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The braincase of *Syllomus aegyptiacus* Lydekker, 1899 (Reptilia, Testudines) from the Middle Miocene Calvert Formation of Virginia

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Abstract

The braincase of the marine turtle *Syllomus aegyptiacus* (Calvert Formation, Virginia, Middle Miocene) is described and figured in detail for the first time. It reveals a ventral crest on the basisphenoid, a high dorsum sellae, an almost subequal diameter of the canals for the internal and lateral carotid arteries at a cross break and a canalis caroticus lateralis and internus that are still far separated from each other at level of the dorsum sellae. The braincase is compared to other known braincases of fossil and extant chelonioid turtles.

Keywords: Celoniidae, Chelonioidea, *Syllomus*, braincase, Miocene, U.S.A.

1. Introduction

Sea turtles are an important group of fossil marine reptiles that are found in almost all marine vertebrate assemblages since their first appearance in the Early Cretaceous. They were first mentioned by Camper (1786) and since that time many studies about fossil marine turtles have been published. Due to their intricate sutures, turtle skulls are usually preserved in articulation and therefore the skulls only expose their external surface in most of the available specimens. Hence, information on braincase anatomy is often quite limited. Characters of the braincase are highly significant for the analysis of phylogenetic relationships in fossil turtles (Gaffney 1979; Hirayama 1994; Matzke 2009; Parham & Pyenson 2010; Cadena & Parham 2015; Evers & Benson 2018). In fossil marine turtles adequate data on braincase anatomy are only available for a limited number of genera, including *Toxochelys* (Zangerl 1953; Matzke 2009), *Ctenochelys* (Zangerl 1953; Hirayama 1994, 1997; Gentry 2016; per. obs.), *Corsochelys* (Zangerl 1960; pers. obs.), *Desmatochelys lowi* (Hirayama 1994), *Euclastes* (Fastovsky 1985; Hirayama & Tong 2003), *Pacifichelys* (Parham & Pyenson 2010), *Puppigerus* (Moody 1974), and *Eochelone* (Casier 1968). Since the advent of CT-scans as a palaeontologcial method to elucidate intricate anatomical structures not usually available for observation, information on internal structures of the skull also became available for *Nichollsemys* (Brinkman et al. 2006), *Mexichelys* ('*Euclastes*' *coahuilaensis* Brinkman et al. 2009) and *Cabindachelys* (Myers et al. 2017). Recently another new phylogeny of all turtles was published (Evers & Benson 2018) that is mainly based on CT-scans of 59 turtle taxa, most of them unpublished so far. We are looking forward to the osteological descriptions of this material.

The purpose of this paper is to provide additional descriptions of the braincase, especially the dorsal surface of the basioccipital and basisphenoid, of *Syllomus aegyptiacus* based on the partial skeleton USNM 187382, originally described in considerable detail by Weems (1980). For discussion on taxonomy and description of the other preserved parts of this specimen, we refer to Weems (1980).

Institutional abbreviations: USNM – National Museum of Natural History (formerly: United States National Museum), Washington, DC, U.S.A.; BMNH – British Museum of Natural History, London, U.K.

Abbreviations used in the illustrations: VI = foramen nervi abducentis, VII = foramen nervi facialis, VIII = foramen nervi acustici, XII = foramen nervi hypoglossi, bo = basioccipital, bsp = basisphenoid, btb = basis tuberculi basalis, ca = canal, cci = canalis carotici interni, ccl = canalis caroticus lateralis, cea = cerebral artery, con = condylus mandibularis, cpt = crista pterygoidea, doo = dorsal oval opening at the pterygoid, ds = dorsum sellae, ex = exoccipital, fj = foramen jugulare, fperi = fenestra perilymphatica, g = groove, ha = hiatus acusticus, ica = internal carotid artery, lc = left crest on basisphenoid enclosing the groove in front of the dorsum sellae, lhv = lateral head vein, opi = opisthotic, pcl = processus clinoideus, pro = prootic, pt = pterygoid, q = quadrate, qj = quadratojugal, rc = right crest on basisphenoid enclosing the groove in front of the dorsum sellae, pi = processus interfenestralis, so = supraoccipital, su pro = sutural facet for prootic, su pt = sutural facet for pterygoid.

Anatomical nomenclature: Throughout this paper the anatomical terminology of turtles established by Gaffney (1972) is followed and therefore the foramen anterior canalis carotici interni = foramen anterior canalis caroticus cerebralis.

2. Systematic palaeontology

Testudines BATSCH, 1788

Cryptodira COPE, 1868

Chelonioidea BAUR, 1893

Cheloniidae OPPEL, 1811

Syllomus LYDEKKER, 1899

Holotype: BMNH R229, partial carapace.

Referred material: USNM 187382 *Syllomus aegyptiacus* almost complete skull with lower jaw and associated postcranial material, including an incomplete carapace and a humerus (WEEMS 1980).

Locality of referred specimen: Plum Point Member, Calvert Formation, Zone 14a, Bluff on the Morris Property, six miles west of Bridge's Creek-Wakefield, Westmoreland County, Virginia, Middle Miocene, U.S.A., collected by MYRICK in 1968.

3. Description

The skull of USNM 187382 is preserved in several parts. The posterior part of the skull is preserved in two pieces which came apart mostly along their sutures, however most of the bones are somewhat damaged. The right part consists of the basioccipital, basisphenoid, exoccipital, opisthotic, prootic, pterygoid and quadrate. The left part consists of exoccipital, supraoccipital, opisthotic, prootic, pterygoid and quadrate. Both parts of the skull are heavily covered with glue and therefore some areas are difficult to interpret.

Basioccipital: The basioccipital is complete. Posteriorly it forms the ventral part of the condylus occipitalis. Laterally the basioccipital is sutured to the right exoccipital. In ventral view, its anterior outline is semi-circular. The main body of the basioccipital is slightly larger than that of the basisphenoid. In dorsal view, the posterior part of the basioccipital narrows triangularly and clearly separates the exoccipitals. The central and posterior parts of the basioccipital are flat and slightly concave respectively. In its anteriormost part the short crista dorsalis basioccipitalis starts which rapidly develops into a rather prominently raised and drawn-out basis tuberculi basalis of oval shape (Fig. 1A, B). A pronounced ridge forming the edge of the basis tuberculi basalis runs on both sides along the anterior and lateral margin of the dorsal surface of the basioccipital and disappears at level with the entrance of the foramen jugulare anterius. At both anterolateral parts the basioccipital forms part of the floor of the hiatus acusticus (Fig. 1A, B). The basioccipital contribution is slightly larger than that of the basisphenoid.

Basisphenoid: As pointed out by WEEMS (1980), the anterior part of the basisphenoid anterior to the dorsum sellae is missing. The posterior part is, however, well exposed from all sides. In ventral view, the basisphenoid is triangular. Two anteriorly rounded, semicircular shaped ventral crests are exposed in its centre in contrast with most other chelonioid turtles where a V-shaped ventral crest is present.

In dorsal view, the remaining posterior part is roughly rectangular and quite thick. In the centre of its posterior part a low but pronounced crista dorsalis basisphenoidalis is exposed which runs anteriorly half way towards the dorsum sellae. Posteriorly the crista leads towards a remarkably shallow basis tuberculi basalis of the basisphenoid that is very small if compared to the one formed by the basioccipital. Just posteriorly to the processus clinoideus the foramen nervi abducentis is visible (Figs. 1, 2). Its anterior exit foramen is covered in dorsal view by the anterolaterally orientated processus clinoideus. The processus clinoideus is quite prominent and situated very close to the dorsum sellae. Its shape is elongated-oval with a blunt end and a broad base. The dorsum sellae is high. However, no anterodorsal process is found, instead a deep groove is leading down towards the missing rostrum basisphenoidale. This groove or channel starts quite narrowly between both processus clinoidei and widens on its way down (Figs. 1, 2).

In left lateral view, the basisphenoid is completely visible and the pterygoid and prootic sutures are exposed. The foramen nervi abducentis anterior is quite large. It faces more laterally than anteriorly and is situated directly below the processus clinoideus. Posterolaterally to the processus clinoideus the rather small sutural facet for the prootic is visible. The largest sutural facet (at least in lateral view) is with the pterygoid (Fig. 1). Both bones together form the canalis caroticus internus. The part that is formed by the basisphenoid is well exposed and runs posteriorly to the level of the missing foramen anterius canalis carotici interni. However, in its anteriormost preserved part a cross section of a very small canal is visible leading from the large canalis caroticus internus up towards the sella turcica. This canal (Fig. 1) is for the cerebral carotids and would lead towards the missing foramen anterius canalis carotici interni (= cerebralis). This feature is better exposed on the left side of the basisphenoid (Fig. 2).

Canalis carotici interni & canalis carotici lateralis: In anterior view of the posterior part of the skull, the remains of the basisphenoid and the cross sections of the two canales are well visible. The left canalis caroticus lateralis is well exposed. It is formed in equal parts by the basisphenoid and the pterygoid at least at the level of the crista pterygoidea of the pterygoid and the processus clinoideus. At this level, just posterior to the foramen nervi abducentis anterior, the canal starts to bend ventrally and is more medially directed. The canal for the internal carotid artery is seen on both sides. On the right side, the canal is well exposed at the basisphenoid. There the internal carotid artery runs anteromedially and at the level of the fracture a channel (for the cerebral carotid) is branching off the main artery and runs dorsomedially towards the groove that is coming down from the dorsum sellae (Fig. 2). The diameter of the cerebral branch of the internal carotid artery is about half the size and therefore we assume that the cerebral and lateral branches are subequal in size.

In mediolateral view of the left pterygoid (Fig. 3), the canal of the internal carotid is well exposed. It is anteriorly equally formed by the basisphenoid and pterygoid (Figs. 1C, D, 3). Just behind the level of the crista pterygoidea, an opening is located at the dorsal surface of the pterygoid, close to the sutural facet for the prootic and it seems that it is formed exclusively by the pterygoid. This dorsal opening is quite large, elongated and definitely connected to the anteriorly exposed canal of the internal carotids. Due to the moderate preservation of the interior structures of the braincase and the fenestra ovalis it is difficult to interpret, but we are confident that it is in fact a dorsal opening

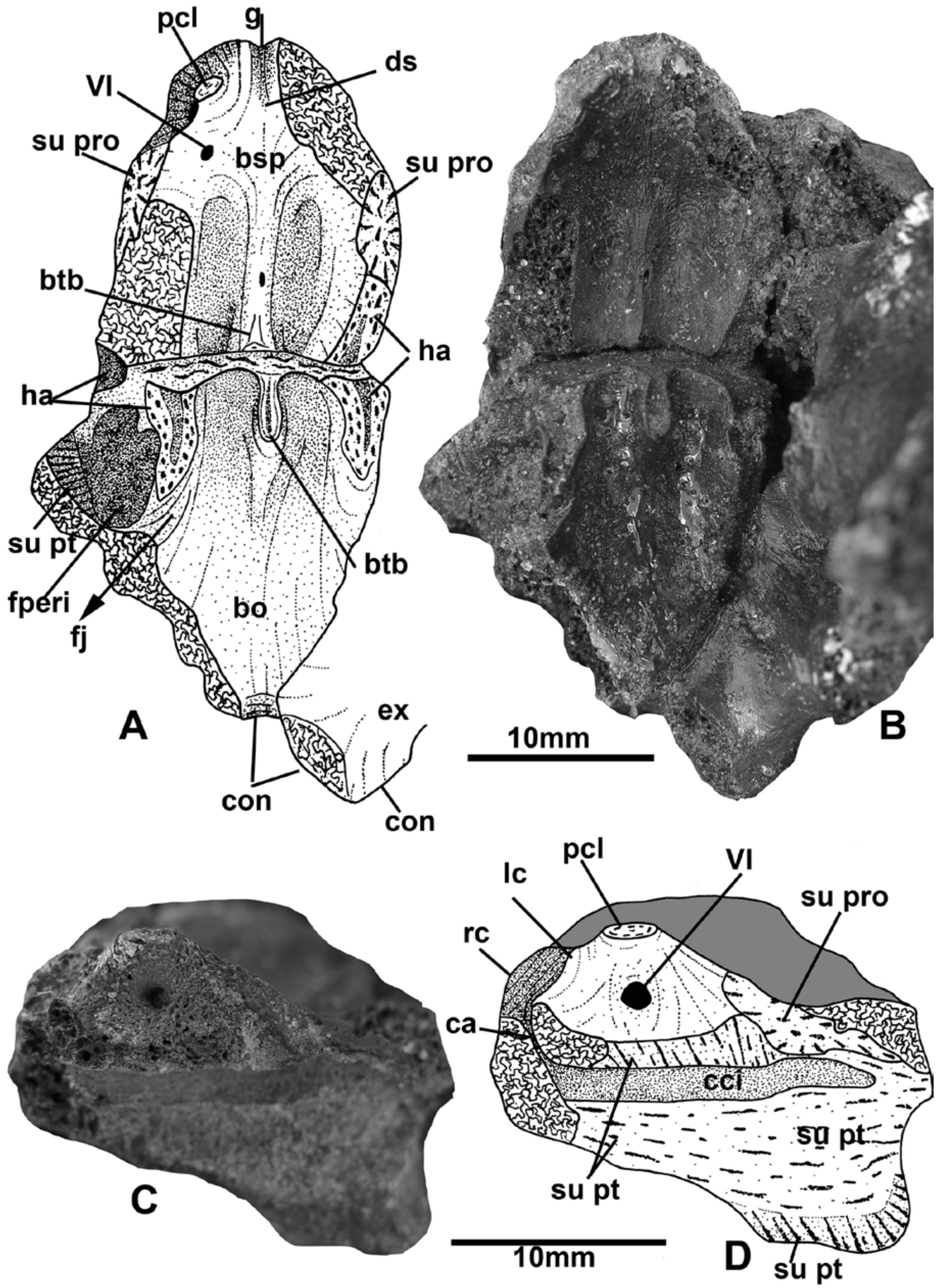

Fig. 1. *Syllomus aegyptiacus* LYDEKKER, 1899; USNM 187382. **A**, **B**: Drawing and photograph of the basisphenoid and basioccipital. **C**, **D**: Photograph and drawing of the basisphenoid in lateral view. Scale bar equals 10 mm.

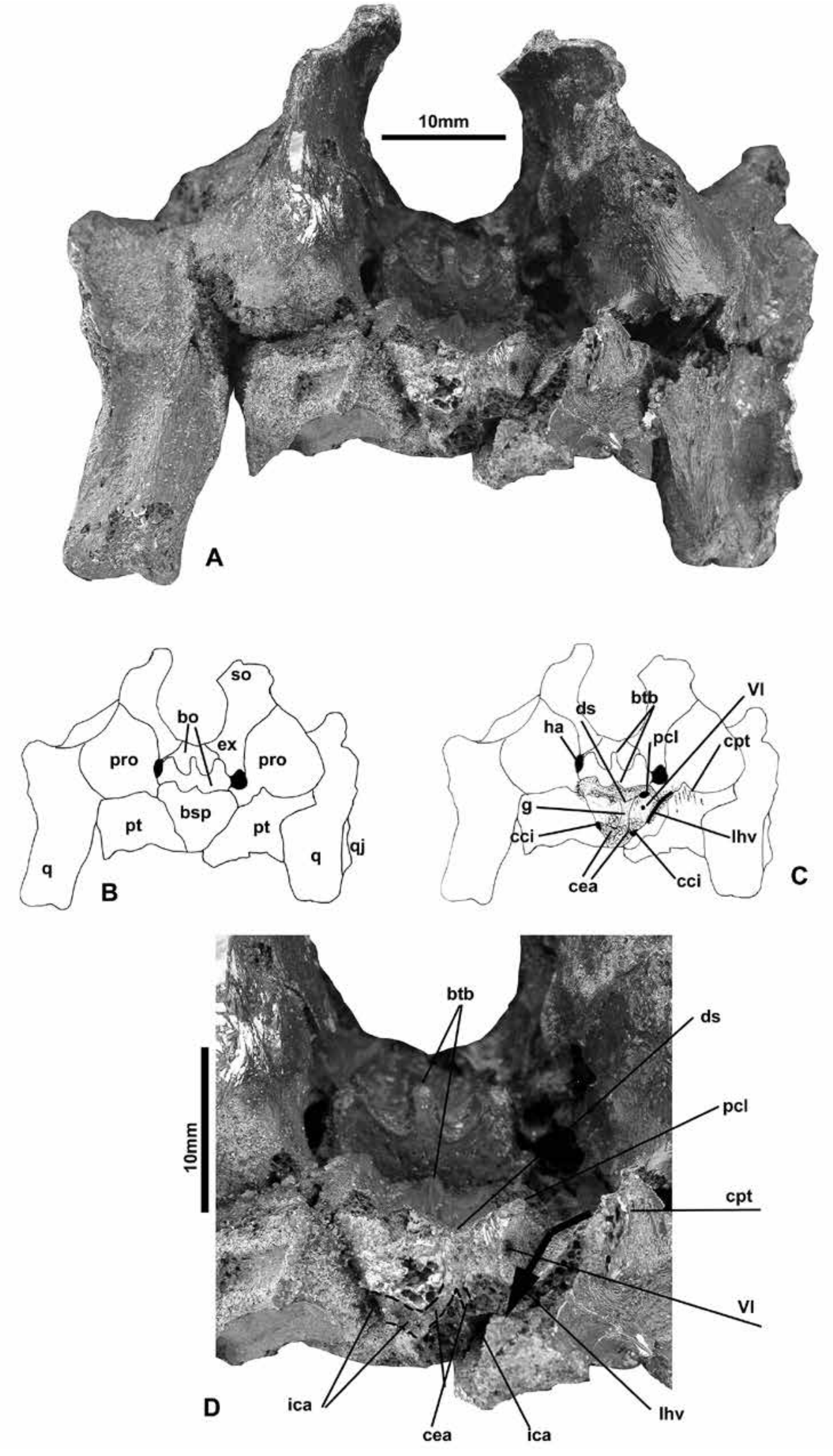

Fig. 2. *Syllomus aegyptiacus* LYDEKKER, 1899; USNM 187382 **A**, **D**: Photograph of the anterior view of the skull with the cross section of the basisphenoid. Scale bar equals 10 mm. **B**, **C**: Sketch of the anterior view of the skull and braincase, not to scale.

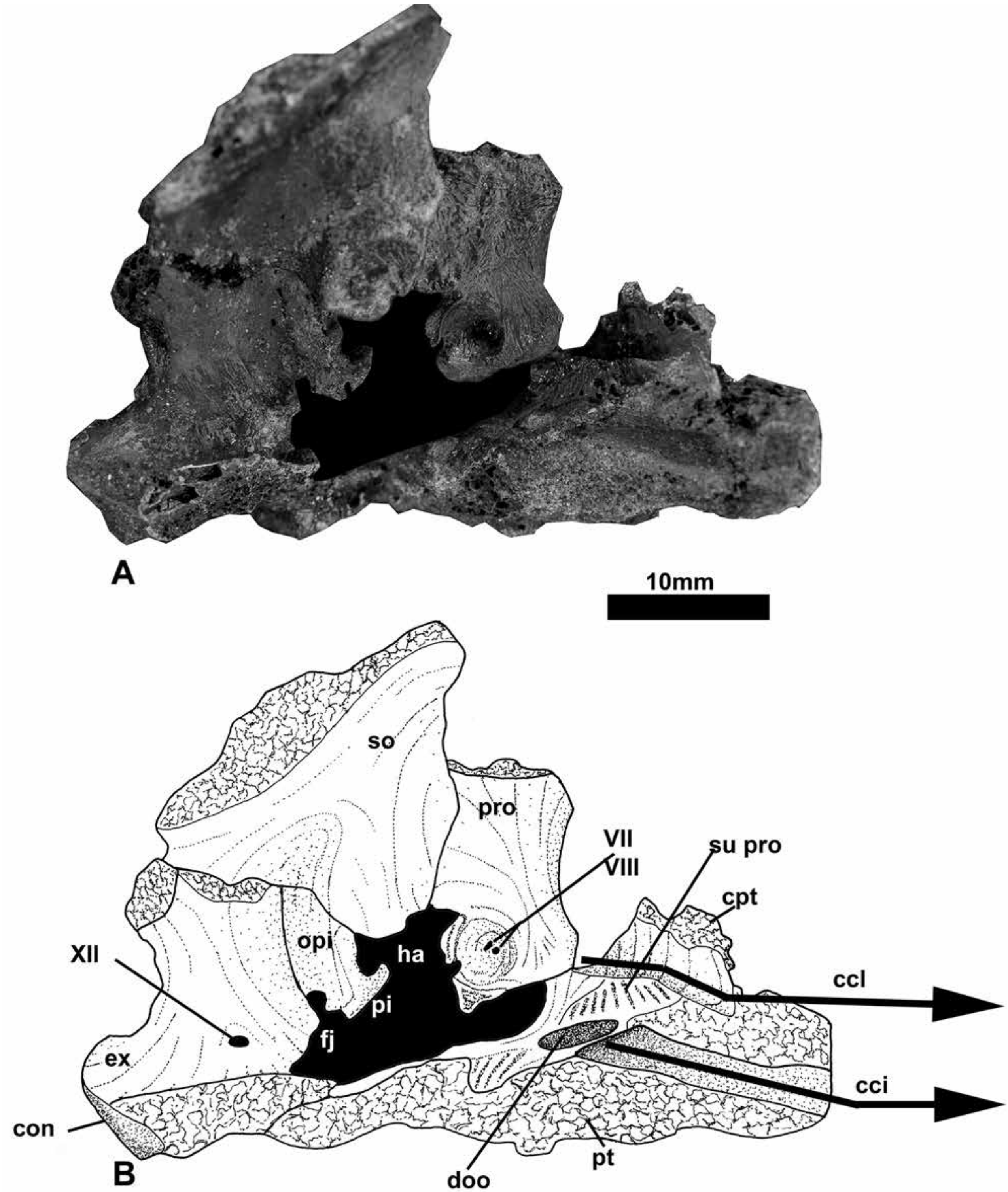

Fig. 3. *Syllomus aegyptiacus* LYDEKKER, 1899; USNM 187382. **A**: Photograph of and **B**, drawing of mediolateral/ sagittal view of the braincase with the hiatus acusticus. Scale bar equals 10 mm.

of the canal for the internal carotids (that usually runs entirely through the pterygoids in extant cheloniids).

At the anterolateral part of the pterygoid (Figs. 2, 3), the canal (canalis cavernosus) for the lateral carotid artery is visible and partially covered by the crista pterygoidea of the pterygoid that extends dorsally and usually contacts the epipterygoid and/or parietal. Anteriorly, at the mediolateral margin, the sutural facet for the basisphenoid is exposed. At the level of the fracture, the canalis carotici lateralis (ccl) and interni (cci) are still separated far from each other (Figs. 2, 3) by a relatively thick bar of bone. Therefore, it is highly likely that both canals are still separated from each other while running anteriorly. This is in contrast to extant chelonioid turtles.

Left lateral wall of the braincase with the hiatus acusticus: In Fig. 3 the left lateral part of the braincase is exposed almost like a sagittal section, with the exoccipital, pterygoid, opisthotic, prootic and supraoccipital visible in median view. Only one of the foramina nervi hypoglossi of the exoccipital is visible medially. The anterior margin of the exoccipital forms the posterior wall of the foramen jugulare anterius. The foramen is formed by the opisthotic anteriorly. It is clearly visible that the ventral part of the foramen jugulare anterius its anteroventrally open and not enclosed by bone. Only a very small part of the opisthotic is visible in medial view and it is by far the smallest bone (Fig. 3). The anteriormost tip of the opisthotic, the processus interfenestralis, leads towards the hiatus acusticus. Posterodorsal to the anterior tip of this processus inside the fenestra ovalis a small emargination is visible which most likely represents the foramen medialis nervi glossopharyngei. The prootic is a rather large element in medial view. Together with the pterygoid it forms the canalis caroticus lateralis. On the posteroventral part of the prootic an almost circular depression is visible. Within this depression are two foramina, interpreted here as the foramen nervi acustici and the foramen nervi facialis. The opisthotic, supraoccipital and the prootic together form the dorsal part of the hiatus acusticus, however, due to the preservation of the specimen no detailed information could be gained.

4. Comparisons

Comparison of the braincase of *Syllomus* to other braincases of fossil and extant marine turtles is somewhat problematic. As pointed out above, data on braincases of fossil marine turtles are limited and only in a few genera detailed descriptions have been published. For comparison to extant taxa we refer to Wegner (1959) for *Dermochelys*, Kensteven (1910) for *Chelonia mydas* and our personal observations on *Dermochelys*, *Chelonia*, *Caretta*, *Eretmochelys* and both species of *Lepidochelys* (Matzke 2008, 2009)

Basioccipital

S h a p e o f a n t e r i o r s u t u r e o f t h e b a s i o c c i p i t a l : The basioccipitals of fossil marine turtles are quite similar in ventral view. The suture with the basisphenoid is extensive and usually longer than the suture with either the pterygoid or the exoccipital. However, the shape of the anterior outline can vary. In *Syllomus aegyptiacus* (USNM 187382, Hasegawa et al. 2005), the suture is semicircular, similar to *Toxochelys* (Zangerl 1953; Matzke 2009), *Ctenochelys* (Zangerl 1953; Gentry 2016; pers. obs), *Nichollsemys* (Brinkman et al. 2006); *Puppigerus* (Moody 1974), *Euclastes* (Hirayama 1994, 1997), *Cabindachelys* (Myers et al. 2017), *Bouliachelys* (Kear & Lee 2006); *Desmatochelys lowi* (Elliot et al. 1997) and Recent cheloniids. The suture can also be only slightly curved anteriorly as in *Mexichelys* (Brinkman et al. 2009), almost straight as in *Desmatochelys padillai* (Padena & Parham 2015) or triangular as in *Eochelone* (Casier 1968) and in one specimen of *Toxochelys latiremis* (USNM 11560, Matzke 2009).

P r o p o r t i o n s o f t h e s i z e o f t h e b a s i o c c i p i t a l a n d b a s i s p h e n o i d : If the size of the ventral exposure of the basioccipital is compared to that of the basisphenoid it is clear that the basioccipital is much larger in *Toxochelys*, *Ctenochelys*, *Nichollsemys*, *Puppigerus*, *Eochelone*, *Euclastes*, *Caretta* and *Desmatochelys lowi* (compare Elliot et al. 1997: 248–249 to Fig. 2D. It is evident from the photograph that the basisphenoid is a small triangular bone and the pterygoid and basioccipital are in broad contact, which is well visible on the left side of the skull. In Elliot et al. 1997, fig. 3C, a drawing of the same skull, the suggested shape of the basisphenoid is therefore incorrect). The basioccipital is only slightly larger in *Syllomus*, *Mexichelys*, *Desmatochelys padillai*, *Cabindachelys* and the Recent marine turtles *Chelonia*, *Lepidochelys* and *Eretmochelys*.

B a s i s t u b e r c u l i b a s a l i s o n t h e b a s i o c c i p i t a l a n d b a s i s p h e n o i d : The basis tuberculi basalis are located at the anterior end of the basioccipital and the posterior end of the basisphenoid as counterparts. The size of the tuberculi is variable within marine turtles. In *Toxochelys moorevillensis*, *Ctenochelys acris* (Gentry 2016), *Nichollsemys* and *Syllomus* the basis tuberculi basalis of the basioccipital are much larger than the one on the basisphenoid. This is also the case in *Chelonia* and *Lepidochelys olivacea* (Matzke 2009). In *Rhinochelys* (Collins 1970), *Eochelone* (Casier 1968) and *Caretta* the one on the basioccipital is only slightly larger than the one on the basisphenoid. Both basis tuberculi basalis are equal in size only in *Toxochelys latiremis*, *Eretmochelys* and *Lepidochelys kempii* (Matzke 2009). In *Puppigerus* (Moody 1974) both tuberculi are reduced and in *Corsochelys* (the basioccipital is unknown) there is no tuberculus visible on the basisphenoid (Zangerl 1960, pers. obs.).

C r i s t a d o r s a l i s b a s i o c c i p i t a l i s : The crista dorsalis basioccipitalis is surprisingly variable within the chelonioid turtles. It is long and forms a sharp crest in *Toxochelys latiremis* and *Nichollsemys*. Whereas it is long, prominent, rounded and branching posteriorly in *Toxochelys moorevillensis*. In *Ctenochelys* (pers. obs.) and *Syllomus* it is long and rounded. A short or almost no crest is found in *Eochelone*, *Puppigerus*, *Caretta*, *Chelonia*, *Lepidochelys*, and *Eretmochelys*.

Basisphenoid

V e n t r a l c r e s t : On the ventral side of the basisphenoids of marine turtles, usually, a ventral crest is exposed which is of variable shape. In *Syllomus* two distinct almost semicircular crest are found - a condition unique in marine turtles. They are located further anterior to the suture with the basioccipital. A V-shaped crest is visible in *Bouliachelys*, *Toxochelys*, *Ctenochelys*, *Mexichelys* and *Puppigerus* that is located more anteriorly to the basisphenoid/basioccipital suture as well. A V-shaped crest that is very close to the suture to the basioccipital is exposed in *Nichollsemys*, *Eochelone*, *Desmatochelys lowi* and Recent turtles. In *Corsochelys* no crest is found, making it almost unique among marine turtles, with the exception of *Dermochelys* and *Desmatochelys padillai*.

Crista dorsalis basisphenoidalis: In dorsal view, the posterior part of the basisphenoid with the crista dorsalis basisphenoidalis and the dorsum sellae is variable in marine turtles. The crista dorsalis basisphenoidalis is completely absent in *Corsochelys* (ZANGERL 1960, pers obs.) as well as the basis tuberculi basalis. The crista dorsalis basisphenoidalis is less pronounced in *Puppigerus*, or moderately developed in *Dermochelys*, *Chelonia*, *Eretmochelys*, *Caretta* and almost absent in *Lepidochelys*. The crista is pronounced in *Toxochelys*, *Eochelone*, *Ctenochelys* (GENTRY 2016, pers obs.) and it extends further anterior up to the level of the foramen nervi abducentis. This is also the case in *Eretmochelys* but the crest is less pronounced. In an adult specimen of *Ctenochelys acris* (GENTRY 2016) the crest is similar to *Toxochelys*, but in a juvenile specimen the crista dorsalis basisphenoidalis is reaching up to the level of the dorsum sellae (GENTRY 2016). A crest that reaches the dorsum sellae is also found in *Nichollsemys*. In *Syllomus* the crest is well visible but not very pronounced and it clearly ends posterior to the foramen nervi abducentis.

Processus clinoideus: The processus clinoideus is large in *Puppigerus* (COLLINS 1970), *Toxochelys* (oval, MATZKE 2009), *Corsochelys* (very large and facing anteriorly, pers. obs.), *Caretta* (elongated, triangular with a sharp tip, MATZKE 2009) and *Lepidochelys* (elongated with oval tips, MATZKE 2009), but their shapes are quite different. The processus is small in *Ctenochelys* (pers. obs.), *Eochelone* (CASIER 1968), *Chelonia* (KESTEVEN 1910) and *Eretmochelys* (MATZKE 2009). It is present in *Nichollsemys* (BRINKMAN et al. 2006) but the exact shape remains unknown. The processus clinoideus in *Syllomus* is quite large with an elongated oval end facing slightly anterolaterally.

Dorsum sellae

The shape of the dorsum sellae is also variable. In *Ctenochelys*, *Toxochelys latiremis* and *Mexichelys* (BRINKMAN et al. 2009, fig. 4A) there is an anterior process overhanging the sella turcica. No process is found in *Eochelone*, *Corsochelys* and Recent cheloniids. A dorsum sellae with a small shallow groove is found in *Syllomus*, *Toxochelys moorevillensis*, *Ctenochelys*, *Puppigerus* (MOODY 1974) and *Eochelone* (CASIER 1968). In all these marine turtles the dorsum sellae is high.

Canalis carotici interni and canalis carotici lateralis

In *Toxochelys*, *Ctenochelys*, *Nichollsemys*, *Cabindachelys*, *Euclastes*, *Mexichelys*, and *Puppigerus* the exit for the canalis carotici interni and therefore the merging of both canals are situated anterior to the foramen anterius canalis carotici interni (cerebralis); whereas in Recent cheloniid turtles both canals are merged posterior to that level (MATZKE 2009).

In the *Syllomus* specimen discussed here the basicranium is broken off just in front of the dorsum sellae. However, at this level both canals are far separated by a bony wall formed by the basisphenoid and pterygoid. Therefore, the canal for the internal carotids and the lateral carotids were definitely separated at least up to the level of the foramen anterius canalis caroticus interni (cerebral artery) and in our opinion even further anteriorly (BRINKMAN 2009).

Size of foramen caroticum laterale and foramen anterius canalis carotici interni (=cerebralis)

In *Toxochelys latiremis* (MATZKE 2009) the foramen caroticum laterale (palatine artery) is much smaller than the foramen anterius canalis carotici interni, this is also the case in *Ctenochelys acris* (GENTRY 2016). In *Toxochelis moorevillensis* (MATZKE 2009) this character is variable. In *Nichollsemys* the foramen caroticum laterale is much larger than the foramen anterius canalis carotici interni, a condition also found in *Cabindachelys* (MEYERS et al. 2017), *Euclastes* (HIRAYAMA 1994) and Recent cheloniids.

As described the basisphenoid is broken off in *Syllomus*, however, at the fracture the cross section of the internal carotid artery is visible as well as the branching for the cerebral artery that will lead towards the missing foramen anterius canalis carotici interni. If we compare both cross sections, we can assume that the cerebral branch is about half the size of the internal carotid artery which leads to the assumption that the arteria palatina and the arteria carotica internus were both subequal in size. This is also the case in *Mexichelys.*

The anterior part of the canalis caroticus interni is formed by the pterygoid and basisphenoid in all marine turtles. Posteromedially to the crista pterygoidea just lateral to the anterior suture to the prootic a small foramen/opening is exposed at the dorsal surface of the pterygoid in *Syllomus*. This unusual foramen is connected to the canalis caroticus interni. Here we interpret it as a short dorsal opening of the canal that is similar but shorter to the one described for a juvenile *Ctenochelys* (MATZKE 2007). Unfortunately, this region of the skull is almost unknown or undescribed in all other fossil marine turtles. A quite similar but longer slit was described in a juvenile specimen of *Lepidochelys* (MATZKE 2008, text-fig. 4E).

5. Conclusions

For the first time the braincase of *Syllomus* is described in detail. Several interesting osteological features could be identified. The ventral crest on the basisphenoid that is usually present in chelonioid turtles is also present in *Syllomus*, but the shape is different. The dorsum sellae is high as in all marine turtles where this region is described. The shape of the dorsum sellae with a small groove leading at least partially down towards the sella turcica is found in *Syllomus* and surprisingly only in the more primitive chelonioid turtles *Ctenochelys* and *Toxochelys moorevillensis*. This character is also figured in Paleogene chelonioids such as *Eochelone* (CASIER 1968) and *Puppigerus* (MOODY 1974) and therefore it is a possibly primitive character for some cheloniids. The foramen anterius canalis carotici interni (cerebralis) are not preserved, but from what is visible, it is clear that they were close together and in front of the dorsum sellae. The foramen caroticum laterale is not preserved in *Syllomus*, but we have the cross sections and therefore it can be assumed that the arteria palatina and the arteria carotici internus are more or less equal in size. Also quite interesting is the fact that the canalis caroticus internus that runs anteriorly through the pterygoids towards the posterolateral end of the basisphenoid, is dorsally open for at least a few millimetres. This opening is at the exact location where the foramen posterius canalis carotici interni (cerebralis) is located in *Desmatochelys padillai* (CADENA & PARHAM 2015) ventrally. It is therefore possible, that in more advanced chelonioid turtles the internal carotid artery was first enclosed by the pterygoid in the posterior part and later more anteriorly.

At the anterior fracture of the basisphenoid the canal for the internal carotids and the lateral carotids are still far separated. This leads to the conclusion that *Syllomus* is much more primitive than extant cheloniids (Brinkman 2009) in this respect.

According to the latest phylogenetic analysis by Myers et al. (2017), which is based on Cadena & Parham (2015), *Syllomus* is closely related to *Mesodermochelys* and *Dermochelys*. Gentry (2016) also used a modified version of Cadena & Parham (2015) with *Syllomus* excluded, but after reintegrating *Syllomus* the results changed and *Syllomus* is now forming a trichotomy with *Ctenochelys* and *Puppigerus*/*Natator*/*Chelonia*. We also recoded *Syllomus* for the Cadena & Parham (2015) matrix, but there was no change the consensus tree. The changed codings are C88=1; C90=1; C92=1; C99=2; C100=1. For character 91 we kept the "?" because, as described above, it remains unclear if the foramen caroticus lateralis is larger than the foramen anterius carotici interni in *Syllomus*, despite the fact that the canals of the cerebral artery and lateral artery are subequal in size. Therefore, the phylogenetic position of *Syllomus* remains somewhat obscure with results placing it within the dermochelyid branch of marine turtles and on the other hand, *Syllomus* is closely related to modern hard-shelled sea turtles (cheloniids).

Currently, the monophyly of marine turtles is questioned (Cadena & Parham 2015). At least the Protostegidae are supposed to be an independent marine radiation (Cadena & Parham 2015), and homoplasies, most likely because of their similar marine adaptations, are affecting the phylogenetic analysis. However, according to the newest phylogenetic analysis (Evers & Benson 2018), the protostegids are placed again within the crown group of chelonioids. In this context, we hope that the description of the braincase of *Syllomus* and future detailed studies on braincases of marine turtles will lead to new ideas for our phylogenetic understanding of marine turtles.

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