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Systematic Palaeontology (Vertebrate Palaeontology)

A new polycotylid plesiosaur from the Late Cretaceous (Turonian) of Morocco

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Abstract

A new Polycotylidae (Plesiosauria) from the Late Cretaceous (Turonian) of southern Morocco is described. *Thililua longicollis* gen. et sp. nov. is based on a complete cranium and 37 associated vertebrae. It differs from other polycotylids in several cranial and especially vertebral characters, such as the occurrence of 30 cervical vertebrae, whose centra are nearly as long as high and bear laterally longitudinal ridges. *Thililua* is the first polycotylid hitherto found in Africa and under subtropical palaeolatitudes. ***To cite this article: N. Bardet et al., C. R. Palevol 2 (2003).***

Résumé

Un nouveau plésiosaure polycotylidé du Crétacé supérieur (Turonien) du Maroc. Un nouveau Polycotylidae (Plesiosauria) provenant du Crétacé supérieur (Turonien) du Sud du Maroc est décrit. *Thililua longicollis* gen. et sp. nov. est basé sur un crâne complet et 37 vertèbres associées. Il diffère des autres polycotylidés par des caractères crâniens et surtout vertébraux, tels que la présence de 30 vertèbres cervicales dont les centres sont presque aussi longs que hauts et portent latéralement des crêtes longitudinales. *Thililua* est le premier polycotylidé trouvé jusqu'à présent en Afrique et sous des paléolatitudes subtropicales. ***Pour citer cet article : N. Bardet et al., C. R. Palevol 2 (2003).***

Keywords: Plesiosauria; Polycotylidae; Late Cretaceous; Turonian; Morocco; New taxon

Mots clés : Plesiosauria ; Polycotylidae ; Crétacé supérieur ; Turonien ; Maroc ; Nouveau taxon

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Introduction

Les Polycotylidae sont des plésiosaures à cou court, connus durant le Crétacé et trouvés essentiellement en Amérique du Nord [4,9,19,20]. La monophylie des Polycotylidae, bien que longtemps mise en doute, est actuellement appuyée par plusieurs travaux [1,4,13]. Classiquement inclus au sein des pliosaures [3,18], les polycotylidés sont de nos jours considérés comme étant plus proches des plésiosaures élasmosauridés à long cou [1,4,5,13], une hypothèse déjà émise il y a près d'un siècle [20].

Contexte géologique

Le spécimen (MNHGr.PA.11710, Muséum d'Histoire naturelle de Grenoble) provient de la région de Goulmima, Province d'Er-Rachidia, Sud du Maroc, bien que sa provenance exacte reste inconnue (Fig. 1). Les gisements localisés lors de travaux de terrain près des villages de Tadirhourst et Asfla ont livré une riche faune de vertébrés marins [2,6], ainsi que des ammonites. Les fossiles sont préservés dans des nodules ovoïdes situés au sommet (unité 4) de la barre calcaire du Cénomanien–Turonien [7,8]. L'unité 4 est d'âge Turonien inférieur (présence de l'ammonite *Mammites* notamment) et correspond à un environnement de plate-forme ouverte, lié au maximum de la transgression cénomano-turonienne [10].

Systématique

Plesiosauria de Blainville, 1835
Polycotylidae Cope, 1869
Thililua gen. nov.

Étymologie. De *Thililua*, dieu aquatique dans la mythologie berbère [12].

Espèce type. *Thililua longicollis*.

Diagnose. Comme pour l'espèce type.

Thililua longicollis sp. nov.

Étymologie. En référence à son long cou.

Holotype. MHNGr.PA.11710, crâne et mandibule subcomplets et 37 vertèbres associées articulées, comprenant les séries cervicale et pectorale complètes ainsi que les quatre premières vertèbres dorsales (Figs. 2 et 3; Tableaux 1 et 2).

Localité et horizon type. Près de Goulmima, province d'Er-Rachidia, Sud du Maroc ; unité 4, Barre calcaire du Cénomanien–Turonien, Crétacé supérieur, Turonien inférieur [10].

Diagnose. Polycotylidé caractérisé par un prémaxillaire portant des processus étendus latéralement entre les narines et les foramens frontaux ; des orbites régulièrement ovales sans processus supraorbitaires ; cinq dents prémaxillaires, au moins 22 maxillaires et 29 dentaires ; une symphyse mandibulaire portant 15 paires de dents ; 30 vertèbres cervicales dont les centres sont presque aussi longs que hauts et qui portent latéralement des crêtes longitudinales qui sont dédoublées de la 19^{e} à la 22^{e} vertèbre.

Discussion

Thililua longicollis est rapporté aux Polycotylidae (sensu [4,5,13]) de par la combinaison des caractères suivants : prémaxillaire dont le processus dorsal est étendu postérieurement et sépare les frontaux (parallélisme avec les pliosauridés) ; contact étendu entre le maxillaire et le squamosal ; jugal formant une barre subrectangulaire horizontale (comme chez les élasmosauridés) ; splénial inclu dans la symphyse mandibulaire.

Thililua longicollis partage également avec tous les polycotylidés (*Dolichorhynchops*, *Georgiasaurus*, *Polycotylus*, *Sulcusuchus*, *Trinacromerum*) [4,5,11,14,16,17,19,20], sauf *Edgarosaurus muddi* (rapportée provisoirement aux polycotylidés, voir [9]), un crâne gracile à long museau, dont la partie préorbitaire représente environ 60% de la longueur totale et une dentition uniforme sans dents caniniformes. De plus, le prémaxillaire contacte le pariétal et il n'y a pas de foramen pinéal, comme chez *Dolichorhynchops osborni*, *Trinacromerum bentonianum* et *Sulcusuchus erraini* (à la différence d'*Edgarosaurus*) [4,9,11]. *Thililua* possède enfin un foramen frontal au-dessus de l'orbite et une symphyse mandibulaire longue (environ la moitié de la longueur totale), comme chez *Dolichorhynchops* et *Trinacromerum* [5]. Ce dernier caractère est aussi présent chez *Polycotylus latipinnis* [16]. En attendant une révision complète du groupe et en l'absence de diagnose consensuelle (comparer [4] et [9]), l'ensemble de ces caractères est ici considéré provisoirement comme caractéristique des Polycotylidae ou de clades moins inclusifs.

Thililua a des dents longues et finement striées, comme chez *Dolichorhynchops* et *Sulcusuchus*, à la

différence de celles de *Polycotylus*, *Trinacromerum* et *Edgarosaurus*, qui sont robustes et fortement striées [4,9,11].

Thililua diffère de *Dolichorhynchops* et de *Trinacromerum* par l'absence d'un processus supraorbitaire, la présence d'un contact prémaxillaire–pariétal situé postérieurement aux orbites et une facette costale portée par le centrum de l'axis seulement [4,5,19]. De plus, son suspensorium est vertical, contrairement à *Trinacromerum* [4].

Finalement, *Thililua longicollis* diffère des autres polycotylidés par les autapomorphies mentionnées dans la diagnose.

D'un point de vue paléobiogéographique, *Thililua* est le premier polycotylidé trouvé jusqu'à présent en Afrique et sous des paléolatitudes subtropicales.

1. Introduction

Polycotylidae is a group of short-necked plesiosaurs exclusive of the Cretaceous. Their remains are essentially known from North America [4,9,19,20], but more fragmentary material has also been described in Asia [15,17], South America [11], Australia and New-Zealand [15]. They stratigraphically range from the Aptian–Albian to the Maastrichtian [15]. The validity of the Polycotylidae is still under debate, but its monophyly has been supported by recent works [1,4,13]. The Polycotylidae currently includes *Polycotylus* Cope, 1869 [4,16,20], *Trinacromerum* Cragin, 1888 [4], *Dolichorhynchops* Williston, 1902 [4,5,19], *Georgiasaurus* Otschev, 1977 [14,17], *Sulcusuchus* Gasparini & Spalletti, 1990 [11] and, tentatively, *Edgarosaurus* Druckenmiller, 2002 [9]. Concerning their phylogenetic relationships within the Plesiosauria, polycotylids have been considered for a long time as pliosauroids [3,18], but Carpenter [4,5] recently reelaborated Williston's [20] suggestion that polycotylids are more closely related to long-necked elasmosaurids than to "pliosaurs", a view supported by cladistic analysis [1,13].

Abbreviations: MNHGr, « Muséum d'Histoire naturelle de Grenoble », France.

2. Geological context

The specimen (MNHGr.PA.11710) comes from the Goulmima region in the southern slope of the High Atlas of Morocco (Fig. 1). Though its exact location remains unknown, fieldwork has allowed us to locate several fossiliferous localities near the villages of Tadirhourst and Asfla, north of Goulmima, Er-Rachidia Province. These sites have yielded a rich fauna of marine vertebrates, including actinopterygians [6], marine reptiles [2], as well as ammonites. The fossils are preserved in ovoid calcareous nodules that occur near the top of a Cenomanian–Turonian limestone bar, a reference level in North Africa [7,8]. The fossiliferous nodules are concentrated in Unit 4 of Ferrandini et al. [10], which is Early Turonian in age according to the ammonite association (mainly *Mammites*). This unit corresponds to an open platform environment related to the maximum of the Cenomanian–Turonian transgressive phase [10].

3. Systematic palaeontology

Plesiosauria de Blainville, 1835
Polycotylidae Cope, 1869
Thililua gen. nov.

Etymology. From *Thililua*, aquatic god in the Berber mythology [12].

Type species. *Thililua longicollis*.

Diagnosis. As for type species.

Thililua longicollis sp. nov.

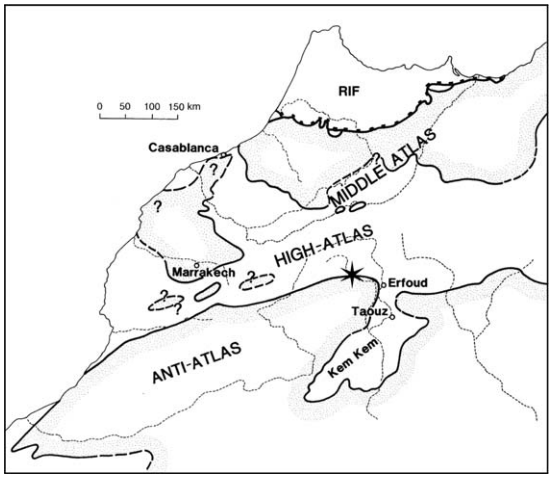


Fig. 1. Palaeogeographical map of the Cenomanian–Turonian transgression in Morocco and location of the fossiliferous site (black star) (after [7,8]).

Fig. 1. Schéma paléogéographique de la transgression cénomano-turonienne au Maroc et localisation du gisement (étoile noire) (d'après [7,8]).

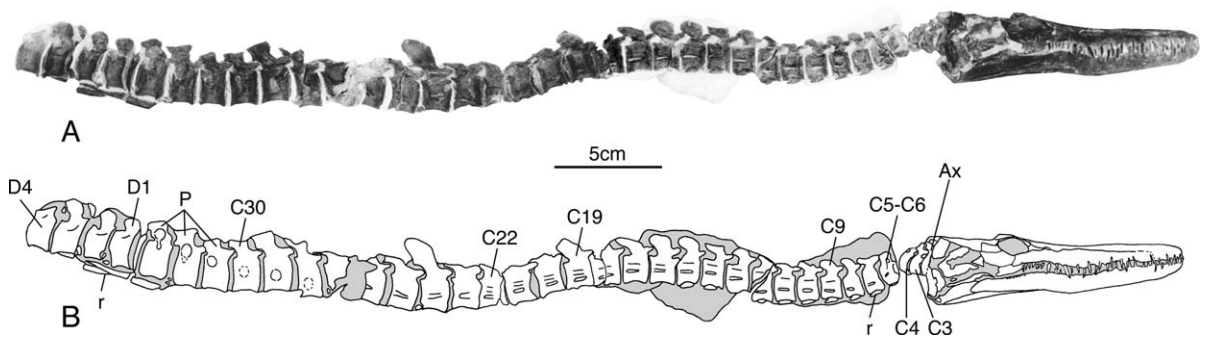


Fig. 2. *Thililua longicollis* gen. et sp. nov., holotype MNHGr.PA.11710, Goulmima region, Turonian, Morocco. **A**, Skull, mandible and associated vertebrae in articulation in right lateral view; **B**, interpretation. Abbreviations: **Ax**, axis; **C**, cervical; **D**, dorsal; **P**, pectoral vertebra; **r**, rib.

Fig. 2. *Thililua longicollis* gen. et sp. nov., holotype MNHGr.PA.11710, région de Goulmima, Turonien, Maroc. **A**, Crâne, mandibule et vertèbres associées en articulation en vue latérale droite ; **B**, interprétation. Abréviations: **Ax**, axis ; **C**, vertèbre cervicale ; **D**, dorsale ; **P**, pectorale ; **r**, côte.

Etymology. The species name alludes to the long neck.

Holotype. MHNGr.PA.11710, a nearly complete skull and mandible, and 37 associated vertebrae, including the entire cervical and pectoral series and the four anteriormost dorsals; preserved articulated in several successive blocks (Figs. 2 and 3).

Type locality and horizon. Near Goulmima, Er-Rachidia Province, southern Morocco; Unit 4 of the Cenomanian–Turonian limestone bar; Late Cretaceous, Early Turonian [10].

Diagnosis. Polycotylid plesiosaur characterized by premaxillae with swollen lateral processes between the external nares and the frontal foramina; orbits regularly oval without supraorbital processes; dental formula consisting of five premaxillary, at least 22 maxillary and 29 dentary teeth; mandibular symphysis bearing 15 teeth; 30 neck vertebrae; cervical centra nearly as long as high, bearing lateral longitudinal ridges which are paired from the 19th to 22th cervical vertebra.

Description. The skull and mandible were found associated and articulated together with 37 vertebrae, including the entire cervical and pectoral series, and the anteriormost dorsals (Fig. 2). Both the cranium and vertebrae have suffered strong lateral compression. The specimen is assumed to be adult as some of the cranial sutures are difficult to trace and the neural arches are all fused to the vertebral centra. Based on comparisons of the skull plus neck length to total body length ratio from reconstruction of *Dolichorhynchops* [19], the estimated overall length of *Thililua* was about 5.5–6 m. For measurements, see Tables 1–2.

Skull. The skull of *Thililua* is long and gracile (Fig. 3). The preorbital segment represents approximately 60% of the total skull length (Table 1). The premaxillae bear five pairs of teeth and extend up to the posterior margin of the orbit to contact the parietal. The premaxillae contribute to the dorsal border of both the external nares and the frontal foramina. Between these pairs of foramina, they are well expanded laterally. Posteriorly, the premaxillae taper to a point located just posterior to the orbital margin. The maxilla contributes

Table 1
Measurements (in mm) of the skull of *Thililua longicollis* gen. et sp. nov. from the Turonian of Morocco. Asterisk indicates the left and right average value measurements
Tableau 1
Mesures (en mm) du crâne de *Thililua longicollis* gen. et sp. nov. du Turonien du Maroc. L'astérisque indique la moyenne des mesures prises à gauche et à droite

Skull length	660
Skull width	105+
Preorbital length	383*
Postorbital length	180*
Maxilla length up to mid orbit	352
External naris length	23
Frontal foramina length	10
Orbit length	90,5*
Supratemporal fenestra length	112,5*
Mandible length	663+
Mandibular symphysis length	290
Coronoid process height	82,5*

Table 2
Measurements (in mm) of the vertebrae of *Thililua longicollis* gen. et sp. nov. from the Turonian of Morocco
Tableau 2
Mesures (en mm) des vertèbres de *Thililua longicollis* gen. et sp. nov. du Turonien du Maroc

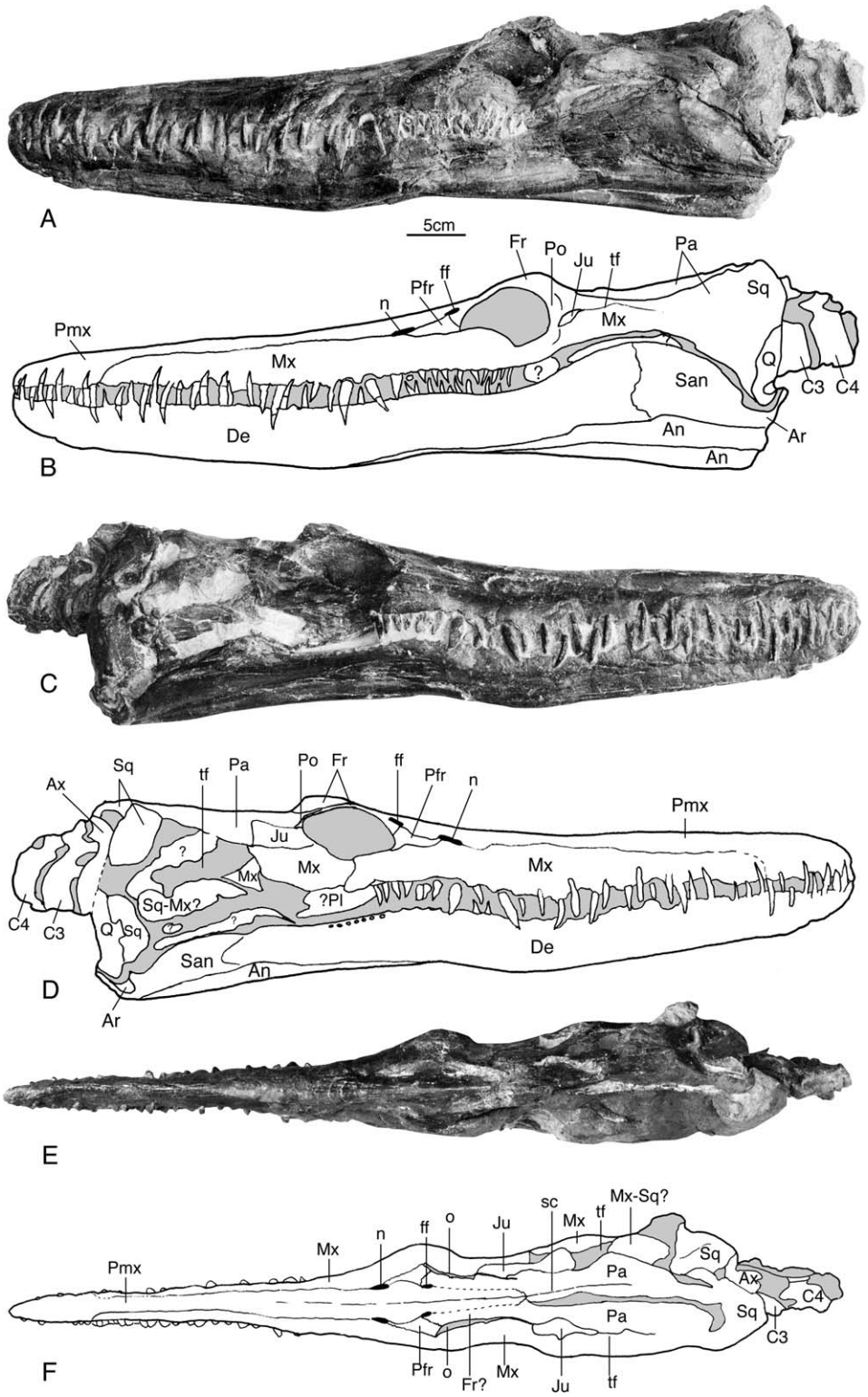
Vertebrae	At-Ax	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19
Centrum length	38+	26	29	?	38	45	47	49	53	55	54	57	57	61	62	64	64	68
Centrum height	44	38	43	?	45	50	52	60	60	64	65	65	66	69	71	70	71	70
Total height	?	?	?	?	?	100	105	111	106	100+	105+	115+	118+	134	137	125+	120+	142+

	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	P1	P2	P3	D1	D2	D3	D4
Centrum length	75	64	69	62	68	60+	65	60+	65	60	60	55	60	60	55	55	50	55
Centrum height	76	73	68	72	72	71	70	64	70	71	72	72	75	75	80	72	80	70
Total height	115+	110+	105+	105+	160	115+	?	95+	110+	135+	115+	115+	135+	125+	115+	115+	130+	100+

to the ventral border of the naris and to the ventral rim of the orbit, extending far posterior to it to contact the squamosal. It bears at least 22 teeth. The external nares are oval-shaped and larger than the frontal foramina. The prefrontal is triangular-shaped and forms the posterolateral margin of the naris and the anterolateral margin of the orbit. Its suture with the frontal is difficult to observe; it seems to be located just anterior to the frontal foramen. The shape of the frontals is unclear. They are separated along the dorsal midline by the premaxillae. The frontals form most of the dorsal rim of the orbit and lack a lateral process. The orbits are regularly oval. Due to crushing, the maxillae are artificially displaced dorsally and the anteroventral rim of the orbits is distorted. The postfrontal and postorbital region is poorly preserved. The right jugal is preserved as a horizontal rectangular bone, while the left one is crushed. It contributes to the posteroventral margin of the orbit and to the anteroventral margin of the temporal fenestra. It contacts the maxilla along a straight suture. The suture with the squamosal is unclear. The temporal fenestrae are larger than the orbits. The right temporal fenestra is preserved and the left one is crushed and reduced to a narrow groove. The parietal apparently bears a low sagittal crest, but this is probably due to poor preservation. There is no evidence of a pineal foramen. The suspensorium is vertically oriented. The squamosal forms the posterolateral margin of the temporal fenestra. Its suture with the quadrate is clearly exposed laterally. The palate is not available. The occipital region is hidden by the anteriormost cervical vertebrae, which are preserved in articulation with the skull.

Mandible. The mandible is complete but the retroarticular processes (Fig. 3). The mandibular rami are very close to each other due to crushing, so that the medial surfaces are not available. The dentary represents three quarters of the total length of the lower jaw. It bears 29 teeth. The symphysis is very long, nearly half the mandible length (Table 1), and includes 15 pairs of teeth. The dentary row extends posteriorly to the level of the middle part of the orbit. Just in front of the top of the coronoid eminence, the suture with the surangular is nearly vertical. Fragments of bone preserved dorsally to the coronoid process could represent ossified cartilage remains of the coronoid, as suggested for *Libonectes* [5]. The surangular is short and subrectangular. Posterior to the coronoid eminence, its dorsal margin descends to the glenoid fossa (articular). The jaw articulation lay slightly lower than the tooth row. The angular is narrow and extends anteriorly ventral to the dentary and surangular. Its suture with the splenial is straight and located just anterior to the level of the external naris. In ventral view, the splenial extends anteriorly to the tenth pair of teeth, taking part into the symphysis.

Dentition. Only the first three pairs of premaxillary teeth are well preserved. The remainder teeth are damaged and most of the crowns have been partially reconstructed, but the tooth count can be established. There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are five premaxillary, at least 22 maxillary and 29 dentary teeth. There is no evidence of caniniform teeth. The dentition is homodont, with the eleventh and twelfth maxillary teeth slightly larger than the others. The teeth are conical, long and slender. A weak anterior carina is present. The enamel crown is ornamented with very fine striations on the posterolingual side, whereas it is nearly smooth on the labial one. The occlusion of the upper and lower tooth rows is deeply interdigitate.

Vertebrae. Thirty cervical, three pectoral and the four anteriormost dorsal vertebrae are preserved in articulation (Fig. 2). The vertebrae are very compressed laterally, and consequently the width of the centra is about half the height. The centra are slightly amphicoelous and bordered by a rugose rim of bone. The lateral surfaces are concave and the ventral ones bear a longitudinal keel that split the nutritive foramina. The zygapophyses are long and robust. The neural spines, as preserved, are low and the dorsal border is nearly horizontal. The ribs are single-headed. From the atlas-axis complex, only the atlas and axis neural spines, the axis centrum and intercentrum are visible. The general shape is similar to that of *Dolichorhynchops* [19], but the facet for the axial rib is confined to the axis centrum. The remainder cervical vertebrae are mainly characterised by centra whose average length is approximately 85–90% of the height (Table 2). The lateral processes are narrow and horizontal from cervical 3 to 27 and become broad and vertically oval in the posteriormost cervicals. The anterior cervical ribs are hatchet-shaped. From cervical 9 to 23, there is a longitudinal ridge located high on the lateral surface of the centrum. This ridge is split into two from the cervical 19 to 22. In the three pectorals, the rib facets are oval to reniform, with a ventral small tubercle, as in *Trinacromerum* [19]. The lateral surface of the anteriormost dorsal centra is excavated and pierced by highly located nutritive foramina. Small bony fragments are present ventrally between the articular surfaces of the posteriormost cervical, pectoral and dorsal centra, deforming them. These structures may be pathological.

4. Discussion

Thililua longicollis is referred to the Polycotylidae (sensu [4,5,13]) on the basis of the following combination of characters (available on the specimen): the dorsal process of premaxillae extend posteriorly and separates the frontals (paralleled in pliosaurids); maxilla forms an expanded posterior contact with the squamosal; jugal forms a subrectangular horizontal bar (as in elasmosaurids); splenial is included in the mandibular symphysis (as typically in longirostrine plesiosaurs).

Thililua longicollis also shares with all other polycotylids but *Edgarosaurus muddi* (provisionnally reported to polycotylids, see [9]) a slender long-snouted skull whose preorbital segment is about 60% of the total length, and a uniform in size dentition, without caniniform teeth. Moreover, the premaxillae contact the parietal and there is no evidence of a pineal foramen, as in *Dolichorhynchops osborni*, *Trinacromerum bentonianum* and *Sulcusuchus erraini* (unlike *Edgarosaurus*) [4,9,11]. Finally, *Thililua* exhibits a frontal foramen above the orbit and a long mandibular symphysis, about half the total length, as in *Dolichorhynchops* and *Trinacromerum* [5]. The latter character is also present in *Polycotylus latipinnis* [16]. In *Edgarosaurus*, there is no evidence of a frontal foramen and the mandibular symphysis is shorter [9]. Pending a complete revision of the group and in the absence of a consensus diagnosis (compare [4] and [9]), the abovementioned features are here provisionally considered as characteristic for the Polycotylidae or less inclusive clades.

Thililua has long and slender teeth, with fine striae as in *Dolichorhynchops* and *Sulcusuchus*, unlike the

Fig. 3. *Thililua longicollis* gen. et sp. nov., holotype MNHGr.PA.11710, Goulmima region, Turonian, Morocco. Skull and mandible in left lateral (**A, B**), right lateral (**C, D**) and dorsal (**E, F**) views. Abbreviations: **An**, angular; **Ar**, articular; **Ax**, axis; **C**, cervical vertebra; **De**, dentary; **ff**, frontal foramen; **Fr**, frontal; **Ju**, jugal; **Mx**, maxilla; **n**, external naris; **o**, orbit; **Pa**, parietal; **Pfr**, prefrontal; **Pl**, palatine; **Pmx**, premaxilla; **Po**, postorbital; **Q**, quadrate; **San**, surangular; **sc**, sagittal crest; **Sq**, squamosal; **tf**, temporal fenestra; ?, unknown.

Fig. 3. *Thililua longicollis* gen. et sp. nov., holotype MNHGr.PA.11710, région de Goulmima, Turonien, Maroc. Crâne et mandibule en vues latérale gauche (**A, B**), latérale droite (**C, D**) et dorsale (**E, F**). Abréviations : **An**, angulaire ; **Ar**, articulaire ; **Ax**, axis ; **C**, vertèbre cervicale ; **De**, dentaire ; **ff**, foramen frontal ; **Fr**, frontal ; **Ju**, jugal ; **Mx**, maxillaire ; **n**, narine externe ; **o**, orbite ; **Pa**, pariétal ; **Pfr**, préfrontal ; **Pl**, palatin ; **Pmx**, prémaxillaire ; **Po**, postorbitaire ; **Q**, carré ; **San**, surangulaire ; **sc**, crête sagittale ; **Sq**, squamosal ; **tf**, fenêtre temporale ; ?, os inconnu.

robust, coarsely striated teeth of *Polycotylus*, *Trinacromerum* and *Edgarosaurus* [4,9,11].

Thililua differs from *Dolichorhynchops* and *Trinacromerum* in the lack of a supraorbital process, in a premaxillae–parietal contact located posterior to the orbits (instead of above the orbits) and in the facet for the axial rib located on the axis centrum (instead of located on both the centrum and the intercentrum of the axis) [4,5,19]. In addition, it is different from *Trinacromerum* in that its suspensorium is vertical (instead of posteriorly inclined) [4]. Unlike *Sulcusuchus*, *Thililua* lacks a longitudinal groove on the lateral surface of both the maxilla and dentary, and a deep notch on the lateral surface of the squamosal [11]. Comparisons with *Georgiasaurus penzensis* are not possible because of the lack of homologous material [14,17].

Thililua longicollis is unique among polycotylids in showing the following autapomorphies:

- the premaxillae have swollen lateral processes between the external nares and the frontal foramina (absent at least in *Dolichorhynchops* and *Trinacromerum* [4,5]);
- the orbits are regularly oval, without lateral processes (unlike *Dolichorhynchops* and *Trinacromerum* [4,5]);
- the mandibular symphysis bears 15 pairs of teeth, much more than in *Edgarosaurus* (6) and less than in *Polycotylus* (20) and *Dolichorhynchus* (18 to 21) [5,9,16];
- the dental formula includes five premaxillary, at least 22 maxillary and 29 dentary teeth (*versus* commonly 5–6/29/25–26 in *Dolichorhynchops*; 5–6/34/34 in *Trinacromerum*; ?/34/38 in *Polycotylus*; 6–7/26/29–31 in *Edgarosaurus* [4,5,9,16]; unknown in *Sulcusuchus* and *Georgiasaurus*);
- the neck includes a relatively high number of cervical vertebrae (30), as compared to *Dolichorhynchops* (19), *Trinacromerum* (20), *Polycotylus* and *Edgarosaurus* (both 26) [4,9];
- all the cervical centra but the anteriormost ones have a length more than 80% of the height, and are nearly as long as high between the cervical 19 to 22 (Table 2) (in other polycotylids, the mid-to-posterior cervical centra are shorter and the ratio length/height does not exceed 0.75 [15]);
- the neck centra bear laterally a longitudinal ridge between the cervical 9 to 22, which is paired from the cervicals 19 to 22 (no lateral ridges are known in other polycotylids). The occurrence of lateral ridges on cervical vertebrae is convergently acquired by long-necked elasmosaurids. However, *Thililua* differs from elasmosaurids in that the number of cervical vertebrae is rather low (30 *versus* more than 40), the centra have rounded (*versus* oval or binocular) articular surfaces, whose length never exceeds the height [1,3,13].

From a palaeobiogeographical point of view, *Thililua* is the first polycotylid plesiosaur hitherto discovered in Africa and under subtropical palaeolatitudes.

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