A description and phylogenetic relationship of a polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous (Turonian) of Goulmima, Morocco

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Contents

Abstract

A Moroccan polycotylid plesiosaur from the early Turonian (Upper Cretaceous) of the Goulmima Formation is described. The specimen, bought from an American fossil dealer in 2002 by the Museum of Natural History, Oslo, is a nearly complete skull of an unknown species. It is compared to the holotypes of *Thililua longicollis* Bardet *et al.* 2003 and *Manemergus anguirostris* Buchy *et al.* 2005, both from the same formation, to investigate the phylogenetic relationship between the three specimens. A phylogenetic analysis and ordinance tests suggest that they are very closely related; still they display enough important morphological differences to signify that the Oslo specimen is different enough from the two other species to warrant a further investigation and description as a new species.

Introduction

The Polycotylidae (Reptilia: Sauropterygia) is a group of short-necked plesiosaurs that existed only during the Aptian-Albian to Maastrichtian (Sato *et al.* 2000). Fossil remains of this group have mainly been found in North America (Carpenter 1996, Druckenmiller 2002, Williston 1903 and 1906, O'Keefe 2004), but some have also been found in Asia (Sato *et al.* 2000, Storrs *et al.* 2001), South America (Gasparini *et al.* 2000), Australia/New Zealand (Sato *et al.* 2000) and North Africa (Bardet *et al.* 2003, Buchy *et al.* 2005). The taxonomy and evolutionary relationship with other Sauropterygia has been much discussed during history. Due to their short necks, large heads and other pliosauroid morphological traits, they have, for most of the last century, been classified as true pliosaurs. Williston (1903) suggested that short necks may have been acquired several times during plesiosaur evolution. Bakker (1993) and Carpenter (1997) proposed that the pliosauroids were not monophyletic, and that there should rather be a sister-group relationship between the polycotylids and the elasmosaurids.

Later, O'Keefe (2001) performed a cladistic analysis of the Plesiosauria, which resulted in showing the pliosauroids as polyphyletic, although with no sister-group relationship between the polycotylids and the elasmosaurids. Instead the analysis found the polycotylids to have been derived from the cryptoclidoid plesiosauroids, most closely related to the Jurassic cryptoclidids *Tricleidus* Andrews 1909, *Cryptoclidus* Phillips 1871 and *Muraenosaurus* Seeley 1874. The analysis involved 34 taxa, scoring the specimens on both cranial and postcranial characters.

O'Keefe's (2001) analysis put the polycotylids firmly into the plesiosauroidea, which resulted in that the pliosauroids, as traditionally defined, was shown as a polyphyletic group. He made a new cladistic analysis of the cranial anatomy of the polycotylids (O'Keefe 2004), redescribed three polycotylid taxa, and used those to make a cladistic using the cryptoclidids as outgroup. He found a monophyletic relationship between the Polycotylidae and the Cimoliasauridae, and that the Cryptoclididae was a paraphyletic group.

The year before, Bardet *et al* (2003) described a new species of polycotylid plesiosaur from Morocco, *Thililua longicollis*. This was followed by the description of *Manemergus anguirostris* two years later, by Buchy *et al* (2005). The following genera of polycotylidae has so far been described: *Polycotylus* Cope 1869 (Carpenter 1996, Schumacher *et al.* 1995, Williston 1906), *Trinacromerum* Cragin 1888 (Cragin 1888, Carpenter 1996, Adams 1997), *Dolichorhynchops* Williston 1902 (Carpenter 1996; 1997, Williston 1903), *Georgiasaurus* Ochev 1976 (Ochev 1976, Storrs *et al.* 2001), *Sulcusuchus* Gasparini & Spaletti 1990 (Gasparini 1990, Gasparini *et al.* 2000), *Edgarosaurus* Druckenmiller 2002 (Druckenmiller 2002), *Thililua* Bardet 2003 (Bardet 2003, see also Buchy *et al.* 2005), and *Manemergus* Buchy *et al.* 2005 (Buchy *et al.* 2005).

Bardet *et al.* (2003) maintained, in their description of the first African species, Carpenter's (1996; 1997) view that the polycotylids are closely related to elasmosaurs, based on the cladistic analysis of Bardet *et al.* (1998). O'Keefe's (2001; 2004) cladistic analysis did not support this and matched them more closely to the cryptoclidids. Buchy *et al.* (2005) described the second African species, which they declared as different enough from *Thililua* to be a new species.

In 2002, a specimen of a polycotylid plesiosaur from the Goulmima Formation in Morocco, was purchased by the Geological Museum, University of Oslo from PaleoDirect, located in Alamonte Spring, Florida, USA, to use as a display item, and was given the registration number PMO201.956. The specimen was a nearly complete skull, much better preserved than other specimens known from the area. It had several clearly visible sutures and foramina, as well as an apparently well-defined bone structure, which provide new details about the morphology and phylogenetic relationship of closely related Moroccan species. For that reason, the present study was undertaken to describe the skull of PMO201.956, and to compare it with previously published descriptions of African polycotylids, namely *Thililua longicollis* Bardet *et al.* 2003 and *Manemergus anguirostris* Buchy *et al.* 2005. An analysis is run to establish how closely related the three taxa are, and to investigate which of the three are most closely related. More specifically, cladistic and ordination analyses are undertaken using informative characters of PMO201.956 that is being compared to the same characters in 36 other Sauropterygia species (3 of them are non-plesiosaurs and are used as an outgroup), mainly derived from the analyses of O'Keefe (2001; 2004), but also Bardet *et al.* (2003) and Buchy *et al.* (2005). Based on this analysis, the taxonomic status of PMO201.956 and the two other African polycotylids is discussed.

Geological setting

All three specimens were found in the Goulmima region of Morocco (Bardet *et al*. 2003a; 2003b, Buchy *et al*. 2005, Oslo specimen) an area rich in the remains of fossil fish (Cavin 1995; 1997; 1999; 2001, Cavin *et al*. 2001, Buchy *et al.* 2005). Recently, marine reptiles have been found in the area (Bardet *et al*. 2000; 2003, Buchy *et al*. 2005). All specimens are preserved within non-laminated calcareous nodules together with a host of fossil remains (Cavin 1999). Extensive bioturbation can be observed in the nodules. Research expeditions in the Goulmima area revealed that these nodules occur in Unit 4, at the top of the section, described by Ferrandini *et al*. (1985). Unit 4 is dated as early Turonian using the *Mammites* ammonites, and was deposited during the Cenomanian-Turonian transgression under open platform conditions (Ferrandini *et al*. 1985, Cavin 1999, Bardet *et al*. 2003).

Material and methods

The skull of PMO201.956 was described and compared to the two other specimens found in Morocco. Drawings of all three skulls can be seen in Figures 1 and 2.

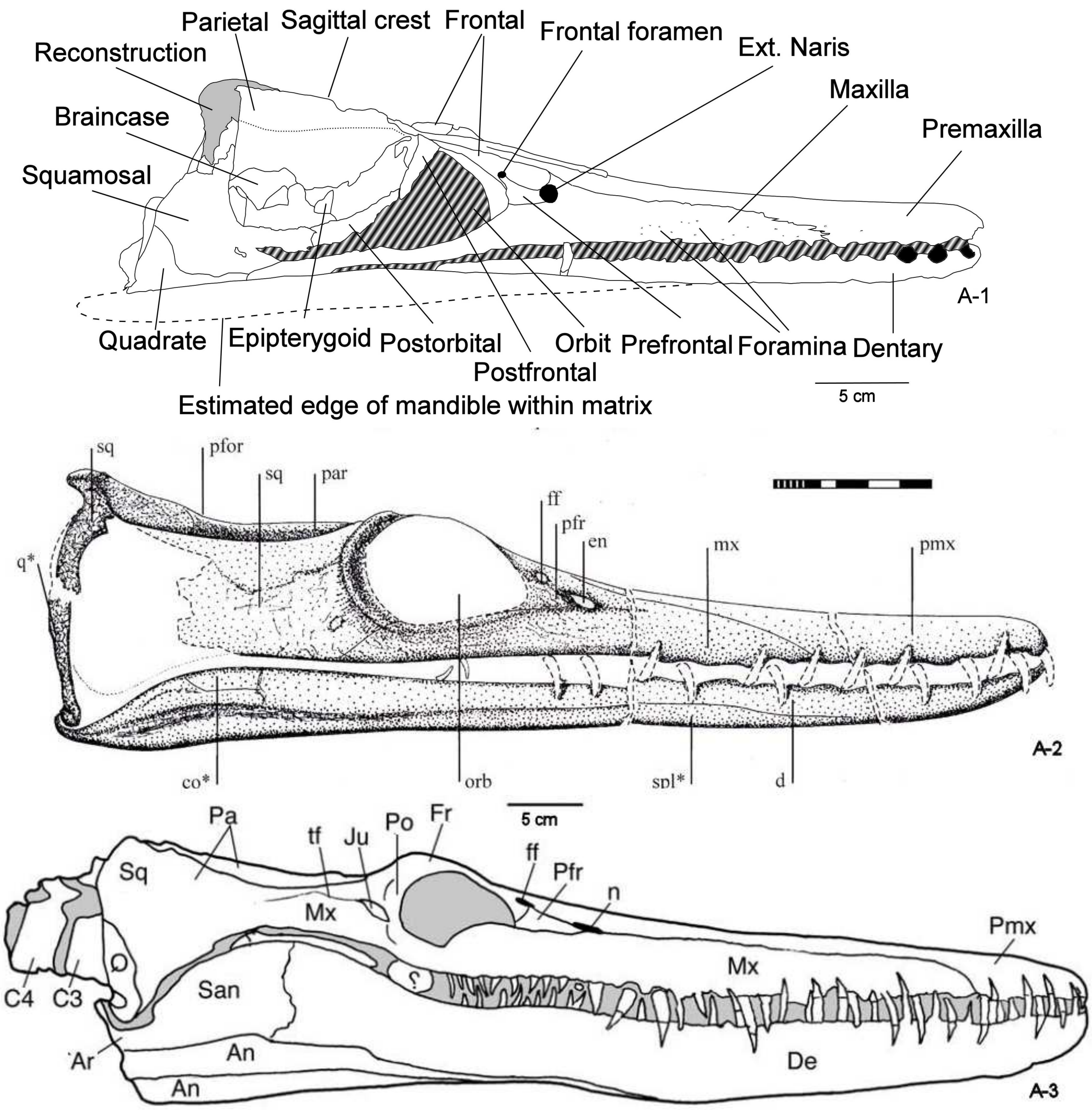

Figure 1
Drawings of the right side of PMO201.956 (A-1) and the left side of the comparative material (*Manemergus anguirostris* (A-2) and *Thililua longicollis* (A-3)). A-2 and A-3 are mirrored to make it easier to compare the three skulls. The splenial of *Manemergus* anguirostris is laterally visible due to heavy weathering (Buchy *et al.* 2005). Abbreviations for *Manemergus anguirostris* Buchy *et al.* 2005 and *Thililua longicollis* Bardet *et al.* 2003 can be found in appendix E.

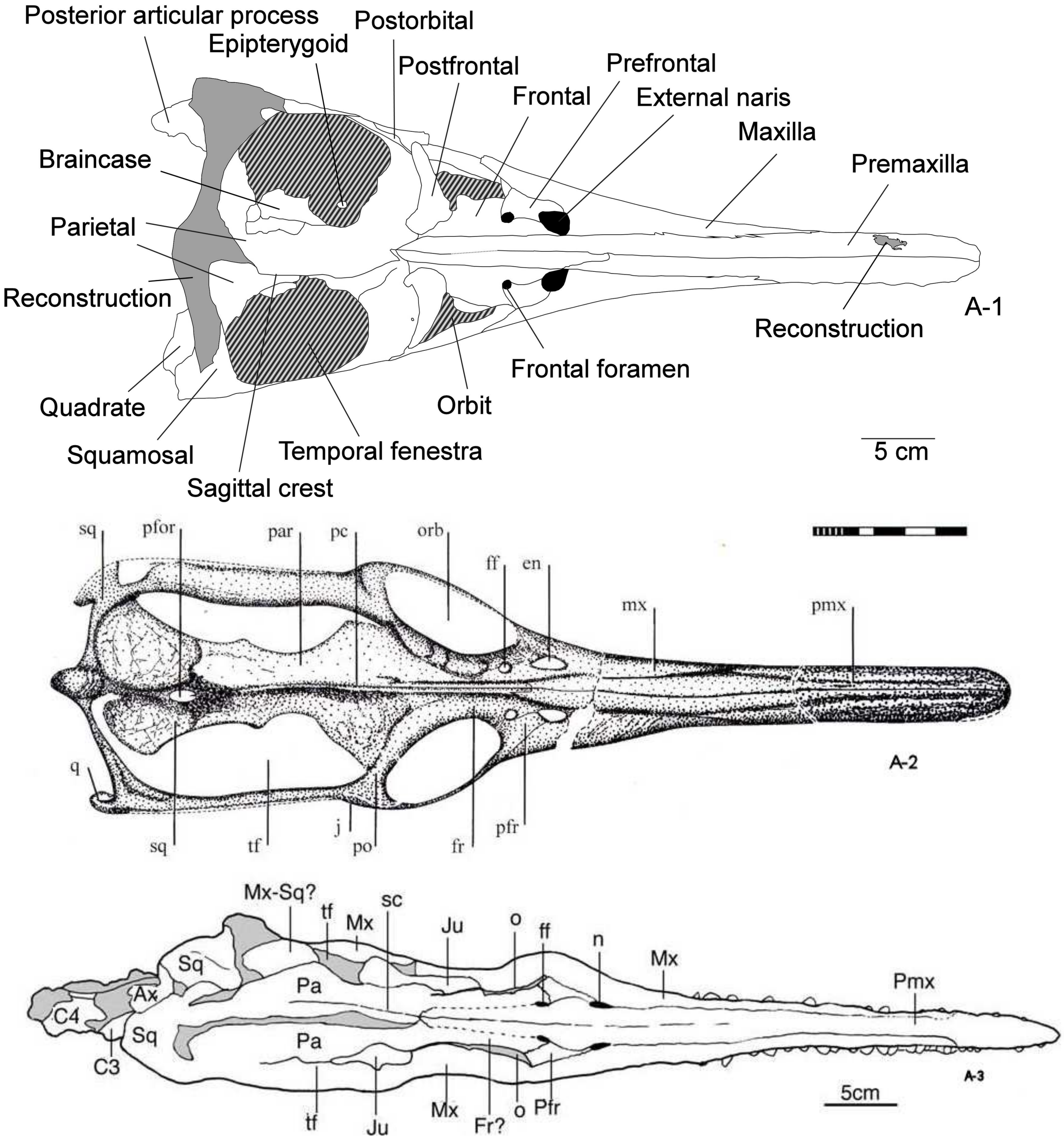

Figure 2
Drawings of dorsal view of PMO201.956 (A-1) and the comparative material (*Manemergus anguirostris* (A-2) and *Thililua longicollis* (A-3)). Abbreviations for *Manemergus anguirostris* Buchy *et al.* 2005 and *Thililua longicollis* Bardet *et al.* 2003 can be found in appendix E.

Cladistic analysis and ordination

The characters of all specimens were scored using O'keefe's (2001; 2004) cladistic analysis of the plesiosauria in general (O'Keefe 2001) and polycotylids in particular (O'Keefe 2004). The new specimen (PMO201.956) was scored against material of *Thililua longicollis* Bardet 2003 (Bardet *et al.* 2003) and *Manemergus anguirostris* Buchy *et al.* 2005 (Buchy *et al.* 2005) and based on published descriptions of these. The dataset was run through different ordination analyses using PAST 1.4 (Hammer *et al.* 2001) to test the fit of the dataset with the three new taxa added. PAUP 4.01b10 (Swofford *et al.* 2001) was used to run a parsimony analysis and bootstrap analysis on the dataset, and also for calculating decay indices.

Skulls

PMO 201.956

This specimen is preserved in a nodule of the same type as those described by Cavin (1995; 1997; 1999; 2001), Bardet *et al*. (2003) and Buchy *et al*. (2004). The skull is gracile, about 48 centimeters long, with a long, slender snout and a robust postorbital segment. The preorbital segment of the skull makes up around 60% of the total length, a normal value for a polycotylid plesiosaur. It is nearly complete, except for partial plastic reconstruction in the squamosal and quadrate area. Apart from the fact that the jugals and the parietals are badly crushed, the remainder of the specimen is intact. There has also been a displacement of the sagittal crest. The skull was originally located within a calcite cemented sandstone concretion, of which the top half has been etched, leaving the specimen partially covered by the lower half of the concretion, so there is no possibility of studying the skull ventrally. It is also matrix-filled internally, with no possibility of removing this matrix, as the skull most likely would collapse. The skull shows some of the defining polycotylid traits; the dorsal process of the premaxillae extend posteriorly and separates the frontals, the missing jugal has most likely been nearly rectangular and formed a horizontal bar behind the orbit, and the maxilla forms an expanded posterior contact with the squamosal.

Comparative material

Both the skulls used for comparison are studied from literature (Bardet *et al.* 2003, Buchy *et al.* 2005). The characters are scored from their descriptions in their respective published articles.

***Thililua longicollis* Bardet *et al.* 2003 Holotype: MHNGr.Pa. 11710.**

(Figures 1A-3 and 2A-3)

The holotype consists of a nearly complete skull, mandible and 37 articulated vertebrae. Both the skull and vertebrae have suffered strong lateral compression. Some cranial sutures are difficult to trace, and the neural arches are fused to the cervical centra. These characters suggest that the specimen is adult (Bardet *et al.* 2003). The comparison is based on Bardet *et al.*'s (2003) description of the skull. Characters in the cladistic analysis are scored on the whole specimen.

Manemergus anguirostris Buchy *et al.* 2005 Holotype: SMNK-PAL 3861

(Figures 1A-2 and 2A-2)

The holotype consists of a heavily weathered skull and articulated axial skeleton. The terminal caudal vertebrae are missing. Also preserved are displaced and incomplete pectorals and pelvic girdles, the left femur and a few phalanges. The neural arches are non-fused, signifying that this is a juvenile. The specimen is badly weathered and also partially destroyed during preparation making it hard to observe most of the sutures of the cranium (Buchy *et al.* 2005). It is preserved in a calcareous nodule, and some of the postcranial elements can only be studied as external moulds. (Buchy *et al.* 2005). The comparison is based on Buchy *et al.*'s (2005) description of the skull, while the characters in the cladistic analysis are scored on the whole specimen.

Description of PMO 201.956

(Figures 3, 4, 5 and 6)

Systematic paleontology

Class Sauropsida Huxley 1864
Subclass Diapsida Osborn, 1903
Order Plesiosauria de Blainville, 1835
Suborder Plesiosauroidea Welles, 1943
Family Polycotylidae Williston, 1908

Figures and drawings

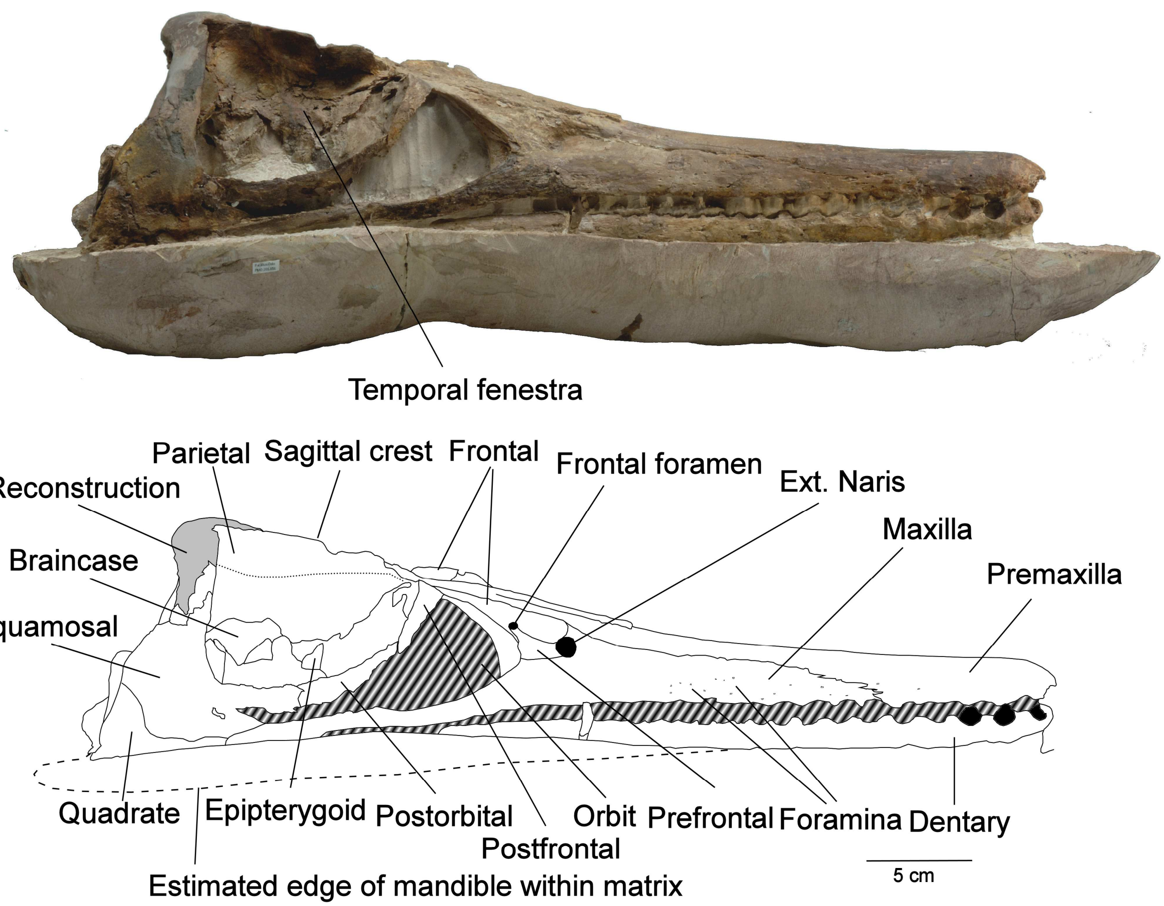

Figure 3
- the skull of PMO201.956 in lateral view. The mandible is reconstructed anteriorly in the drawing (A-2), as it is covered by the matrix from the calcareous nodule. The jugal is missing, and would have been located on the edge of the orbit, in the crushed (striped) area behind the orbit. The parietals are suggested by a dotted line just below the sagittal crest. The left side of the skull was not chosen, as it is heavily reconstructed in the squamosal area.

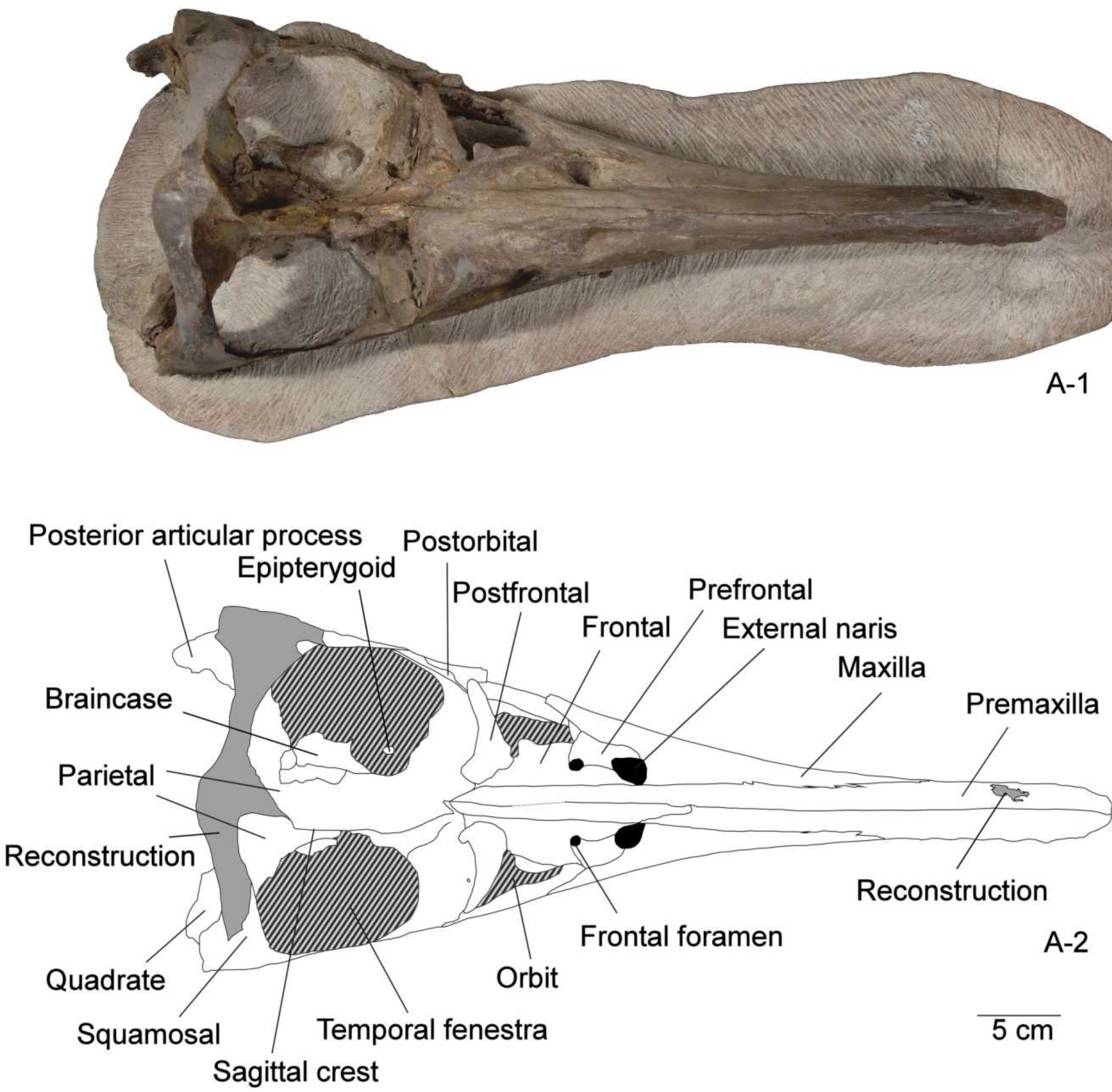

Figure 4
- the skull of PMO201.956 in dorsal view. The sutures on the skull roof can be clearly observed.

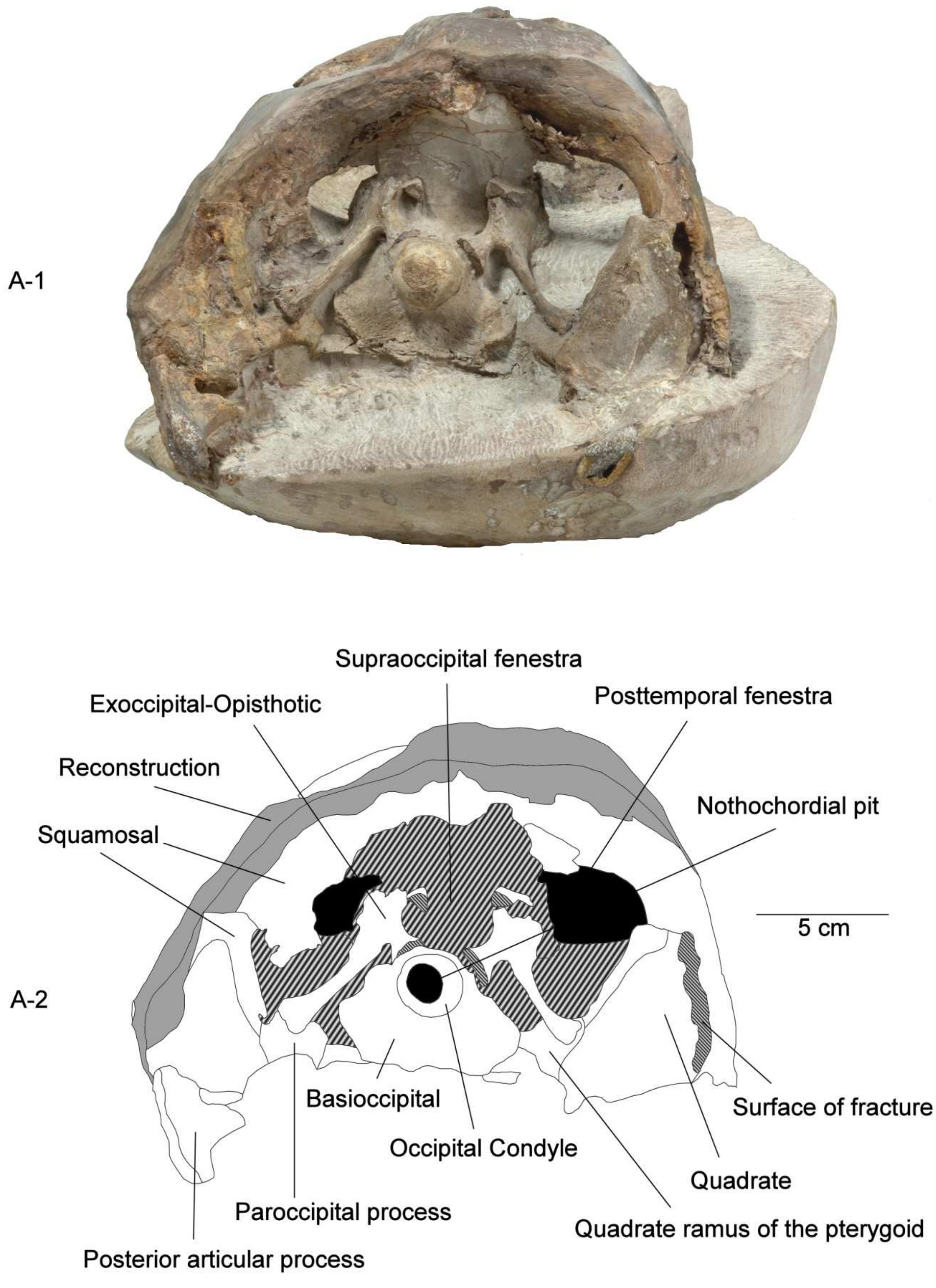

Figure 5
- the skull of PMO201.956 in posterior view

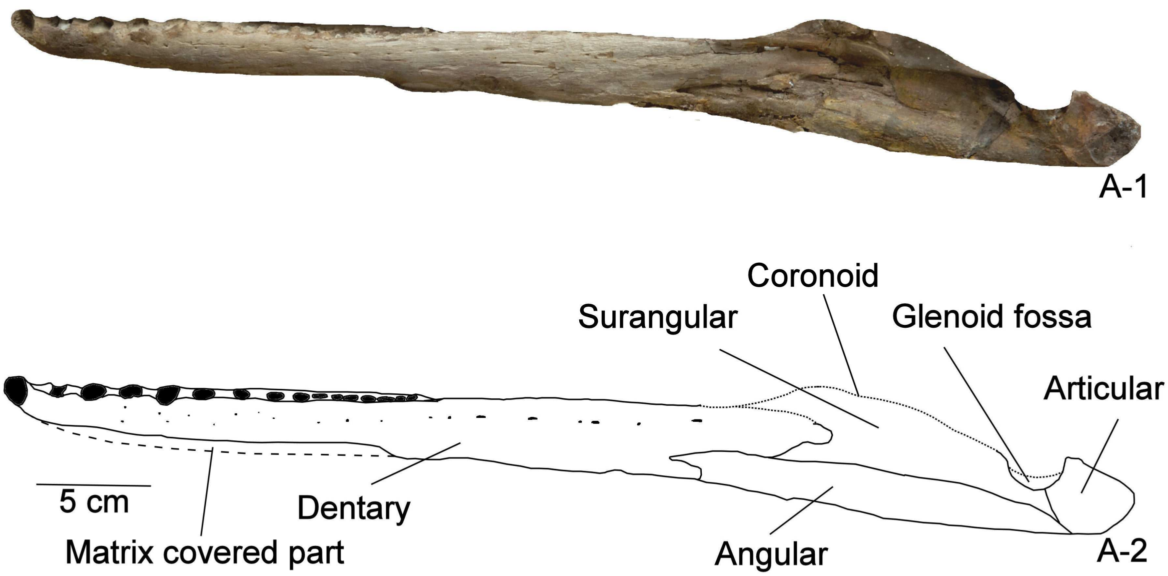

Figure 6
- the left mandible of PMO201.956 in lateral view. A small part of the anterior end is reconstructed as it is covered by matrix (A-2). The coronoid and part of the surangular is reconstructed in the drawing (A-2), as it is partially covered by plastic reconstruction.

Skull openings and foramina

External Nares

The external nares (Figures 3 and 4) are situated posteriorly on the snout, and are placed between the premaxillae, maxillae and frontals. They are dorsally bordered by the premaxillae, the posterior edges are formed by the frontals, and the ventral and anterior edges are bordered by the maxillae. Only the left opening is visible in the specimen. This opening is round and tilts backwards and outwards. The right opening is partly matrix-filled. Anteriorly the external nares have large grooves of about twice the length of the openings themselves. No nasals are present.

Frontal Foramina

The frontal foramina (Figures 3 and 4) are small round openings located about two centimeters posterior to the external nares. They are bordered ventrally by the prefrontals, and dorsally by the frontals.

Orbit

The orbits (Figures 3 and 4) are large, round to triangular in shape. They tilt slightly forward, with slightly overlapping view indicating stereopsis. The orbits are located two thirds down the length of the skull. The prefrontals and maxillae form the anterior and dorsal rims of the orbit together with the anteriormost parts of the postfrontals. These continue posteriorly and form the upper posterior rim of the orbits. The middle anterior rims are formed by the postorbitals, which end about halfway down the complete posterior rim. The lower posterior rims are probably formed by the jugals. The orbits are bordered ventrally by the maxillae. There are no lacrimals.

Supratemporal fenestrae

The supratemporal fenestrae (Figures 3 and 4), hereby referred to as temporal fenestrae, are huge, and contribute to most of the postorbital section of the skull. Their length is approximately two thirds of the total postorbital length. Their exact form is difficult to determine, since the parietals are badly crushed and are pressed down to cover the laterodorsal part of the braincase. The opening is bordered anteriorly by the postorbitals. The anteriormost parts of the ventral rims of the fenestrae are made up of the maxillae. The posterior ventral and posterior rims are formed by the squamosals. The crushed parietals form the dorsal rims, while the braincase forms the inner wall of the fenestrae. The anterior walls of the temporal fenestrae are composed of the pterygoid flanges, postorbitals and postfrontals.

Pineal foramen

After preparation, only faint traces of the pineal foramen are left and the pineal foramen was most likely positioned anteriorly to the parietals, on the suture between these and the premaxillae.

Posttemporal fenestrae

The posttemporal fenestrae (Figure 5) are large, round openings. The one on the right is partly matrix-filled, but the left one is fully excavated. Their dorsal and outer edges are bordered by the squamosals, while the ventral edges are lined by the quadrate rami of the pterygoids. The inner and lower edges are partly covered by matrix.

Foramen magnum

The foramen magnum (Figure 5) is partially covered by matrix, but can be clearly seen to be bordered ventrolaterally by the exoccipital-opisthotic.

The optic foramina are not visible, as they are covered by matrix.

Skull Roof (Figures 3 and 4)

The snout is long and slender, and is composed of the premaxillae and the maxillae. The postorbital section is dominated by the temporal fenestrae.

Premaxilla

The premaxillae are long and slender and form the anterior and most of the dorsal side of the snout. They support five pairs of teeth and form long facial processes, which run between the external nares and terminate between the orbits. They form long sutures with the maxillae, starting in a zigzag pattern at the sixth pair of teeth, straightening out above the ninth pair, and ending at the start of the external nares. The premaxillae continue past the external nares and form sutures with the frontals. These sutures continue posteriorly and terminate in another suture with the parietals. There is also an almost completely straight suture between the two premaxillae. The premaxillae contain some small foramina, running just above the tooth margins, starting between the third and fourth pair of teeth.

Maxilla

The maxillae are robust bones, making up the main part of the snout together with the premaxillae. Each has at least 24 teeth. They form the anterior and ventral edges of the external nares, before continuing posteriorly to the sutures with the prefrontals. They also form the ventral edges of the orbits. Posterior to this, they would have met the now missing jugals before ending as wedges into the squamosals. The bones end medially on the ventral edge of the temporal fenestrae. There are at least two rows of small foramina running along the maxillae, just above the tooth margin. These foramina end at the thirteenth pair of teeth.

Prefrontal

The prefrontals are small, nearly rectangular bones starting medially on the ventral edges of the external nares, and end up as small parts of the anterior orbit edges. They form sutures with the maxillae, running from the external nares, to the anterior orbit edge. The suture between the prefrontals and the frontals runs from the external nares, via the frontal foramina, down to the anterior orbit edges.

Frontal

The frontals are long and thin, forming sutures with the premaxillae from the middle of the external nares back to the parietals. They have posterior lateral processes on the dorsal orbit border, giving them a brow-like shape.

Postfrontal

The postfrontals are vaguely triangular, and are placed as a wedge between the orbits and the temporal fenestrae. They form sutures with the ventral edges of the frontals, and border anteriodorsally to the parietals. Ventrally they meet the postorbitals. They cover roughly one third of the anterior walls of the temporal fenestrae.

Postorbital

The postorbitals are long and thin, and also serve as the lower anterior edges of the temporal fenestrae. Anteriorly, they form sutures with the postfrontals, and ventrally they meet the jugals in sutures that run backwards until they meet the squamosals.

Jugal

Posteroventral to the postorbital on the left side of the skull, a small part of the jugal is preserved. This forms a suture with the postorbital dorsally and the squamosal posteriorly. The jugal on the right side is missing. However, it is possible to judge where the jugals were located and they seem to have been a part of the lower posterior rims of the orbits, directed posteriorly between the postorbitals and maxillae and extending to the squamosal and medial to the temporal fenestrae. Most likely the jugals have been subrectangular in shape, as it is a defining trait for a polycotylid.

Squamosal

The squamosals (Figures 3, 4, and 5) have been cosmetically reconstructed by a commercial preparator by covering these and the outside of the quadrates with a thin layer of plastic. However, their shapes are visible through the transparent plastic. The squamosals form the ventral and posterior rims of the temporal fenestrae, starting at the posterior end of the jugals, making a vertical suture with them, as can be seen on the left side of the specimen. On the lower end of this suture, they meet the posterior parts of the maxillae. The squamosals form a large arch posteriorly to the temporal fenestrae together with the quadrates, meeting the sagittal crest dorsally. The dorsal surface of this arch has been partly reconstructed, making it hard to see its exact form. The descending rami of the squamosals form, together with the quadrate, solid pillars to support the arch. The sutures between the squamosal and quadrate are clearly visible on the right side of the skull. The ventral end of the right squamosal has a fracture just above the squamosal/quadrate suture. The suture between the squamosals and parietals cannot be clearly seen.

Quadrate

In posterior view the quadrates (Figures 4 and 5) are robust and triangular-shaped, forming wedges into the ventral part of the squamosals. Together with these rami, they form the base for the squamosal arch dorsally. Ventrally they are a part of the jaw hinges, and are articulated with the articulars.

Parietal

The parietals are crushed onto the inner sides of the temporal fenestrae, but their shape can clearly be seen to have formed a dorsal bar over the temporal fenestrae. They bear a tall sagittal crest, which anteriorly forms short sutures with the postorbitals before bifurcating anteriorly to form another suture with the posterior end of the premaxillae. This anterior bifurcating part of the crest contains the remains of the parietal foramen. The parietals are fused to each other and seem to have had ventrolateral edges that have been supported by the epipterygoids. The latter protrude up from the matrix medially on the inner walls of the temporal fenestrae, which is formed by the braincase. They are robust pillars, widening ventrally, pointing straight up at the parietals thus bracing them against the pterygoid. The pterygoid is covered in matrix. The braincase is partly buried in matrix ventrally, and is dorsally covered by the crushed parietals.

Pterygoid flange

The pterygoid flanges protrude from the matrix as a part of the anterior walls of the temporal fenestrae. They cover about half the height of the walls, and there are clear sutures along the dorsal edge where they meet the postfrontals and postorbitals.

Posterior view (Figure 5)

Quadrate ramus of the pterygoid

When the skull is viewed posteriorly, the quadrate rami of the pterygoids run from the ventral portion of the basioccipital to the quadrates, forming the ventral edges of the posttemporal fenestrae. The sutures between the rami and the basioccipital are not connected, and the bones are pushed forward under the paroccipital processes and fractured. Their anterior ends are covered by matrix.

Paroccipital processes and exoccipital-opisthotic

The paroccipital processes run from the squamosals to the exoccipital-opisthotic. They form a steep angle, supporting the rear of the skull against the quadrates. The exoccipital-opisthotic and forms a support between the occipital condyle and the supraoccipital, which is not visible. The sutures between the exoccipital-opisthotic and the occipital condyle are fractured, and the prootic bones are fractured anteriorly against the braincase. This is due to a slight dorsal compression of the skull.

Basioccipital and occipital condyle

The basioccipital itself is connected to the ventral side of the occipital condyle, and the shape of the bone is somewhat like an inverted butterfly. The occipital condyle is almost perfectly round, and contains the notochordal pit, which is roughly half the diameter of the condyle itself.

Mandible (Figure 6)

The mandible is partly embedded in the hard sandstone matrix, with only the dentary above the matrix visible on the right side, but it is almost complete on the left side. Only the outer surface and the general shape is possible to describe.

Dentary

The dentary is a long, slender bone, and represents about three quarters of the total length of the mandible. It bears at least 36 teeth. Anteriorly, the teeth are large, based on the size of the alveoli, and they get smaller and smaller posteriorly. Based on the shape of the dentary, the mandibular symphysis can be estimated to around 40% of the length of the dentary, or about 30% of the total mandible length. If this estimate is correct, it bears 11 of the teeth of the lower jaw. The row of teeth of the dentary extends posteriorly to the posterior rim of the orbit. The suture with the surangular is hard to discern, due to the heavy plastic reconstruction in this area, but some remains of it can be seen just posterior to the coronoid.

Surangular

The surangular is nearly rectangular in shape. The suture with the articular is just visible under the microscope where it can be seen extending from the anterior part of the anterior transverse crest to the medial of the glenoid fossa.

Angular

The angular begins medially to the anterior rim of the orbit, and forms a diagonal suture with the dentary that ends just posteriorly to the coronoid eminence. Here, it forms another suture with the surangular that runs posteriorly until it forms another suture with the articular just posterior to the posterior transverse crest.

Coronoid

The coronoid is half-moon- shaped, forming a suture with the dentary anteriorly. Ventrally, it meets the surangular in a suture which runs posteriorly until it forms another short suture with the articular.

Articular

The articular is small, but large enough to hold the glenoid fossa, anteriorly forming a suture with the surangular, before meeting the angular in a suture which runs almost to the posteriormost part of the long retroarticular process.

Dentition

Only one tooth remains in the right maxilla of the specimen and even this has been damaged during preparation. The rest of the teeth are missing. The one remaining tooth is the tenth tooth of the maxilla on the right side of the skull. This tooth is long and slender, and nearly conical. The posterior side of the tooth has been damaged and no possible serration can be seen. The anterior side of the tooth is complete, but no edge can be seen. There is some faint evidence of striation, but the tooth is too worn to discern any pattern. Despite the lack of teeth it is possible to make a tooth count using the moulds. The premaxillae bears five teeth each, while the maxillae has at least 24 each, a number compatible with previous counts of pliosauroid teeth.

The premaxillary teeth seem to have been the largest, together with the seven or eight anterior pairs of dentary teeth. The teeth diminish in size towards the posterior of the jaws, both in the maxillae and in the dentary. This has been estimated from the size of the sockets, which clearly diminish in diameter from the anterior ends of the jaws to the posterior. This change is gradual in a posterior direction. The diameter of the anterior sockets is twice that of the posterior sockets and it appears as if the teeth of the maxillae have been larger than the teeth of the dentary.

The angle of the sockets suggests that the teeth were interdigitate, possibly extending past the rim of the opposite jaw. The shape of the sockets suggests that the dentition is homodont. The anterior teeth seems to have been protruding forwards as well as laterally, with the most anterior pair of teeth in both upper and lower jaw directed almost straight forwards. Just posterior to the diastema, the teeth appear to have straightened upwards and point at an angle laterally. The sockets are partly filled with matrix, but it is possible to see that the teeth were deeply imbedded in the jaw. The combined characters of the dentition seem to indicate a strong, tough structure well suited for catching and gripping prey.

Cladistic analysis

Characters

In the first data matrix, used for assigning the three taxa *Thililua* Bardet *et al.* 2003 (Bardet *et al.* 2003, Buchy *et al.* 2005), *Manemergus* Buchy *et al.* 2005 (Buchy *et al.* 2005) and Oslo specimen into the plesiosaur hierarchy, the characters used were those defined by O'Keefe (2001) to confirm the assignment of the first two to the polycotylids. The data matrix includes 34 plesiosaur taxa, which are scored for 166 characters. Of these, 107 are characters of the skull and 59 are from the post-cranium. Ninety characters of similarity and differences were usable for placing the three taxa on the tree, and a further 15 characters based only on differences between the three specimens were added later. The characters are described in O'Keefe (2001), and are scored with a (0) for a primitive character and the complete matrix is represented in appendix A. O'Keefe scored some taxa with an x, for inapplicable, but since part of the analysis was run in PAST (Hammer *et al.* 2001), they had to be converted to "?" for the program to run. Character states are described in O'Keefe (2001). In this analysis, the three above mentioned taxa were added bringting the total to 37. As in O'Keefe's cladistic analysis, the non-plesiosaur genera *Simosaurus*, *Cymatosaurus* and *Pistosauridae* were used as out-groups. Furthermore, some characters that only apply to these out-groups were included in the matrix to help with establishing their topology (O'Keefe 2001).

In the second data matrix, used to identify the relationship between the three Moroccan taxa, the characters were scored after O'Keefe (2004). This data set is scored on 95 characters from16 taxa including the three (*Thililua* Bardet *et al.* 2003, *Manemergus* Buchy *et al.* 2005 and Oslo specimen) introduced for this analysis. Fifty-nine of the characters are cranial, while the remaining 36 are based on postcranial material. Forty-four of the characters were useable for this comparison. Thirty one of these characters scored the same for all three specimens. Because only 13 cranial characters (see below) represent differences between the three taxa, there is low bootstrap support for the internal relationship in the clade.

Differing characters, discussion

All characters and character numbers are taken from O'Keefe (2004).

The pineal foramen of the Oslo specimen is located between the orbits where the processes of the premaxillae meet the parietals; hence the posterior processes of the premaxillae contact the parietals at the pineal foramen (Character 8). In *Manemergus* the foramen is located in the posterior end of the parietals, just anterior to the squamosal arch, behind the sagittal crest, not between the frontal and the anterior extension of the parietal. In the Thililua specimen, there is no evidence of the pineal foramen, so the frontals contact the parietals directly.

In PMO201.956 the premaxillae contact the external nares (Character 9), as in *Thililua*. In *Manemergus*, the premaxillae narrow at the external nares and are not in contact. The external nares in PMO201.956 and in *Manemergus* are in contact with the frontals (Character 13), while in *Thililua* the frontals end in sutures with the prefrontals at the frontal foramina. PMO201.956 has posterolateral processes on the frontals (Character 11), giving them a brow-like look. *Manemergus* does not have these processes. In *Thililua*, this is uncertain, due to the heavy crushing of the specimen. These processes project into the orbit on PMO201.956 (Character 15). The postorbitals of PMO201.956 extend posteriorly along the margins of the temporal fenestrae (character 90). In *Manemergus* and *Thililua* they end medially on the posterior orbit margin.

All three specimens have 5 premaxillary teeth, but *Manemergus* has only 9-10 maxillary teeth, while *Thililua* has 22+ and PMO201.956 has 24+ (Character 57). Another character, which O'Keefe did not score for, is number of dentary teeth. Here, *Manemergus* has only 15, with 9 in the symphysis. This is relatively few for a polycotylid, and could be because the specimen is that of a juvenile. *Thililua* has 29 dentary teeth, with 15 symphyseal, and PMO201.956 has 36 or more dentary teeth, with only 11 in the symphysis. This is a significant difference in number and distribution between both *Thililua* and especially *Manemergus,* and PMO201.956. In PMO201.956 and *Manemergus*, there is a long retroarticular process (character 92), while in *Thililua* the process cuts off abruptly straight below the quadrate. Both *Thililua* and *Manemergus* have a low sagittal crest (character 94), In *Thililua* this may be because of distortion, and in *Manemergus* it may be because it is a juvenile, but the only one of the three specimens that has a high crest is PMO201.956

Thililua has 30 cervical vertebrae (Character 60) with backwards angling neural spines (Character 70), while *Manemergus* has a reduced number with only 25. There is no angling of the neural spines in *Manemergus*. PMO201.956 is missing postcranial material, and so the scores for these characters are unknown.

Placement within the Plesiosauria

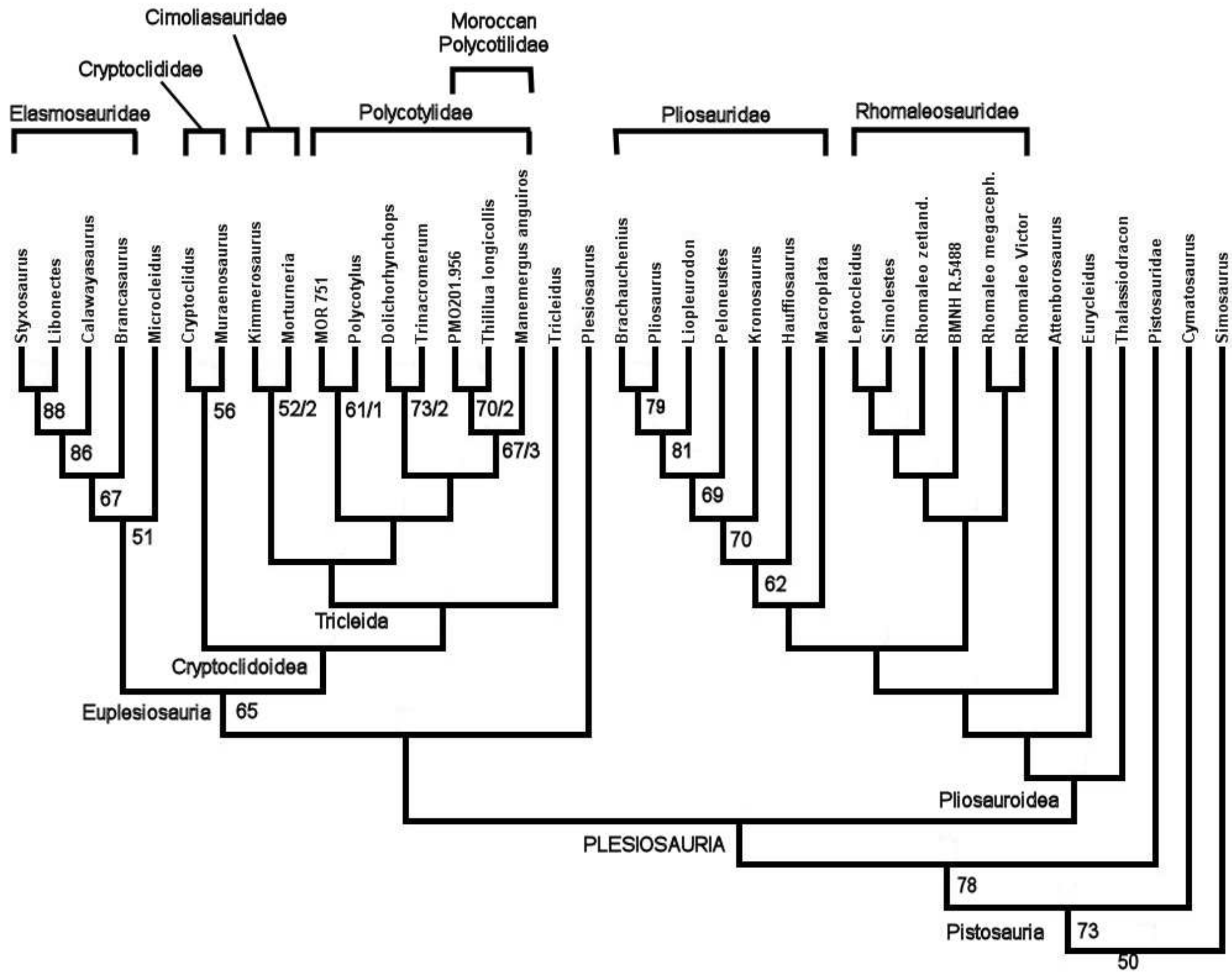

Figure 7
- phylogenetic relationships of the plesiosauria. Strict consensus of 12 most parsimonious trees. Tree lengths 460. Ci = .44, Ri = .70, RCi = .31. Numbers given are bootstrap values/decay indices. Where there is no value, The bootstrap support is under 50%. List of the taxa with holotypes can be found in appendix A.

A parsimony analysis (TBR) was run in PAUP 4.0b10 (Swofford *et al.* 2001). Of the 166 characters in this data set, 139 were parsimony informative. The data matrix was analyzed with tree bisection-reconnecting (TBR) branch-swapping. The analysis resulted in twelve most parsimonious trees, the strict consensus of which can be seen in Figure 7. The trees had a length of 460. The consensus tree had a consistency index of 0.44, a retention index of 0.70 and a rescaled consistency index of 0.31. The polycotylids are well ordered within the plesiosaurids as in O'Keefe's analysis, and the three added taxa are shown to be a stable group within the

Polycotylidae. The analysis placed *Thililua* Bardet 2003 and PMO201.956 closest, with *Manemergus* Buchy *et al.* 2005 as a close relative. The *Thililua*/PMO201.956 pairing had a bootstrap support of 70 and a decay index of 2. The analysis confirmed the three specimens as polycotylids, supporting their placement within the group with a decay index of 3 and a bootstrap support value of 67. This is a clear indication that they are more closely related to each other than to the rest of the polycotylids. This was expected, since they are all found in the same area. The rest of the polycotylids had a decay index of 3. Decay indexes and bootstrap support values are shown in Figure 7. The tree as a whole is well supported, with the exception of the internal relationships of the rhomaleosaurs and the cryptoclidoids.

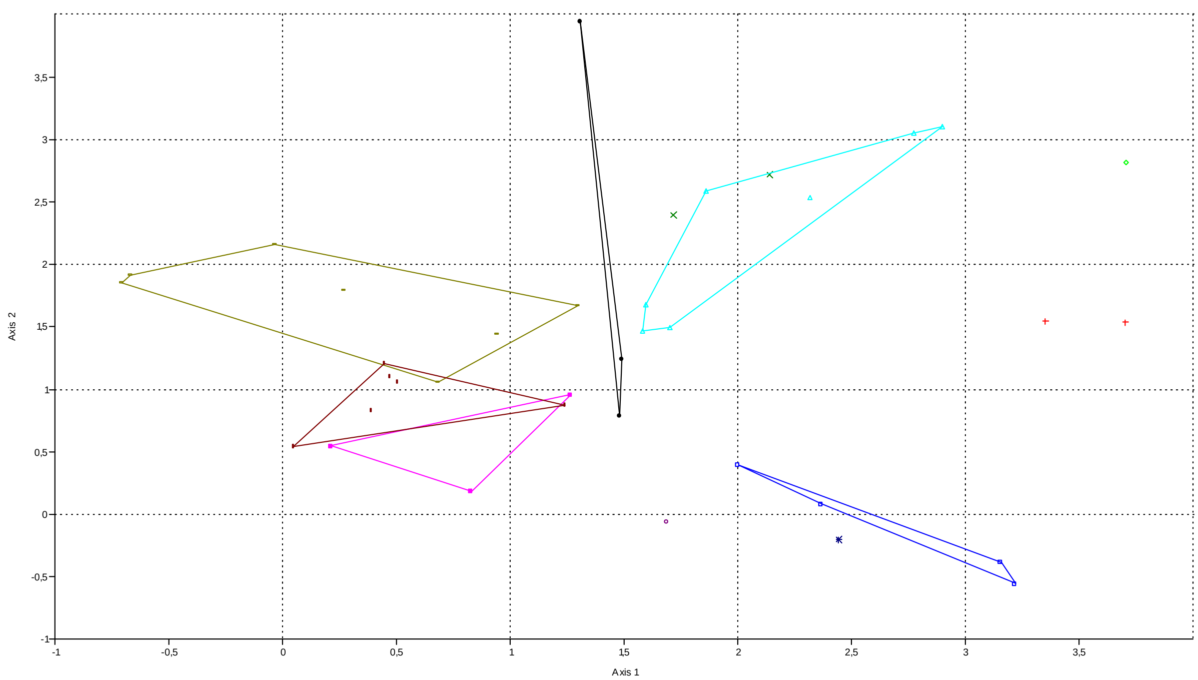

Figure 8
- detrended correspondence analysis (DCA) of O'Keefe's (2001) dataset with three added taxa. Cyan: Polycotylidae, Blue: Elasmosauridae, Brown: Rhomaleosauridae, Yellow: Pliosauridae, Pink: *Thalassiodracon, Euryclideus, and Attenborosaurus*, Black: Outgroup.

Finally, PAST 1.68 was used to run DCA and NMDS analyses on the data matrix, and they both showed that the polycotylids grouped together with no overlapping to any other group. The DCA (Figure 8) showed them as closely related to the cryptoclidids, as the Cryptoclididae are contained within the polycotylid convex hull. On one side of the outgroup we find the Cryptoclididae, Cimoliasauridae, Elasmosauridae and Polycotylidae. On the other side we have Pliosauridae and Rhomaleosauridae. This is a clear indication of the placement of the Polycotylidae within the plesiosauroids. Closer examination of the plot shows that *Manemergus, Thililua* and PMO201.956 are all grouped together on one side of the polycotylids, towards the center of the plot. This could be because all share the same pliosauromorph characters. All the other polycotylids were grouped together on the other side of the convex hull. This indicates that the Moroccan polycotylids are slightly different from the rest of the Polycotylidae.

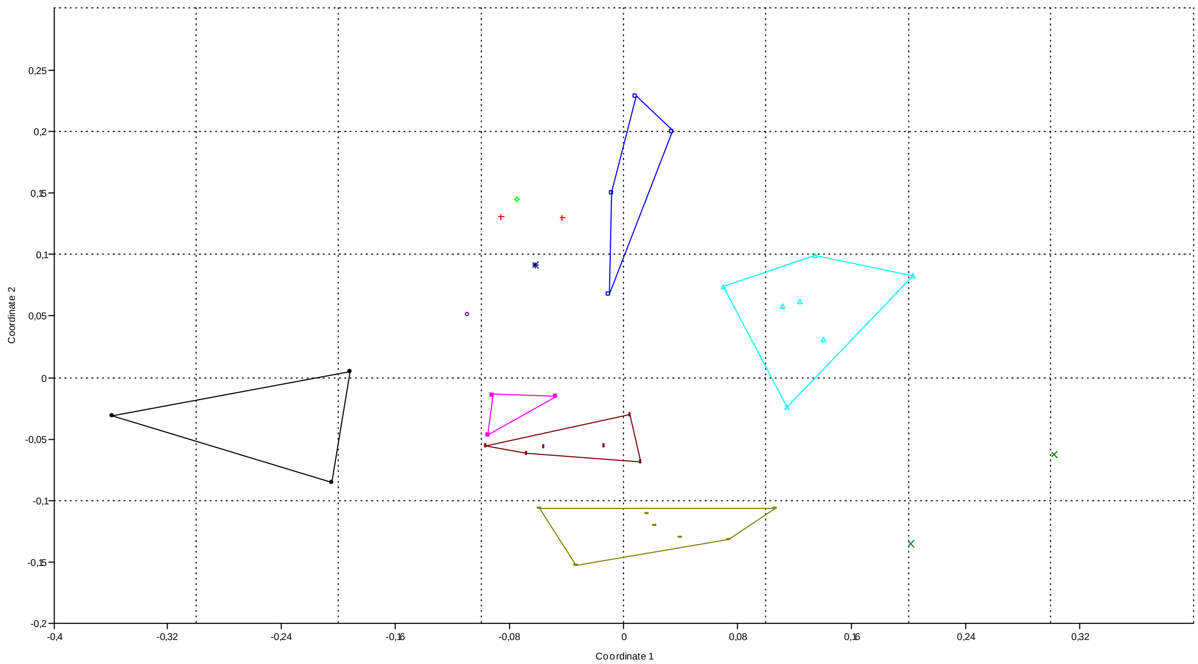

Figure 9
- non metric multidimensional scaling (NMDS) scatter plot of the O'Keefe (2001) data set with three added taxa. Cyan: Polycotylidae, Blue: Elasmosauridae, Brown: Rhomaleosauridae, Yellow: Pliosauridae, Pink: *Thalassiodracon, Eurycllideus, and Attenborosaurus*, Black: Outgroup

The NMDS analysis (Figure 9) shows a clear grouping of the different plesiosaur groups. There are no overlapping groups, and the polycotylids are clearly defined on one side of the plot. Here, the outgroup taxa are separated from the plesiosaurs, but a trend can be seen in the placement of the ingroup taxa. The plesiosauroids are moving towards the top of the plot, and the pliosauroids to the bottom. This supports the view that the polycotylids are plesiosauroids. This plot also indicates a slight difference between the Moroccan polycotylids and the other Polycotylidae.

Relations inside the polycotylid group

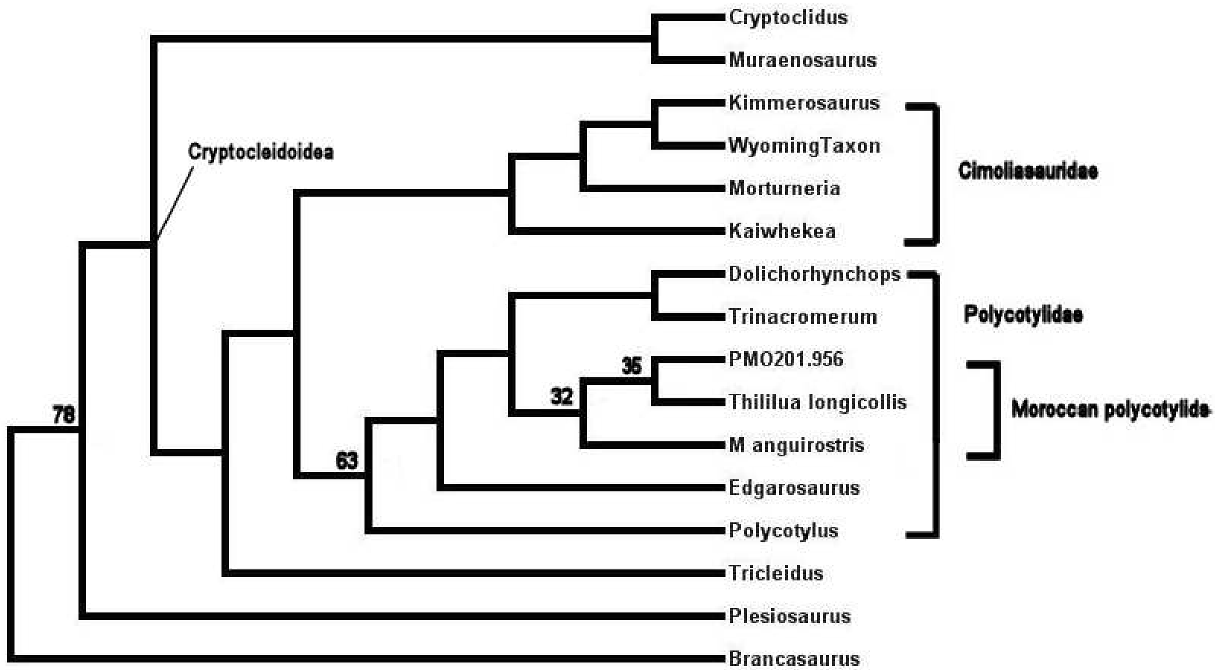

Figure 10
- phylogenetic relationship of the Polycotylidae. Strict consensus of 4 most parsimonious trees. Tree lengths 182. Ci = .65, Ri = .64, RCi = .42. Numbers given are bootstrap values. Where there is no value, The bootstrap support is under 50%. List of the taxa with holotypes can be found in appendix B.

Following O'Keefe (2004) the three taxa were scored to test their assignment to the polycotylidae, their relationship to each other, and to examine the robustness within the group. Of the 95 characters in the matrix, 71 was parsimony informative. The outgroup used was the same as in O'Keefe (2004), and a parsimony analysis run in PAUP 4.0b10 (Swofford *et al.* 2001) yielded 4 most parsimonious trees with a length of 182, a consistency index of 0.65, a retention index of 0.64 and a rescaled consistency index of 0.42 (Figure 10). The strict consensus of the trees is shown in Figure 10. PMO201.956 and the two other taxa was placed with the true polycotylids, which forms a sister group to the Cimoilasauridae, as in O'Keefe (2004). The group with the three new taxa, however, is not completely stable internally, with a bootstrap value of only 35 for *Thililua* and PMO201.956. This indicates that they are very closely related.

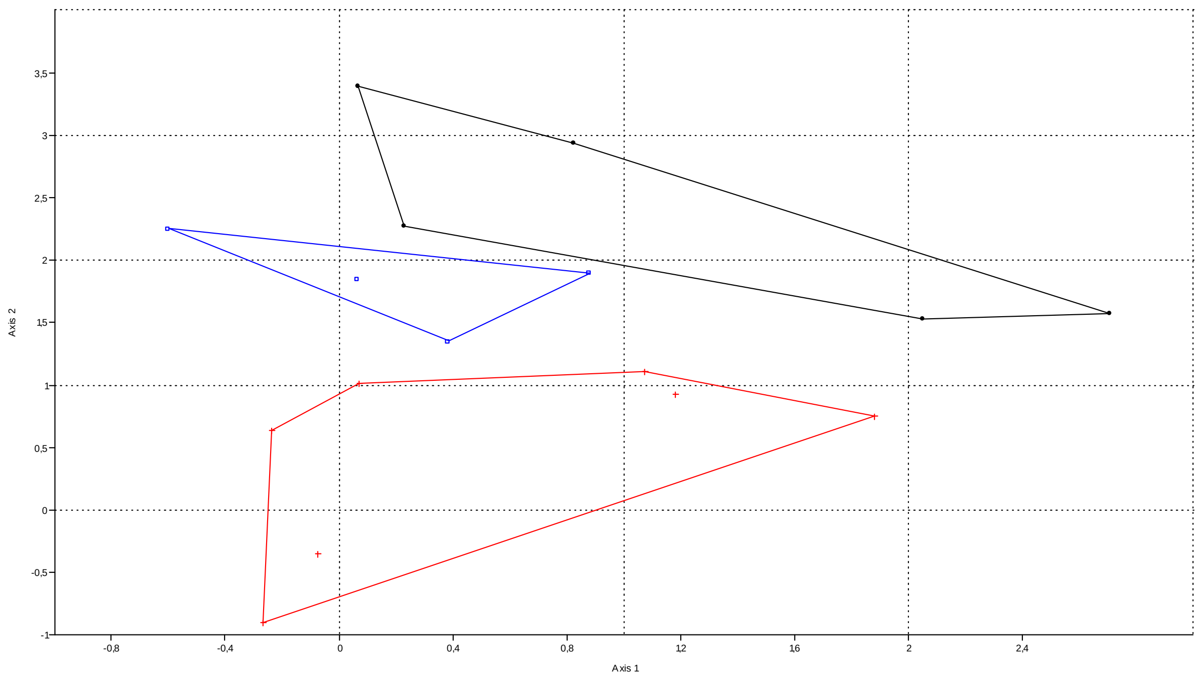

Figure 11
- detrended correspondence analysis (DCA) of O'Keefe's (2004) dataset with three added taxa. Red: Polycotylidae, Blue: Cimoliasauridae, Black: Outgroup.

PAST 1.68 was again used to run DCA and NMDS analyses on the smaller data set. The DCA (Figure 11) had no overlapping groups, and the polycotylidae were shown as closely related to the Cimoliasauridae. The three Moroccan taxa are located towards the middle of the plot, away from the Cimoliasauridae. This supports the parsimony analysis in that the North African taxa are more removed from the Cimoliasauridae than the other polycotylids. The larger analysis showed that the Moroccan taxa are somewhat different from the other taxa in the group, and this view is supported by this closer analysis of the polycotylids.

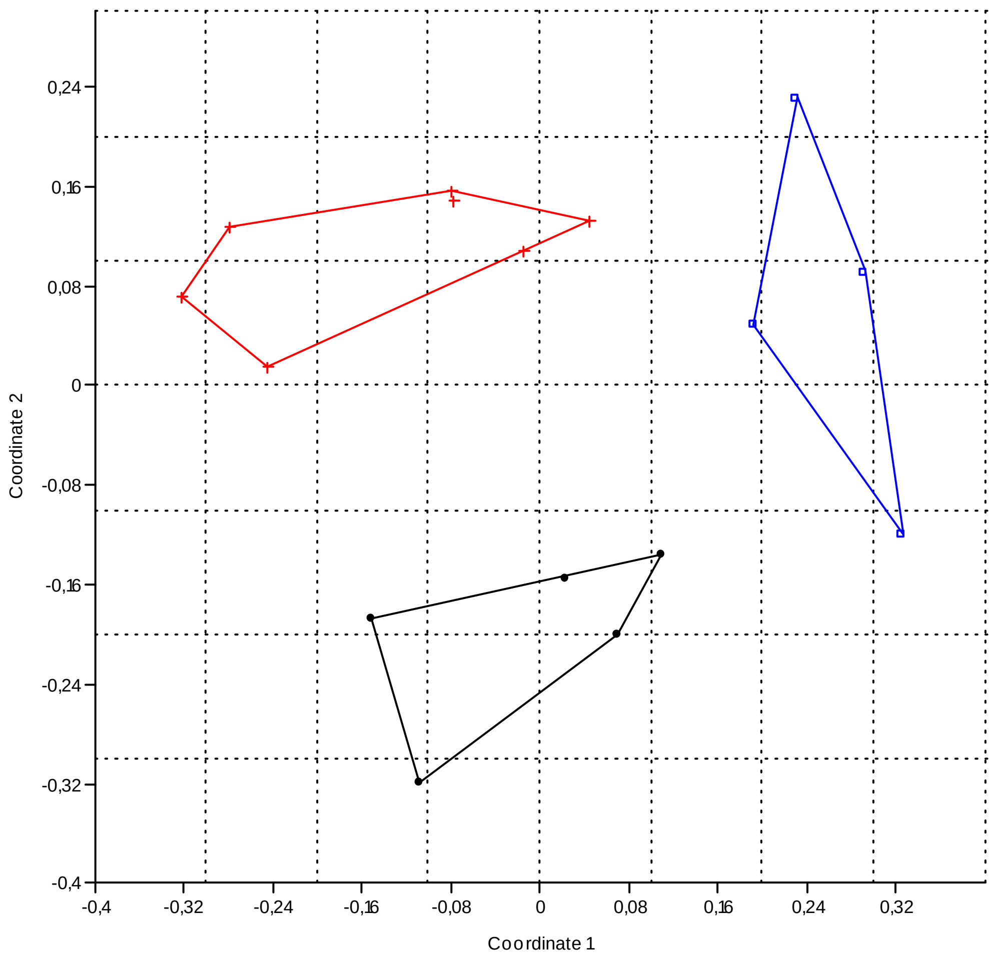

Figure 12
- non metric multidimensional scaling (NMDS) scatter plot of the O'Keefe (200) data set with three added taxa. Red: Polycotylidae, Blue: Cimoliasauridae, Black: Outgroup

The NMDS analysis (Figure 12) shows a clear separation of the polycotylid and cimoliasaurid groups. There are no overlapping groups, and the polycotylids are clearly defined on one side of the plot. The trend in grouping can be clearly seen, with both Polycotylidae and Cimoliasauridae towards the top of the plot, and the outgroup towards the bottom. The African taxa are furthest removed from the Cimoliasauridae, and furthers the view of a different Moroccan clade.

Discussion

The analyses all place PMO201.956, *Thililua longicollis* and *Manemergus anguirostris* as a group firmly located within the Polycotylidae. They form a sister group to *Dolichorhynchops* and *Trinacromerum*, and have derived characters from *Edgarosaurus* and *Polycotylus*. However, the African taxa do not seem to be as closely related to the other polycotylids as they are to each other. They end up further away from the Cryptoclididae and Cimoliasauridae in the ordination analyses, and in the parsimony analysis they form their own clade within the polycotylids. Within this clade, the analyses all show PMO201.956 and *Thililua* to be the more closely related taxa, but this is not strongly supported by bootstrap analyses and decay indices. This suggests that the three taxa are very closely related. The holotype of *Manemergus* is believed to be a juvenile specimen, which could mean that if it was more mature, it would have scored as more closely related to PMO201.956 than is seen in this analysis.

There is, however, morphological evidence on the three skulls that show that none of the three are the same species.

Comparison with Thililua longicollis *Bardet* et al. *2003*

(Figures 1A-3 and 2A-3)

Some of the traits that differ between PMO201.956 and *Thililua* are not scored in the data sets. This is due to limited access to the different material, so there was no possibility of scoring the other 34 taxa for these traits. The dentary of *Thililua* looks much more robust than on PMO201.956, the surangular does not extend anteriorly in *Thililua*, as it does in PMO201.956, and the dentary bone of the former has fewer teeth, but more in the mandibular symphysis (29(15) as opposed to 36+(11)). The articular process is also shorter, almost absent, in *Thililua* than in PMO201.956.

The orbits are different in the two; in *Thililua* it is round and the posterior rim slants forward, but in PMO201.956 the orbit is more triangular, and the posterior rim slants backwards. The jugal in *Thililua* is located higher on the orbit edge than in PMO201.956, and seems to have had a slightly different shape. The postorbitals are also different shapes. In *Thililua* it is a small, slender bone, in PMO201.956 it is more triangular, pointing posteriorly.

Comparison with Manemergus anguirostris *Buchy* et al. *2005*

(Figures 1A-3 and 2A-3)

Other differences that were not scored in the sets are between PMO201.956 and *Manemergus*. At first glance, the two seem to be morphologically very similar, but there are a few differences.

Firstly, the number of teeth is significantly different, even taking into account that *Manemergus* is a juvenile. It has only 15 teeth in the dentary, with 9 in the symphysis. Possibly this number could increase with age, but PMO201.956 has 36+ teeth in the dentary, with 11 in the symphysis. This means that it has more teeth by a factor of 3+.

Secondly, the orbits are again different, with *Manemergus* having oval orbits, while in PMO201.956 they are triangular. The postorbitals are in different positions in the two; In *Manemergus* it forms the dorsal posterior edge of the orbit, while in PMO201.956 it forms the medial posterior edge. The quadrates are larger and the squamosals are far more slender in *Manemergus*, but this could be due to the specimen being a juvenile.

Conclusion

On the basis of cladistic analysis, *Manemergus anguirostris*, *Thililua longicollis* and PMO201.956 are shown to be very closely related and all form a sister group to existing polycotylids. This North African clade is quite stable in its arrangement, even though it is not completely stable within. More material from Morocco for comparison might remedy this.

Although the phylogenetic analyses did not completely resolve the relationship between the three taxa, it does show that *Thililua* and PMO201.956 are closer to each other than both are to *Manemergus.* Enough morphological traits are present in the three specimens to indicate that PMO 201.956 warrants a further analysis and description as a new species. It is, however, so closely related to the other African polycotylids (esp. *Thlilua longicollis*) that it might belong to the *Thililua* genus. It will, in the case of the erection of a new species, be the third African polycotylid species.

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Appendix A – Taxa and holotypes in O'Keefe (2001)

Table with taxa in O'Keefe (2001), with list over holotypes and, if applicable, the namer of the holotype. Institutional abbreviations can be found in appendix E.

Taxon	Author	Holotype	Museum number	Holotype author
Styxosaurus	Welles, 1943	Styxosaurus snowii	KUPV 1301	Williston 1890
Libonectes	Carpenter, 1996	Libonectes morgani	SMUSMP 69120	Welles 1949
Cal l awayasaurus	Carpenter, 1999	Callawayasaurus columbienesis	USMP 38349	Welles 1962
Brancasaurus	Wegner, 1914	Brancasaurus Brancai	N/A - Münster	
Microcleidus	Owen, 1865	Microcleidus homalospondylus	YORM G.502	
Cryptoclidus	Phillips, 1871	Cryptoclidus eurymerus	lost - Neotype BMNH R.2860	Neo: Brown 1981
Muraenosaurus	Seeley, 1874	Muraenosaurus leedsii	BMNH R.2421	
Kimmerosaurus	Brown, 1981	Kimmerosaurus langhami	BMNH R.8431	
Morturneria	Chatterjee & Small, 1989	Morturneria seymorensis	TT VP9219	
MOR 751 (Edgarosaurus muddi)	Druckenmiller 2002	Edgarosaurus muddi	MOR 751	
Polycotylus	Cope, 1869	Polycotylus latipinnis	USNM 27678	
Dolichorhynchops	Williston, 1903	Dolichorhynchops osborni	KUPV 1300	
Trinacromerum	Cragin, 1888	Trinacromerum bentonianum	USNM 10945	
PMO201.956	N/A	N/A	PMO201.956	N/A
Thililua longicollis	Bardet et al. 2003b	Thililua longicollis	MNHGr.PA.11710	
Manemergus anguirostris	Buchy et al. 2005	Manemergus anguirostris	SMNK-PAL 3861	
Tricleidus	Andrews, 1909	Tricleidus seeleyi	BMNH R.3539	
Plesiosaurus	De la Beche & Conybeare, 1821	Plesiosaurus dolichodeirus	BMNH R.39490	Conybeare 1824
Brachau ch enius	Williston, 1903	Brachauchenius lucasi	USNM 4989	
Pliosaurus	Owen, 1841	Pliosaurus brachydeirus	OXFUM J.9245 A,B	
Liopleurodon	Sauvage, 1873	Liopleurodon ferox	BMNH R.3536	
Peleoneustes	Lydekker, 1889b	Peleoneustes philarchus	CAMSM J.46913	Seeley 1869
Kronosaurus	Longman, 1924	Kronosaurus queenslandicus	N/A - Queensland museum	
Hauffiosaurus	O'Keefe 2001	Hauffiosaurus zanoni	N/A - Hauff museum	
Macroplata	Swinton, 1930	Macroplata longirostris	MCZ 1033	Blake 1876
Leptocleidus	Andrews, 1922	Leptocleidus capensis	BMNH R.4828	Andrews 1911a
Simolestes	Andrews, 1909	Simolestes vorax	BMNH R.3319	
Rhomaleosaurus zetlandicus	Phillips, 1854	N/A	YORYM G503	
BMNH R.5488	N/A	?Macroplata tenuiceps	BMNH R.5488	
Rhomaleosaurus megacephalus	Stuchbury, 1846	N/A	Lost - Neotype LEICT G221.1851	Neo: Cruickshank 1994a
Rhomaleosaurus victor	Fraas, 1910	N/A	SMNS 12478	
Attenborosaurus	Bakker, 1993	Attenborosaurus conybeari	lost;BMNH R.1339 (cast)	Sollas 1881
Eurycleidus	Andrews, 1922	Eurycleidus arcuatus	BMNH 2030	Owen 1840
Thalassiodracon	Storrs & Taylor, 1996	Thalassiodracon hawkinsii	BMNH 2018	Owen 1838
Pistosauridae	Zittel, 1887	Pistosaurus longaevus/Augustasaurus hagdorni	N/A - Oberfränkisches Erdgesicht. Mus./FMNH PR 1974	N/A / Sander et al. 1997
Cymatosaurus	v. Fritsch, 1894	Cymatosaurus fridericanus	N/A - Inst. Für Geowiss. - Martin-Luther Uni.	
Simosaurus	Meyer, 1842	Simosaurus gaillardoti	Lost - Neotype: SMNS 16700	Rieppel 1994a

Appendix B – Taxa and holotypes in O'Keefe (2004)

Table with taxa in O'Keefe (2001), with list over holotypes and, if applicable, the namer of the holotype. Institutional abbreviations can be found in appendix E.

Taxon	Author	Holotype	Museum number	Holotype author
Cryptoclidus	Phillips, 1871	Cryptoclidus eurymerus	lost - Neotype BMNH R.2860	Neo: Brown 1981
Muraenosaurus	Seeley, 1874	Muraenosaurus leedsii	BMNH R.2421	
Kimmerosaurus	Brown, 1981	Kimmerosaurus langhami	BMNH R.8431	
Wyoming Taxon	O'Keefe 2004	Tatenectes laramiensis, not holotype		O'Keefe & Wahl 2003
Morturneria	Chatterjee & Small, 1989	Morturneria seymorensis	TT VP9219	
Kaiwhekea	Cruickshank & Fordyce 2002	Kaiwhekea katiki	OU 12649	
Dolichorhynchops	Williston, 1903	Dolichorhynchops osborni	KUPV 1300	
Trinacromerum	Cragin, 1888	Trinacromerum bentonianum	USNM 10945	
PMO201.956	N/A	N/A	PMO201.956	N/A
Thililua longicollis	Bardet et al. 2003b	Thililua longicollis	MNHGr.PA.11710	
Manemergus anguirostris	Buchy et al. 2005	Manemergus anguirostris	SMNK-PAL 3861	
Edgarosaurus	Druckenmiller 2002	Edgarosaurus muddi	MOR 751	
Polycotylus	Cope, 1869	Polycotylus latipinnis	USNM 27678	
Tricleidus	Andrews, 1909	Tricleidus seeleyi	BMNH R.3539	
Plesiosaurus	De la Beche & Conybeare, 1821	Plesiosaurus dolichodeirus	BMNH R.39490	Conybeare 1824
Brancasaurus	Wegner, 1914	Brancasaurus Brancai	N/A - Münster	

Appendix C – Data matrix based on O'Keefe (2001)

This data matrix is based on O'Keefe (2001), where his unapplicable characters (x) are converted to (?), and three taxa (*Thililua longicollis, Manemergus anguirostris,* and PMO201.956) added.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Simosaurus	0	0	0	0	2	2	?	0	0	0	0	?	0	1	2	0	0	0
Cymatosaurus	0	?	?	?	?	2	?	0	1	0	0	?	0	0	?	1	0	1
Pistosauridae	0	0	?	1	?	0	?	1	0	0	0	?	0	0	1	1	0	1
Cryptoclidus	2	0	0	1	2	0	1	0	0	0	0	0	0	0	?	0	0	0
Muraenosaurus	2	1	0	1	2	0	1	0	0	0	0	0	0	0	?	0	0	0
Brancasaurus	2	1	2	1	0	0	0	0	0	0	0	0	0	1	?	0	0	1
Calawayasaurus	2	1	2	0	2	0	0	0	0	0	0	0	0	0	?	0	1	1
Libonectes	2	1	?	0	?	0	0	0	0	0	2	0	0	?	?	?	1	?
Styxosaurus	2	1	?	?	?	0	0	0	0	0	2	0	?	?	?	0	1	0
Kimmerosaurus	?	?	?	?	?	2	?	3	0	0	0	?	?	0	?	0	?	0
Morturneria	?	?	?	?	?	2	1	3	0	0	?	?	?	?	?	?	?	?
Dolichorhynchops	1	2	1	1	0	1	1	2	0	0	1	0	0	?	?	0	0	0
Manemergus anguirostris	1	1	1	0	?	1	?	2	0	0	1	1	0	?	?	0	1	0
MOR 751	0	2	?	?	?	0	1	1	0	0	0	1	0	0	?	0	0	0
PMO201.956	1	?	?	?	?	1	?	2	0	0	2	0	0	?	?	1	0	0
Polycotylus	?	2	1	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?
Thililua_longicollis	1	1	?	?	?	1	?	2	0	?	2	0	0	?	?	?	?	0
Trinacromerum	1	2	1	1	1	1	1	2	0	0	1	0	0	?	?	0	?	0
Plesiosaurus	0	0	2	1	0	0	0	0	0	0	0	0	0	0	?	1	0	0
Tricleidus	2	0	?	1	0	2	1	0	0	0	0	0	0	0	?	?	?	0
Brachauchenius	1	2	?	?	?	1	?	2	1	0	1	1	0	?	?	0	0	0
Hauffiosaurus	1	0	2	1	0	1	0	2	1	0	?	?	?	?	?	?	?	?
Kronosaurus	1	2	2	1	?	1	?	2	?	?	?	?	?	?	?	?	?	?
Liopleurodon	1	2	1	1	1	1	1	2	2	0	1	1	0	?	?	0	0	0
Macroplata	1	0	2	1	0	1	0	2	0	0	?	1	0	?	0	0	?	?
Peloneustes	1	2	1	1	1	1	1	2	1	0	1	1	0	?	?	0	0	0
Pliosaurus	1	2	?	?	?	1	?	2	2	0	1	1	0	?	?	0	0	0
BMNH R.5488	1	0	1	1	1	0	1	1	1	0	?	0	1	0	?	?	0	0
Leptocleidus	?	2	?	1	?	0	1	1	1	0	1	0	1	?	?	0	0	0
Rhomaleo_megaceph.	0	0	0	1	0	0	0	1	1	0	0	1	0	0	?	1	0	0
Rhomaleo_Victor	1	0	0	1	2	0	0	1	1	?	?	0	?	?	?	?	?	?
Rhomaleo_zetland.	0	2	?	?	0	1	?	1	1	0	1	0	1	?	?	0	0	0
Simolestes	1	2	1	1	1	0	1	1	1	0	1	0	?	?	?	0	?	?
Attenborosaurus	1	0	1	1	0	0	0	1	1	0	0	?	?	0	0	?	0	?
Eurycleidus	0	?	0	?	?	0	0	1	1	0	0	?	0	0	0	1	0	0
Thalassiodracon	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0
Microcleidus	2	1	0	1	0	0	0	0	0	0	0	0	0	?	?	0	?	1

Taxon	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Simosaurus	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cymatosaurus	?	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0
Pistosauridae	?	1	0	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0
Cryptoclidus	1	1	1	0	0	0	2	1	1	0	1	2	0	0	1	1	2	?
Muraenosaurus	0	1	1	?	0	0	2	1	1	0	1	2	0	0	?	?	?	?
Brancasaurus	?	1	1	0	0	0	2	1	1	0	1	2	0	0	0	1	2	?
Calawayasaurus	?	1	1	0	0	0	2	1	1	1	1	2	0	0	0	1	2	?
Libonectes	?	1	1	0	0	?	2	1	?	1	1	2	0	0	0	1	2	?
Styxosaurus	?	?	?	0	0	0	2	1	1	1	1	2	0	0	0	1	2	?
Kimmerosaurus	?	1	1	?	0	0	2	1	1	?	1	?	?	?	1	1	?	?
Morturneria	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	1	?	?
Dolichorhynchops	?	1	0	0	0	1	2	1	1	0	1	2	0	0	0	1	2	?
Manemergus anguirostris	0	0	0	0	0	0	2	0	1	?	1	2	?	0	0	1	2	?
MOR 751	1	1	0	0	0	0	2	1	1	0	1	2	0	0	0	1	2	?
PMO201.956	0	?	?	0	0	1	2	?	1	0	1	2	0	0	0	1	2	?
Polycotylus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Thililua_longicollis	1	?	?	0	0	0	2	0	1	0	1	2	0	0	0	1	2	?
Trinacromerum	?	1	?	0	0	1	2	1	1	0	1	2	0	0	0	1	2	?
Plesiosaurus	0	1	0	0	0	0	2	0	1	0	1	1	0	0	0	1	2	0
Tricleidus	?	1	0	0	0	0	2	1	1	?	1	2	0	0	1	1	2	?
Brachauchenius	0	1	0	0	0	0	2	0	1	1	1	0	0	1	0	1	1	1
Hauffiosaurus	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0	1	?	?
Kronosaurus	?	?	?	?	?	?	?	0	1	?	1	?	?	1	?	1	?	?
Liopleurodon	1	1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0
Macroplata	0	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0
Peloneustes	1	1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0
Pliosaurus	?	1	0	0	0	0	2	?	1	1	1	0	0	1	0	1	1	1
BMNH R.5488	1	1	?	0	0	0	2	?	1	?	1	0	0	?	0	?	1	0
Leptocleidus	?	1	0	0	0	0	2	0	1	0	1	0	0	?	0	1	?	?
Rhomaleo_megaceph.	1	1	0	0	0	0	2	0	1	?	1	0	0	?	0	1	1	0
Rhomaleo_Victor	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
Rhomaleo_zetland.	1	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0
Simolestes	?	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0
Attenborosaurus	?	1	0	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0
Eurycleidus	?	1	0	0	0	0	2	0	1	0	1	?	0	?	0	1	?	?
Thalassiodracon	1	1	0	0	0	0	2	0	1	0	1	1	0	0	0	1	1	0
Microcleidus	?	1	1	?	0	0	2	1	1	?	1	?	0	?	0	1	2	?

Taxon	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Simosaurus	0	0	0	1	0	0	0	0	0	?	0	?	?	0	0	0	?	0
Cymatosaurus	0	?	0	0	0	?	?	1	1	?	?	?	?	?	?	?	?	0
Pistosauridae	0	1	0	1	0	?	?	1	?	?	?	?	?	?	?	1	?	0
Cryptoclidus	0	?	1	1	0	1	1	1	?	0	1	0	0	?	0	?	?	1
Muraenosaurus	0	?	?	1	?	0	1	1	?	0	?	0	?	?	?	?	?	1
Brancasaurus	0	?	1	1	1	0	0	1	?	0	?	0	?	?	?	?	?	0
Calawayasaurus	0	?	1	1	1	0	0	1	1	0	2	0	1	1	1	?	?	0
Libonectes	0	?	1	1	?	0	0	1	1	0	2	0	1	1	1	1	?	0
Styxosaurus	0	?	1	1	1	?	?	1	?	?	?	?	?	?	1	1	0	0
Kimmerosaurus	?	?	?	1	?	1	1	1	1	0	0	0	0	?	0	?	?	1
Morturneria	?	?	?	?	?	0	0	?	1	1	0	?	1	?	?	?	?	1
Dolichorhynchops	0	?	1	1	2	0	0	1	1	0	1	1	1	0	0	0	0	1
Manemergus anguirostris	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MOR 751	0	?	1	1	2	0	0	1	1	1	?	?	?	?	0	?	?	?
PMO201.956	1	?	1	1	2	0	1	1	1	0	1	1	1	0	1	0	1	1
Polycotylus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Thililua_longicollis	0	?	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?
Trinacromerum	0	?	1	1	2	?	0	1	?	0	1	1	?	0	?	0	0	1
Plesiosaurus	0	?	1	1	1	?	0	1	?	0	?	?	?	?	1	1	1	1
Tricleidus	0	?	?	1	0	0	0	1	1	0	1	1	0	0	0	?	?	1
Brachauchenius	0	0	1	0	0	?	?	1	?	1	?	0	?	?	?	1	1	1
Hauffiosaurus	?	?	?	?	0	?	1	?	?	?	?	?	?	0	0	?	?	1
Kronosaurus	?	?	?	?	?	?	1	1	1	0	2	0	1	0	0	?	?	?
Liopleurodon	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	1	1
Macroplata	1	0	0	?	?	0	1	1	1	0	0	0	0	0	0	?	0	?
Peloneustes	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	1
Pliosaurus	0	?	?	0	0	0	1	1	?	1	?	?	1	?	?	0	0	1
BMNH R.5488	1	?	0	0	?	0	1	1	?	1	?	0	?	?	?	0	0	?
Leptocleidus	?	?	0	?	1	0	?	1	?	?	?	?	1	0	?	0	0	1
Rhomaleo_megaceph.	1	0	0	?	1	?	1	1	1	1	?	0	1	0	1	0	0	?
Rhomaleo_Victor	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Rhomaleo_zetland.	1	0	0	0	?	?	1	1	?	1	1	1	1	0	1	0	0	1
Simolestes	?	0	?	?	?	0	1	1	?	1	0	0	1	?	?	0	0	1
Attenborosaurus	?	0	?	0	0	?	?	1	?	0	?	?	?	?	?	?	?	1
Eurycleidus	0	?	0	?	?	0	1	1	1	0	0	?	?	0	0	?	?	1
Thalassiodracon	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	1	?	1
Microcleidus	0	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?

Taxon	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Simosaurus	?	0	0	0	0	0	0	?	?	?	0	0	0	?	?	?
Cymatosaurus	?	?	?	2	0	0	0	?	?	?	0	0	?	?	?	?
Pistosauridae	0	?	?	?	0	0	1	0	?	?	0	?	0	0	0	?
Cryptoclidus	0	1	1	1	0	2	1	0	0	?	0	1	0	0	0	1
Muraenosaurus	0	?	1	1	0	2	1	0	0	?	0	1	0	0	0	1
Brancasaurus	0	1	1	1	?	0	1	?	?	0	?	?	0	0	?	0
Calawayasaurus	0	1	1	1	1	0	1	1	0	0	0	1	0	0	0	0
Libonectes	0	1	1	1	1	0	1	2	0	0	0	1	0	0	0	0
Styxosaurus	0	1	1	?	?	?	?	?	?	0	?	?	?	0	?	?
Kimmerosaurus	0	1	1	1	0	2	1	0	0	?	0	?	0	1	0	?
Morturneria	?	?	1	?	?	?	1	?	0	?	?	?	0	?	?	1
Dolichorhynchops	0	1	1	1	0	2	1	2	0	0	0	1	1	1	0	1
Manemergus anguirostris	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
MOR 751	0	?	1	1	0	2	1	1	0	0	0	1	1	1	0	1
PMO201.956	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Polycotylus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Thililua_longicollis	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trinacromerum	0	?	?	1	1	2	1	2	0	0	0	?	1	1	0	1
Plesiosaurus	0	0	0	1	0	1	1	0	0	?	0	0	0	0	0	0
Tricleidus	0	?	?	1	0	2	1	0	0	?	0	1	0	1	0	1
Brachauchenius	1	?	?	1	0	0	1	1	1	0	0	0	0	0	3	0
Hauffiosaurus	?	?	?	2	0	0	1	1	1	0	1	0	0	0	2	0
Kronosaurus	1	?	?	2	0	0	1	1	?	0	?	?	?	0	2	?
Liopleurodon	1	?	0	2	0	1	1	1	1	0	0	0	0	0	3	0
Macroplata	1	?	?	1	0	0	1	0	1	?	?	?	0	0	0	0
Peloneustes	1	1	0	2	0	0	1	1	1	0	1	0	0	0	2	0
Pliosaurus	1	?	?	2	0	?	1	1	?	0	?	?	0	?	3	?
BMNH R.5488	1	1	0	1	?	?	1	1	1	?	0	0	0	0	0	0
Leptocleidus	1	?	?	1	1	2	1	1	1	1	0	0	0	0	0	0
Rhomaleo_megaceph.	1	?	?	1	1	2	1	1	1	1	0	0	0	0	0	0
Rhomaleo_Victor	?	?	?	1	1	2	1	1	1	1	0	?	0	0	?	?
Rhomaleo_zetland.	1	?	?	1	1	2	1	?	1	?	0	?	0	0	0	0
Simolestes	1	?	0	1	?	?	1	1	1	?	0	0	0	0	0	0
Attenborosaurus	1	?	?	2	0	?	1	0	1	?	0	0	0	0	1	0
Eurycleidus	1	1	0	1	0	2	1	0	1	?	0	0	0	0	0	0
Thalassiodracon	1	0	0	1	0	2	1	0	1	?	0	0	0	0	0	0
Microcleidus	0	?	?	?	1	0	1	0	1	0	0	?	0	0	0	0

Taxon	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Simosaurus	?	?	?	?	0	?	0	0	0	0	0	0	0	0	?	0	0	0
Cymatosaurus	?	?	?	?	?	?	0	0	0	0	1	0	1	1	0	0	?	?
Pistosauridae	1	0	?	0	?	?	0	0	0	0	0	0	0	1	?	0	?	?
Cryptoclidus	0	2	1	0	0	0	0	0	0	0	?	0	0	0	?	0	1	0
Muraenosaurus	0	1	1	0	0	0	0	0	1	0	0	0	1	0	?	0	1	0
Brancasaurus	?	?	1	0	?	0	0	?	0	0	1	?	1	?	?	0	?	0
Calawayasaurus	1	2	1	?	0	0	0	0	0	0	1	0	1	0	?	1	1	0
Libonectes	1	2	1	?	0	0	0	?	0	0	1	0	1	0	?	?	1	0
Styxosaurus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	?	0
Kimmerosaurus	0	2	1	1	?	?	?	?	?	0	?	?	?	0	?	?	?	0
Morturneria	?	2	?	1	0	1	?	?	0	?	1	?	?	?	?	0	1	0
Dolichorhynchops	0	2	1	1	0	1	0	0	0	0	1	0	0	0	?	0	?	0
Manemergus anguirostris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
MOR 751	?	2	1	?	?	?	0	?	?	?	?	0	?	0	?	0	?	0
PMO201.956	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Polycotylus	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Thililua_longicollis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Trinacromerum	0	2	1	1	?	1	0	0	?	?	?	0	?	0	?	0	?	0
Plesiosaurus	?	1	?	0	0	0	0	?	0	0	0	0	0	0	?	0	?	0
Tricleidus	0	2	1	1	0	1	?	?	?	0	0	?	0	0	?	0	1	0
Brachauchenius	2	2	?	0	?	0	?	0	?	1	?	1	1	1	0	0	0	?
Hauffiosaurus	2	2	?	0	?	0	0	0	0	0	1	0	1	1	1	0	?	0
Kronosaurus	?	?	?	0	?	0	0	?	?	?	?	?	?	1	?	?	?	0
Liopleurodon	2	2	?	0	?	0	0	1	1	1	1	1	1	1	1	0	1	0
Macroplata	2	2	0	0	?	0	?	?	0	0	1	?	1	0	?	0	0	0
Peloneustes	2	2	?	0	0	0	1	0	0	0	1	1	1	1	2	0	0	0
Pliosaurus	?	?	?	?	?	0	?	?	1	?	1	?	1	1	?	0	0	0
BMNH R.5488	0	2	?	0	?	0	?	?	?	?	?	?	?	?	?	1	?	1
Leptocleidus	1	2	?	0	0	0	1	?	?	0	1	1	0	1	0	1	?	?
Rhomaleo_megaceph.	1	2	?	0	0	0	?	1	0	0	1	1	?	1	1	1	0	1
Rhomaleo_Victor	1	1	?	?	?	0	?	1	1	0	1	0	0	1	?	?	0	1
Rhomaleo_zetland.	?	2	?	0	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Simolestes	?	2	?	0	?	0	?	1	?	?	?	?	?	1	?	?	0	1
Attenborosaurus	0	2	0	0	0	0	1	?	?	?	?	1	?	0	?	0	0	1
Eurycleidus	2	2	0	0	0	0	?	?	0	0	?	?	0	0	?	0	1	1
Thalassiodracon	2	2	0	0	0	0	0	?	?	0	1	?	1	0	?	0	?	0
Microcleidus	?	2	1	0	0	?	?	0	?	?	?	0	?	0	?	0	1	0

Taxon	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106
Simosaurus	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	?	0
Cymatosaurus	2	?	?	?	?	?	?	?	?	?	1	?	1	1	0	0	?	0
Pistosauridae	1	?	?	?	?	?	?	?	?	?	0	?	1	0	?	0	?	0
Cryptoclidus	0	0	0	0	0	0	1	0	1	0	0	?	0	0	0	0	0	1
Muraenosaurus	0	0	0	0	0	0	1	0	1	0	0	?	0	0	0	0	0	0
Brancasaurus	?	?	?	?	?	?	?	?	?	?	0	?	0	0	0	0	?	0
Calawayasaurus	1	0	0	0	0	?	0	0	0	1	0	?	0	1	0	0	?	0
Libonectes	1	0	1	0	0	0	0	0	0	1	0	?	0	1	0	0	?	0
Styxosaurus	1	?	?	0	?	?	0	?	?	1	0	?	0	1	0	0	?	0
Kimmerosaurus	0	0	?	0	1	0	1	?	1	1	?	?	0	0	2	0	?	3
Morturneria	?	?	?	?	?	0	?	?	0	1	0	?	0	0	2	0	?	2
Dolichorhynchops	3	2	0	0	0	0	1	0	1	1	0	?	0	0	0	0	?	0
Manemergus anguirostris	3	1	?	0	0	?	1	1	?	?	?	1	0	0	0	0	2	0
MOR 751	2	1	0	0	0	?	1	0	1	1	0	?	0	1	1	0	?	1
PMO201.956	3	?	?	1	0	?	1	?	?	0	1	0	0	?	0	0	?	0
Polycotylus	?	?	0	?	0	0	1	0	1	1	?	?	?	?	1	0	?	?
Thililua_longicollis	3	?	?	0	0	?	1	1	?	0	?	0	0	0	0	0	1	0
Trinacromerum	3	2	?	0	?	0	1	0	1	1	0	?	0	0	0	0	?	0
Plesiosaurus	0	?	?	?	?	0	0	?	0	0	0	?	0	0	0	0	0	0
Tricleidus	0	0	0	0	0	0	?	0	1	1	0	?	0	0	0	0	0	0
Brachauchenius	2	1	?	1	?	?	0	?	0	0	1	?	0	0	1	0	?	?
Hauffiosaurus	3	1	0	?	?	?	?	?	0	0	1	1	0	0	0	0	?	2
Kronosaurus	3	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?
Liopleurodon	2	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0
Macroplata	3	1	?	1	?	?	?	0	0	0	?	?	0	0	0	0	0	?
Peloneustes	3	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	0	1
Pliosaurus	2	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	1	1
BMNH R.5488	2	1	?	?	?	?	?	?	?	0	1	?	?	0	1	0	0	1
Leptocleidus	2	?	0	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0
Rhomaleo_megaceph.	2	1	1	?	?	?	?	?	0	0	1	?	1	0	1	0	0	0
Rhomaleo_Victor	2	1	1	?	?	?	?	0	0	0	?	?	1	0	1	0	?	?
Rhomaleo_zetland.	2	1	?	?	0	?	0	0	0	0	1	?	1	0	1	0	0	?
Simolestes	2	1	?	1	0	1	0	0	0	0	?	?	1	0	1	0	0	0
Attenborosaurus	2	1	?	0	0	?	?	0	0	0	1	?	0	0	1	0	0	0
Eurycleidus	2	1	?	?	0	?	0	0	0	0	1	1	?	0	0	0	?	?
Thalassiodracon	2	1	?	?	?	?	0	?	0	0	0	?	0	0	0	0	0	0
Microcleidus	1	0	?	0	?	0	0	?	0	1	0	?	0	?	0	0	0	?

Taxon	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124
Simosaurus	0	?	?	?	0	0	0	0	0	0	0	0	?	0	0	0	?	0
Cymatosaurus	0	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?
Pistosauridae	0	?	?	?	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Cryptoclidus	0	1	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	1
Muraenosaurus	0	1	0	1	1	1	0	0	0	?	1	1	0	2	1	1	1	1
Brancasaurus	?	?	1	0	1	1	?	?	0	0	1	1	0	2	1	0	?	0
Calawayasaurus	0	?	?	?	3	1	1	?	0	1	1	1	0	2	1	0	?	0
Libonectes	0	1	?	0	3	1	1	?	1	1	1	1	0	2	1	1	?	0
Styxosaurus	?	?	?	?	3	1	?	?	1	1	1	1	0	2	1	1	?	0
Kimmerosaurus	2	1	?	?	?	2	?	0	0	0	1	1	0	2	?	1	1	?
Morturneria	2	0	0	2	?	2	?	?	0	1	1	1	0	2	?	0	?	?
Dolichorhynchops	0	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1
Manemergus anguirostris	0	?	?	?	2	0	0	0	?	0	1	?	?	?	0	1	0	?
MOR 751	0	1	1	2	2	2	?	1	0	0	1	1	0	?	?	0	?	?
PMO201.956	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polycotylus	?	1	1	2	2	2	0	?	0	0	1	1	0	1	1	0	?	1
Thililua_longicollis	1	1	?	0	0	2	0	1	?	0	1	0	?	?	0	?	?	1
Trinacromerum	1	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1
Plesiosaurus	?	?	?	0	1	0	?	0	0	0	0	1	0	2	1	0	0	0
Tricleidus	?	1	?	1	0	0	1	0	0	0	1	1	0	2	1	0	1	1
Brachauchenius	?	?	?	?	2	2	?	?	0	0	1	1	1	2	?	0	?	0
Hauffiosaurus	1	?	?	?	0	0	0	?	0	0	0	?	0	2	?	0	?	?
Kronosaurus	?	?	1	?	2	2	?	?	?	?	1	1	?	2	?	0	?	0
Liopleurodon	1	?	?	?	2	2	0	0	0	0	0	1	1	2	1	0	1	0
Macroplata	1	0	?	0	0	0	?	1	0	0	0	1	0	2	0	0	?	0
Peloneustes	1	0	0	0	2	2	0	1	0	0	0	1	0	2	0	0	1	0
Pliosaurus	1	?	?	?	?	2	?	0	0	0	0	1	1	2	?	0	?	0
BMNH R.5488	?	0	1	0	0	2	0	1	0	0	0	1	0	1	?	0	?	0
Leptocleidus	0	?	?	?	2	2	0	1	0	0	1	1	0	2	0	0	?	0
Rhomaleo_megaceph.	?	?	?	?	0	2	?	1	0	0	0	1	0	1	?	0	0	0
Rhomaleo_Victor	?	?	?	?	0	?	0	?	0	0	?	?	0	?	?	0	0	?
Rhomaleo_zetland.	?	?	?	?	2	2	0	1	0	0	0	1	0	1	?	0	?	0
Simolestes	?	?	?	0	2	2	?	0	0	0	0	1	0	1	1	0	1	0
Attenborosaurus	0	?	?	?	0	0	0	?	0	0	0	1	?	2	?	0	0	0
Eurycleidus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Thalassiodracon	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0
Microcleidus	?	0	?	?	1	1	1	0	1	1	0	1	0	2	?	1	0	0

Taxon	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142
Simosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?
Cymatosaurus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pistosauridae	?	1	0	0	?	0	?	1	0	?	0	0	0	1	1	?	0	0
Cryptoclidus	1	1	1	1	2	1	?	0	0	0	1	1	2	1	1	0	0	1
Muraenosaurus	1	1	1	1	2	1	?	0	0	1	1	1	2	1	1	0	0	1
Brancasaurus	0	1	1	1	2	1	1	0	0	0	1	?	2	1	1	0	1	1
Calawayasaurus	1	1	1	1	2	1	?	0	0	0	1	0	?	1	1	0	1	1
Libonectes	1	?	1	1	?	1	?	0	0	0	2	0	2	1	1	?	1	1
Styxosaurus	1	?	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Kimmerosaurus	1	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Morturneria	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dolichorhynchops	1	1	1	1	2	0	?	0	0	2	0	1	1	1	1	1	0	1
Manemergus anguirostris	1	1	1	?	?	?	1	?	0	?	?	?	?	?	1	?	?	1
MOR 751	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
PMO201.956	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polycotylus	1	1	1	1	2	0	?	0	0	2	0	1	1	1	1	1	?	?
Thililua_longicollis	0	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Trinacromerum	1	1	1	1	2	0	?	0	0	2	0	1	1	1	1	1	0	1
Plesiosaurus	1	1	1	1	2	1	?	0	1	0	0	0	1	1	1	0	0	1
Tricleidus	1	1	1	1	2	0	0	0	0	2	1	0	2	1	1	0	0	1
Brachauchenius	1	1	1	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?
Hauffiosaurus	?	?	1	1	?	0	?	0	?	?	0	0	?	1	1	0	0	1
Kronosaurus	0	?	1	1	2	0	?	?	?	?	0	?	0	1	1	?	0	?
Liopleurodon	0	1	1	1	2	0	?	0	?	?	0	?	?	1	1	0	0	1
Macroplata	0	?	1	1	0	0	?	?	?	?	?	?	?	?	1	?	?	?
Peloneustes	0	1	1	1	2	0	0	0	?	?	0	0	0	1	1	0	0	1
Pliosaurus	0	1	1	1	?	0	?	?	?	?	?	?	?	?	?	0	?	?
BMNH R.5488	0	1	1	1	?	0	?	0	0	0	0	0	1	1	1	0	0	0
Leptocleidus	0	1	1	1	?	0	0	0	0	0	0	0	1	1	1	0	0	1
Rhomaleo_megaceph.	0	1	1	1	2	0	?	0	?	?	?	?	?	?	1	?	0	?
Rhomaleo_Victor	?	?	?	1	2	?	?	?	0	?	0	0	1	1	1	0	0	1
Rhomaleo_zetland.	?	1	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Simolestes	?	1	1	1	?	0	?	0	?	?	0	?	0	1	1	0	0	0
Attenborosaurus	0	1	1	1	0	0	?	0	0	0	0	0	0	1	1	0	0	1
Eurycleidus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Thalassiodracon	0	1	1	1	2	0	?	0	0	0	0	0	1	1	1	0	0	1
Microcleidus	1	1	1	1	2	1	?	0	?	?	1	?	2	?	1	0	0	1

Taxon	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Simosaurus	0	0	0	?	0	0	0	0	0	?	0	?	?	0	0	0	1	2
Cymatosaurus	?	1	?	?	1	?	?	0	0	?	?	?	?	?	?	?	0	1
Pistosauridae	0	?	1	?	?	1	1	0	0	?	0	?	?	1	1	0	1	?
Cryptoclidus	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2
Muraenosaurus	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	2
Brancasaurus	1	0	1	1	1	1	1	1	1	?	?	0	0	1	?	0	1	2
Calawayasaurus	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	1	2
Libonectes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Styxosaurus	?	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?
Kimmerosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Morturneria	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?
Dolichorhynchops	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2
Manemergus anguirostris	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MOR 751	?	?	?	?	?	?	?	1	1	1	1	0	0	1	1	0	1	2
PMO201.956	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polycotylus	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	2
Thililua_longicollis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trinacromerum	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2
Plesiosaurus	1	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	2
Tricleidus	1	1	1	0	1	1	?	1	1	1	1	0	0	1	1	0	1	2
Brachauchenius	?	?	?	?	?	?	?	1	1	?	?	0	1	?	?	0	?	?
Hauffiosaurus	1	1	1	?	1	1	?	1	1	0	0	0	0	1	1	1	1	2
Kronosaurus	?	1	1	1	1	1	?	?	1	?	?	0	0	?	?	0	1	2
Liopleurodon	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	2
Macroplata	1	1	1	1	1	1	?	1	1	0	0	0	0	1	1	?	1	2
Peloneustes	1	1	1	0	1	1	1	1	1	0	0	0	0	1	1	0	1	2
Pliosaurus	1	1	1	0	1	1	?	1	1	0	0	0	1	1	1	0	1	2
BMNH R.5488	1	1	1	1	1	1	1	0	1	?	0	0	0	1	1	1	1	2
Leptocleidus	?	?	?	?	?	?	?	1	1	0	0	?	0	1	?	?	?	?
Rhomaleo_megaceph.	1	1	1	?	1	1	1	0	1	0	0	0	0	1	1	1	1	2
Rhomaleo_Victor	?	1	1	1	1	1	?	0	1	0	0	0	0	1	1	1	1	2
Rhomaleo_zetland.	?	?	1	?	?	?	?	0	1	0	0	0	0	1	1	1	1	2
Simolestes	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	2
Attenborosaurus	1	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1	2
Eurycleidus	1	1	1	0	1	1	1	?	1	?	?	?	?	?	?	?	?	?
Thalassiodracon	1	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	2
Microcleidus	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	2

Taxon	161	162	163	164	165	166
Simosaurus	0	0	0	0	0	1
Cymatosaurus	?	?	?	?	?	0
Pistosauridae	0	0	0	?	?	0
Cryptoclidus	1	1	1	1	0	0
Muraenosaurus	1	1	1	1	0	0
Brancasaurus	1	?	1	1	?	0
Calawayasaurus	1	0	1	1	1	?
Libonectes	?	?	?	?	?	?
Styxosaurus	?	?	?	?	?	?
Kimmerosaurus	?	?	?	?	?	?
Morturneria	1	?	?	1	?	?
Dolichorhynchops	1	3	1	1	1	?
Manemergus anguirostris	?	?	?	?	?	?
MOR 751	1	?	1	1	1	?
PMO201.956	?	?	?	?	?	?
Polycotylus	1	3	1	1	?	0
Thililua_longicollis	?	?	?	?	?	?
Trinacromerum	1	3	1	1	1	0
Plesiosaurus	0	1	1	1	0	0
Tricleidus	1	2	1	1	?	0
Brachauchenius	1	?	1	1	?	?
Hauffiosaurus	0	2	1	1	0	0
Kronosaurus	1	?	?	1	?	?
Liopleurodon	1	0	1	1	0	0
Macroplata	0	?	?	1	?	?
Peloneustes	1	0	1	1	0	0
Pliosaurus	1	?	?	1	?	0
BMNH R.5488	0	?	?	1	?	0
Leptocleidus	?	?	?	1	?	?
Rhomaleo_megaceph.	0	?	?	1	?	0
Rhomaleo_Victor	0	3	1	1	0	0
Rhomaleo_zetland.	0	?	?	1	?	?
Simolestes	0	0	?	1	?	?
Attenborosaurus	0	0	1	1	0	0
Eurycleidus	?	?	?	?	?	?
Thalassiodracon	0	0	1	1	0	0
Microcleidus	0	1	1	1	0	0

Appendix D – Data matrix based on O'Keefe (2004)

This data matrix is based on O'Keefe (2004), where his unappliccable characters (x) are converted to (?), and three taxa (*Thililua longicollis, Manemergus anguirostris,* and PMO201.956) added.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Brancasaurus	2	1	2	0	0	0	0	0	0	1	0	1	?	1	0	2	1	0	2	0	1	0
Cryptoclidus	2	0	0	2	0	1	0	0	0	0	0	0	1	1	0	2	1	0	2	1	0	1
Muraenosaurus	2	1	0	2	0	1	0	0	0	0	0	0	0	1	0	2	1	0	2	?	?	0
Tricleidus	2	0	?	0	2	1	0	0	0	0	?	0	?	0	0	2	1	?	2	1	0	0
Plesiosaurus	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	?
Dolichorhynchops	1	2	1	0	1	1	2	1	0	?	0	0	?	0	1	2	1	0	2	0	2	0
Polycotylus	?	2	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trinacromerum	1	2	1	1	1	1	2	1	0	?	0	0	?	?	1	2	1	0	2	0	2	?
PMO201.956	1	?	?	?	1	?	2	2	0	?	1	0	0	?	1	2	?	0	2	0	2	0
Thililua_longicollis	1	1	?	?	1	?	2	2	0	?	?	0	1	?	0	2	0	0	2	0	2	?
Manemergus anguirostris	1	1	1	?	1	?	2	1	1	?	0	0	0	0	0	2	0	?	2	0	?	?
Edgarosaurus	0	2	?	?	0	1	1	0	1	0	0	0	1	0	0	2	1	0	2	0	2	0
Wyoming Taxon	?	?	?	?	?	?	?	0	?	0	?	?	?	?	0	?	1	?	?	1	?	1
Kaiwhekea	2	0	?	?	2	1	0	1	0	?	0	?	1	0	0	2	1	?	?	?	1	?
Kimmerosaurus	?	?	?	?	2	?	3	0	?	0	0	0	?	1	0	2	1	?	?	1	?	1
Morturneria	?	?	?	?	2	1	3	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0

Taxon	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Brancasaurus	0	0	?	0	?	?	?	?	0	1	?	0	?	?	?	0	0	0	?	0	0	0
Cryptoclidus	1	0	1	0	0	0	?	?	1	1	0	2	0	0	1	0	0	1	2	0	0	0
Muraenosaurus	1	0	?	0	?	?	?	?	1	1	0	2	0	0	1	0	0	1	1	0	0	1
Tricleidus	0	0	1	1	0	0	?	?	1	?	0	2	0	0	1	0	1	1	2	1	1	?
Plesiosaurus	0	0	?	?	?	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0
Dolichorhynchops	0	0	1	1	1	0	0	0	1	1	0	2	2	0	1	1	1	1	2	1	1	0
Polycotylus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Trinacromerum	0	0	1	1	?	?	0	0	1	?	1	2	2	0	?	1	1	1	2	1	1	?
PMO201.956	1	0	1	1	1	1	0	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?
Thililua_longicollis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Manemergus anguirostris	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Edgarosaurus	0	1	?	?	?	0	?	?	?	1	0	2	1	0	1	1	1	1	2	?	?	?
Wyoming Taxon	1	?	?	?	?	?	0	?	?	?	?	2	?	1	?	0	1	1	?	1	1	?
Kaiwhekea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kimmerosaurus	1	0	0	0	0	0	?	?	1	1	0	2	0	0	?	0	1	?	2	1	?	?
Morturneria	0	1	0	?	1	?	?	?	1	1	?	?	?	0	?	0	?	1	2	1	1	0

Taxon	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Brancasaurus	1	?	1	?	?	?	?	?	?	0	0	0	?	1	0	1	1	?	?	0	2	1
Cryptoclidus	?	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	2	0
Muraenosaurus	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	?	2	1
Tricleidus	0	?	0	0	0	0	?	1	1	0	0	0	?	?	1	0	0	1	0	0	2	1
Plesiosaurus	0	0	0	0	?	?	0	0	0	0	0	0	?	?	0	1	0	?	0	0	2	1
Dolichorhynchops	1	1	0	3	2	0	1	1	1	0	0	0	0	1	2	2	2	1	?	0	2	1
Polycotylus	?	?	?	?	?	0	1	1	1	?	1	?	?	1	2	2	2	0	?	0	1	1
Trinacromerum	?	1	?	3	2	?	1	1	1	0	0	0	1	1	2	2	2	1	?	0	2	1
PMO201.956	?	?	?	3	?	0	1	?	0	?	0	0	1	?	?	?	?	?	?	?	?	?
Thililua_longicollis	?	?	?	3	?	0	1	?	0	0	0	0	1	?	0	0	2	0	1	0	?	0
Manemergus anguirostris	?	?	?	3	1	0	1	?	?	0	0	0	0	?	?	2	0	0	0	0	?	0
Edgarosaurus	?	0	?	2	1	0	1	1	1	1	1	1	0	1	2	2	2	?	1	0	?	?
Wyoming Taxon	?	?	?	?	?	?	?	?	?	?	2	?	?	?	2	?	2	?	0	1	2	0
Kaiwhekea	?	?	?	0	0	?	?	?	0	?	2	2	2	?	?	1	2	?	1	1	2	?
Kimmerosaurus	?	?	?	0	0	1	1	1	1	0	2	3	2	?	?	?	2	?	0	0	2	?
Morturneria	1	?	?	?	?	?	?	0	1	0	2	2	2	0	2	?	2	?	?	1	2	?

Taxon	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Brancasaurus	0	?	0	0	1	1	0	0	1	?	2	0	1	0	1	1	?	?	0	1	?	?
Cryptoclidus	1	1	1	1	1	?	0	0	1	1	2	0	0	1	0	1	1	0	0	1	1	0
Muraenosaurus	1	1	1	1	1	?	0	1	1	1	2	0	0	1	0	1	1	1	0	1	1	0
Tricleidus	0	1	1	1	0	0	0	2	1	0	2	0	0	1	0	1	1	1	0	1	2	?
Plesiosaurus	0	0	0	1	1	?	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0
Dolichorhynchops	0	?	1	1	0	?	0	2	0	1	1	1	0	1	0	1	1	0	0	1	3	1
Polycotylus	0	?	1	1	0	?	0	2	0	1	1	1	?	1	0	1	1	1	0	1	3	?
Trinacromerum	0	?	1	1	0	?	0	2	0	1	1	1	0	1	0	1	1	0	0	1	3	1
PMO201.956	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Thililua_longicollis	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Manemergus anguirostris	1	0	?	1	?	1	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Edgarosaurus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	?	1
Wyoming Taxon	0	1	1	0	0	?	?	?	1	?	0	0	0	?	?	1	1	1	?	1	?	?
Kaiwhekea	0	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Kimmerosaurus	1	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Morturneria	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?

Taxon	89	90	91	92	93	94	95
Brancasaurus	0	0	?	1	0	0	0
Cryptoclidus	1	0	0	0	1	0	0
Muraenosaurus	1	?	0	0	1	0	0
Tricleidus	1	0	0	0	1	0	0
Plesiosaurus	0	1	1	1	0	0	0
Dolichorhynchops	1	0	0	1	2	1	1
Polycotylus	1	?	?	0	1	0	1
Trinacromerum	1	0	0	1	2	0	1
PMO201.956	?	1	?	1	?	1	?
Thililua_longicollis	?	0	?	0	?	0	?
Manemergus anguirostris	?	0	?	1	?	0	?
Edgarosaurus	?	0	?	0	2	0	?
Wyoming Taxon	1	?	?	?	?	?	0
Kaiwhekea	1	?	?	0	?	1	?
Kimmerosaurus	1	0	?	0	1	0	?
Morturneria	1	?	?	?	?	?	?

Appendix E – Abbreviations

Institutional abbreviations

1. AMNH: American museum of Natural History, New York, New York, USA
2. BMNH: The Natural History Museum, London, UK
3. BRI: Banque de la República de Villa de Leyva, Bogota, Columbia
4. BRSMG: Bristol Museum and Art Gallery, Bristol, UK
5. CAMSM: Sedgwick Museum, Cambridge, UK
6. FHSM: Sternberg Museum of Natural History, Fort Hayes, Kansas, USA
7. FMNH: Field Museum of Natural History, Chicago, Illinois, USA
8. GPIT: Institut und Museum für Geologie und Paläontologie, Tübingen, Germany
9. Hauff: Urwelt Museum Hauff, Holzmaden, Germany
10. KUPV: Kansas Museum of Natural History, Lawrence, Kansas, USA
11. LEICT: Leicester City Museum, Leicester, UK
12. MAN UM: Manchester Museum, Manchester, UK
13. Münster: Geologisch- Paläontologisches Museum der Universität Münster, Münster, Germany
14. MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
15. MOR: Museum of the Rockies, Bozeman, Montana, USA
16. NMW: National Museum of Wales, Cardiff, Wales
17. OXFUM: Oxford University Museum of Natural History, Oxford, UK
18. PETMG: Peterborough Museum and Art Gallery, Peterborough, UK
19. SM: Strecker Museum, Baylor University, Waco, Texas, USA
20. SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany
21. SMUSMP: Southern Methodist University Museum of Palaeontology, Dallas, Texas, USA
22. TTVP: Texas Technical Institute, Lubbock, Texas, USA
23. UCMP: University of California Museum of Paleontology, Berkeley, California, USA
24. USNM: Smithsonian Institution, Washington, D.C., USA
25. UW: University of Wyoming, Laramie, Wyoming, USA
26. YORYM: Yorkshire Museum, York, UK
27. YPM: Yale-Peabody Museum, New Haven, Connecticut, USA

Abbreviations in Buchy et al. *2005*

an: angular
co: coronoid
d: dentary
en: external naris
ff: frontal foramen
fr: frontal
j: jugal
mx: maxilla
orb: orbit
par: parietal
pc: parietal crest (sagittal crest, authors remark)
pfor: parietal foramen (pineal foramen, authors remark)
pmx: premaxilla
po: postorbital
prf: prefrontal
q: quadrate
san: surangular
spl: splenial
sq: squamosal
tf: supratemporal fenestra

Abbreviations in Bardet et al. *2003*

An: angular
Ar: articular
Ax: axis
C: cervica vertebra
De: dentary
ff: frontal foramen
Fr: frontal
Ju: jugal
Mx: maxilla
n: external naris
o: orbit
Pa: parietal
Pfr: prefrontal
Pmx: premaxilla
Po: postorbital
Q: quadrate
San: surangular
sc: sagittal crest
tf: temporal fenestra
?: unknown