, or those proposed by Brochu ? How these characters are distributed in your trees ??

A: This paragraph just demonstrates that the results obtained are in agreement with the previous analyses performed by Brochu (2011) and Blanco et al. (2014). The position of *Allodaposuchus* in the tree are not unresolved. To discuss the position of the genus in all the other trees is illogical and no informative; the most important is the strict consensus tree. Additionally, to discuss the distribution and history of each character in the whole tree would extend the length of the paper and it is beyond of the scope of this study.

The position of the *Allodaposuchus* is not unresolved ? : “the clade ‘Allodaposuchia’ was included within Crocodylia, placed in a more derived position than Gavialoidea, and forming a polytomy with *Borealosuchus*, *Planocraniidae* and the clade *Brevirostres* (Crocodyloidea + *Alligatoroidea*)”

“To discuss the position of the genus in all the other trees is illogical and no informative”:

This is your opinion..... not mine. If “Allodaposuchia” is alternatively located close to *Brevirostre* or *Planocraniids*, it is not as if it is alternatively closely related to

Borealosuchus or Crocodylia (Gavialoids excluded).... This has consequences on the characters history.

“Additionally, to discuss the distribution and history of each character...”:

I was not clear in my review. Sorry. As your result strongly differs from the “classical” relationships of Allodaposuchus, which characters support the location of Allodaposuchus as more inclusive as in the “classical” view? (why your result differs from the “classical” view?). But the list of the characters supporting the “new” relationships is provided in the text.

Moreover, some of the characters cited are problematic:

3) frontoparietal suture concavo-convex: the suture is not concavoconvex in Allodaposuchus.

A: We understand that the different authors disagree between the different characters and its significance to decipher the relationships within Crocodylia. However, as previously noted, this character has been found informative in previous studies and the codification of this character (not only in the reported specimen) has been discussed in the literature and agrees with our matrix. See also the answer for the question of the L446.

See above.

1) slender postorbital bar: The postorbital bar is huge in Allodaposuchus.

A: We are sorry to disagree with the reviewer, but previous works (and the present one) demonstrate the morphology of the postorbital bar. We refer the reviewer to check Delfino et al. (2008) considered it as “slender” because, “although it is not as slender as in *Crocodylus cataphractus*, its thickness is far from the massive condition shown at maturity by *Gavialis gangeticus* (the only living taxon with a massive postorbital bar)”. Moreover, this character is only codified in *A. subjuniperus* and *A. precedens*, and the codification of others species exceeds the aim of this paper.

Absolutely! I was wrong here (don’t know why I wrote this !!)!! I apologize !

L573: supretmporal: supratemporal

L664: Crocodrylus: Crocodylus

A: We solved the above mentioned punctual comments in the revised version.

Comments to the editor

The two reviewers agree that your manuscript is interesting, but they also agree that several parts of it should be modified and improved. The major issue concerns your diagnosis of *Allodaposuchus hulki* and the limitation of the comparisons given the poor preservation of your material. The two reviewers actually question whether you truly have a new species in hand. At the very

least, you must provide a differential diagnosis that clearly tells in which features *A. hulki* is different from each other species of *Allodaposuchus*. You must also improve your comparative section, paying special attention to the possible effects of individual variations and poor preservation. If you are still confident that you can define a new species based on this material, you need to address these issues. Alternatively, you may want to consider Massimo Delfino's suggestion to not erect a new species based on this material and focus on the other morphological aspects of your study.

The two reviewers have done an excellent job and provided very detailed reports. I strongly urge you to revise your manuscript following their suggestions and comments. Your manuscript should also be checked by a native English speaker. Please, do not consider this last comment lightly. There are numerous issues with English in your manuscript.

We are grateful for most of the reviewer's comments and suggestions to this study. The aim of this paper is to describe a new specimen. A whole revision of the genus exceeds the goal of this study and of course we only can compare the new specimen with the published material. We would like to remark that unfortunately there are some unpublished material, also discussed by the reviewers but that cannot be considered to make comparisons until it will be published.

Concerning to the major issue of the revisions, we have reconsidered the possibility of intraspecific variation. In this way, all the characters were carefully checked again. The first author studied in first hand the type material of *A. precedens* (Budapest) and *A. subjuniperus* (Huesca). However, intraspecific variability is poorly studied among fossil (and many extant) crocodylomorph and particularly in *Allodaposuchus*. Unfortunately to date any study focused in the intraspecific variability, although surely could be of great interest, and don't discard to work on this issue in a future work, following the reviewer suggestion. Nonetheless, in the present study it is not possible to consider and the morphological differences found in the new specimen represent in our opinion an interspecific variation that force us to erect a new taxon. In turn, many of these differential characters are phylogenetically diagnostic, according to previous studies (See Brochu 2011 and references therein).

We concur with the reviewers, particularly Dr. Massimo Delfino, that the previous version required a 'Differential Diagnosis' section to clarify the differences between our specimen and the other species. We think that the revised version improves this major concern of the revision and we followed most of the reviewer comments to address these issues.

Lastly, we also would like to annotate that the reviewer Stéphane Jouve disputes our scientific objectivity being in our opinion excessively critical and severe underestimating our codings of morphological characters. The reviewer also commented that he is currently working in the same genus, preparing a new study and sometimes claims that we should make comparisons with still unpublished material, which is impossible. We don't dispute the impartiality of the reviewer but we don't want to be in a conflict of interest due to the in progress study: the

reviewer underestimates our codings of morphological characters and, even sometimes, contradicts the published papers describing the other species.

Taking into account all these reasons we have been able to answer to the major comments of this reviewer, providing accurate answers to his queries, as well as, giving supporting literature. Except for this issue, we have corrected all other queries and comments provided for you as well as Massimo Delfino.

Detailed comments:

Diagnosis:

L166:

-“*Allodaposuchus* differs from all other eusuchians by the presence of the canalis quadratosquamosoexoccipitalis, or cranioquadrate passage, laterally open and represented by a sulcus (broader than in *Hylaeochampsia vectiana* Owen).”:

Should not be included in the diagnosis of the new species.

-“*Allodaposuchus hulki* differs with *Allodaposuchus palustris* in having a linear frontoparietal suture” :

As discussed above: the frontoparietal suture is equally concave (or linear) in both species.

-“*a small foramen aëreum*”

Is this difference exclude intraspecific variability ? I am not sure.

-“*lacking false-zipodont teeth*”.

Not sure this could be asserted with only two dentary teeth.

-“*Allodaposuchus hulki* differs with *A. subjuniperus* in having the incisive foramen abutting premaxillary tooth row, located between the first and second alveoli,”

-“*the premaxillary-maxillary suture does not reach the incisive foramen*”

The suture does not reach the Fi in *A. subjuniperus*. It would be better to consider a shorter distance between the posterior margin of the FI and the suture.

-“*external naris opened in anterodorsal direction,*”

-“*no elevation around the rim of external naris*”

As the rim is described as “slightly elevated” in *A. subjuniperus*, it would be due to intraspecific variability. (some crest are absent or present in extant species, depending on the age/sex or individuals).

-“*absence of interorbital ridge*”

I don't think that its presence anterior to the preserved portion of the specimen can be excluded with certainty.

-“*a very large medial jugal foramen,*”

Puertolas et al., 2012 wrote: “A large medial jugal foramen placed anteriorly to the postorbital bar is not visible due to the poor preservation of this area.”

Consequently this character must be excluded.

-“*quadratojugal spine nearly absent and located near of the ventral angle in the infratemporal fenestra,*”

-“*medial articular hemicondyle of the quadrate without ventral expansion*”

In my opinion, the difference is too weak to exclude intraspecific variability.

-“*and teeth without longitudinal grooves in lingual side.*”

Not sure this could be asserted with only two teeth.

-“*Allodaposuchus hulki differs with A. precedens in having the premaxilla wider than long with four teeth positions, being the third the largest, a smaller and key-shaped external naris,*”

-“*no elevation around the rim of external naris,*”

See above.

-“*incisive foramen located between the first and second alveoli,*”

-“*dermal bones of skull roof overhanging supratemporal fenestra rim,*”

-“*two crests in the ventral surface of the quadrate without association of any tubercle,*”

-“and capitate processes of laterosphenoid anteroposteriorly oriented,

Anteroposteriorly oriented in the Holotype of *A. precedens*.

-“and teeth with smooth enamel.”

Not sure this could be asserted with only two teeth.

-“Allodaposuchus hulki shows the following autapomorphies: Quadratojugal does not extend along the infratemporal fenestra.”

Along the dorsal margin of the fenestra, or quadrate participates to the fenestra would be better ?

-“Spine of quadratojugal significantly reduced.”

Should be excluded from the diagnosis. The QJ spine is unknown in *A. precedens* (“*There is no indication of a quadratojugal spine owing to preservation.*” Buscalioni et al., 2001; “*The development of the quadratojugal spine ... cannot be evaluated due to its incompleteness*”, Delfino et al., 2008; “*The occurrence of a spine is impossible to establish because the bone is broken at this level.*”, Martin et al., 2010), and both species are described as sister taxa. This reduced spine could be a *A. precedens/A. hulki* synapomorphy. Moreover, as the shape of the spine is unknown in other *Allodaposuchus* (except in *A. subjuniperus*), it is not possible to know if on the contrary, the long QJ spine is a *A. subjuniperus* autapomorphy, and the short spine an *Allodaposuchus* plesiomorphy.

-“Absence of fossa or shelf at anteromedial corner of the supratemporal fenestra.”

Plesiomorphic for *Allodaposuchus* (see above)

-“No ridge surrounds the foramen aëreum.”

Weak ridge in other *Allodaposuchus*, and the difference is so weak, that I recommend to the authors, as Massimo did it, to consider it as intraspecific variation.

-“Teeth bear smooth enamel, low-developed mesial and posterior carinae, and absence of longitudinal grooves in lingual side.”

Only two teeth herein, and poorly known teeth in other species (Carinae present in isolated teeth of cf *A. precedens*).

-“Aside of the previous characters, A. hulki has the following ambiguous autapomorphies:

-“Spine of quadratojugal significantly reduced. No ridge surrounds the foramen aëreum.”

Both characters are included in the list of autapomotrphic characters.....

-“Anterolateral, anteromedial and olecranon processes of the ulna well developed. Ulnar shaft lateromedially compressed with lateral and medial grooves. Distal condyles of the ulna turned lateroposteriorly, causing a lateral crest in the shaft. We prefer coding all these autapomorphies as ambiguous, due to the absence of these characters in other species of Allodaposuchus and probable variability concerning to the ridge surrounding the foramen aëreum. New discoveries may reveal if they are autapomorphies of A. hulki or sinapomorphies of the genus.”

Ok, but as it is not possible to know if these characters are autapomorpies for the species or genus, they should also be excluded from the ambiguous autapomorphies. (they are discussed and described elsewhere in the text).