

## INTRODUCTORY NOTES

I enjoyed reading this well-written and well-illustrated MS and would like to congratulate the authors on their work.

The descriptive work within this paper is comprehensive, and only restricted by the crushed preservation of the specimen. I appreciate the careful taxonomic approach of (i) not naming a new species on the basis of the new material based on the probability that the skull pertains to *Hyaelochelys*, but also (ii) being careful about the referral to *Hyaelochelys*, which is otherwise only known from postcranial material (i.e. there is no overlap in material that could provide concrete evidence for the referral). The authors perform a phylogenetic analysis, and their usage of the Evers & Benson (2019) matrix over alternatives is well reasoned and explained. Comparative descriptive comments as well as their phylogeny support the systematic identification of their new material as belonging to the Thalassocheilydia. Re-running their deposited matrix reveals the exact results as presented in this paper. The deposition of the 3D model of the cranium is much appreciated, facilitated easy review, and will be useful for future systematic work including this taxon.

The comparative work aimed to distinguish the new specimen from paracryptodiran turtles reveals some interesting observations on the latter group. This extra bit of information makes the present paper relevant beyond thalassocheilydian anatomy and systematics.

I have a few specific comments, and also very few general comments that I would like to see addressed. All of those are outlined below. However, all potential changes to the manuscript are very minor, so that I hope that this paper can be published in due course.

With best regards,  
Serjoscha Evers

## GENERAL COMMENTS

### Carotid description of new skull

In the descriptive section of the features related to the carotid circulation, it would be nice if the authors differentiate the patterns for thalassocheilydians a bit more clearly. For instance, the ventrally exposed groove for the internal carotid artery is compared to other thalassocheilydians by stating: "This is clearly reminiscent of the condition in some thalassocheilydians, such as *Plesiochelys etalloni*, *Plesiochelys bigleri*, and *Jurassichelon oleronensis* (Gaffney, 1976; Rieppel, 1980; Anquetin et al., 2015; Püntener et al., 2017)." However, this list disregards variation among thalassocheilydians: Although the arteries are indeed exposed in a trough in *Plesiochelys bigleri* and *Jurassichelon oleronensis*, the course of the internal carotid is ventrally entirely covered by bone in *Portlandemys* (Gaffney 1975) and *Neusticemys* (Gonzalez-Ruiz et al. 2019) [and also *Solnhofia*, although this taxon probably is a sandownid rather than a 'true' thalassocheilydian], whereas it seems largely

embedded in *Plesiochelys planiceps* (own observation; but see also works of Gaffney). The situation in *Plesiochelys etalloni* may be variable across specimens, but at least in NMS 40870, the artery lies in a trough anteriorly, but is posteriorly embedded, so that in this specimen, technically a fenestra caroticus (sensu Rabi et al. 2013) is present.

I would recommend that the authors include these additional taxon/specimen citations, because only the full list gives an unbiased view on the variation that is present within thalassochelydians.

Additionally, I would suggest to cite Raselli & Anquetin (2019) in this section, as that paper specifically compares at least some aspect of carotid variation among plesiochelyids.

### **Paracryptodiran carotid system**

I appreciate the comments of the authors regarding the paracryptodiran carotid system, because they align well with my own observations. The forward position of the fpcci (i.e. the posterior foramen for the internal carotid artery) has long been stated as basically the only synapomorphy of paracryptodires (i.e. some concept of baenids + pleurosternids). I agree with the authors, however, that the pleurosternids system is quite different from that of baenids, and that the proposed and often-cited synapomorphy is indeed not present.

It would be interesting if the authors could comment on potential consequences of this observation. In my latest phylogenetic developments of the Evers & Benson (2019) matrix (not yet published), I fail to retrieve a monophyletic Paracryptodira, and upon checking the literature, there are actually very few global studies that do 'manage to get' a monophyletic Paracryptodira (and they all include the erroneous synapomorphy of the carotid system). Do the authors think that they're carotid observations have any consequences for paracryptodiran relationships, and if so, how?

### **Additional citations**

I have suggested a few additional citations throughout my comments, but I want to highlight that I think the cranial description of *Neustiqemys neuquina* (Gonzalez Ruiz et al. 2019; Journal of Palaeontology, doi: 10.1017/jpa.2019.74); the paper discussing carotids in some specimens of *Plesiochelys* (Raselli & Anquetin. 2019. PLoS ONE 14(5): e0214629); one or several papers for protostegid comparisons regarding the laterally open foramen palatinum posterius (e.g. Williston 1898; Hirayama 1998; Kear & Lee 2006; Cadena & Parham 2015; Raselli 2018; Evers et al. 2019); and possibly the recent cranial description of *Sandownia harrisi* (Evers & Joyce. 2020. Royal Society Open Science 7: 191936) could be cited.

For full disclosure, the *Sandownia* paper is a recent paper of mine, and the authors could not have known of this paper when they prepared the MS at hand. So I consider this an optional additional citation.

### **SPECIFIC COMMENTS**

In line 96, the authors write “For a recent reassessment of basal paracryptodire taxonomy, the reader is referred 96 to Joyce and Anquetin (2019).” I disagree with the use of the word ‘basal’ here: The primary comparisons listed in this section are *Glyptops* and *Pleurosternon*, both members of the Pleurosternidae. Pleurosternids are most commonly inferred to be the sister-group to baenids. However, as the sister to baenids they are no more ‘basal’ than baenids themselves. I think this problem can be easily circumvented by using ‘non-baenid paracryptodire’ or ‘pleurosternid’ instead of ‘basal paracryptodire’.

Line 243ff: Regarding the jugal description, the authors do not comment about whether a medial jugular process is present or absent. This process is commonly absent in plesiochelyids or thalassochelydians, and it seems that this is also the case here, although the region is obscured by crushing... It would be nice if the authors could specifically comment on this feature and its preservation.

Line 280/281: The usage of ‘arms’ in respect to the diverging rami of the maxillae is somewhat unusual, and I recommend rephrasing the sentence.

Line 282: The authors describe the lingual ridge of the maxilla to be ‘serrated’. I have checked the images and the 3D file, and know what is meant. However, the pattern is a bit irregular on both skull sides, and serrations immediately remind of testudinid-like structures that are present in the rhamphotheca. Do the authors think that the observed ‘serrations’ are features that would have been mirrored in the horny beak, or are those simply roughened areas of bone, possibly linked to the innervation and blood supply of the beak? It would be nice to comment on this with one or two sentences.

In line 306, the authors note that “The foramen supramaxillare opens in the posterior part of the orbit floor along the suture between the maxilla and jugal (visible only on the left side)”. This is interesting, because we recently described this foramen to be within the jugal of *Sandownia harrisi* (also an angolachelonian; Evers & Joyce 2020). The foramen supramaxillare is usually fully and clearly formed by the maxilla, so the position of this foramen here in comparison with *Sandownia* is intriguing. I leave it open if the authors want to include a comparison with *Sandownia*, as it is a paper of my own, and as it only came out so recently that the authors could not have included this particular comparison a few weeks ago.

line 310: ‘excepting’ seems to be linguistically incorrect in this instance. I would suggest using ‘with exception of’ instead.

Line 315 ff: Palatine description. The presence/absence of an interpalatine/vomer-pterygoid contact is only briefly mentioned in the section describing the pterygoid. The authors seem to infer that an interpalatine contact is absent. This has also been described for many thalassochelydians (e.g. *Neusticemys*; Gonzalez-Ruiz et al. 2019; see also Gaffney 1975), but not for all (e.g. *Plesiochelys planiceps*: Gaffney 1975). Given that the respective sutures are difficult to see in the specimen at hand, it would be good of the authors discuss this particularly possible contact, or their interpretation thereof, in a bit more detail here, possibly citing the above studies that provide evidence for variation of this feature in thalassochelydians.

In line 327, the authors write “It is known only in some thalassochelydians (*Plesiochelys* spp. and *Jurassichelon oleronensis*) and some early pan-chelonioids, whereas modern sea turtles lack the foramen altogether (e.g., Gaffney, 1976; Joyce, 2007; Anquetin et al., 2017)”. I think it would be helpful to cite instances of pan-chelonioids that have the feature of the ‘open’ foramen palatinum posterius. Citing instances would be important, because the feature is not present in ‘random’ pan-chelonioids, but in protostegids (e.g. Williston 1898; Hirayama 1998; Kear & Lee 2006; Cadena & Parham 2015; Raselli 2018; Evers et al. 2019). Protostegids have repeatedly been hypothesized to be closely related to thalassochelydians (e.g. Joyce 2007; but many others), so that this comparison is highly relevant to both the positions of thalassochelydians and protostegids – both of which are debated.

Line 351: The infolding ridge of the quadrate is also present in sandownids, and not only in thalassochelydians (Evers & Benson 2019; Evers & Joyce 2020).

Line 383: ‘briefly’ is usually a term used for durations. I would recommend something like ‘along a short contact’

line 544: the word ‘sterile’ seems misplaced in this context; maybe exchange with something like ‘ascertained’?

line 568: you could delete the ‘somewhat’; the conclusion is definitely supported by your results.

line 568: Please include a figure reference to Fig 6. here.