Anatomy and relationships of the bizarre Early Cretaceous pliosaurid *Luskhan itilensis*

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Pliosaurid plesiosaurians are iconic marine reptiles that regulated marine trophic chains from the Middle Jurassic to the early Late Cretaceous. However, their evolution during the Cretaceous remains poorly documented. Recent discoveries from the Hauterivian–Aptian interval suggest that the radiation of brachaucheniine pliosaurids produced a wide disparity of forms following the *Pliosaurus*-dominated assemblages of the Late Jurassic. Among the most bizarre of these early brachaucheniines is *Luskhan itilensis*, from the Hauterivian of Russia. We describe the osteology of this tusked, longirostrine pliosaurid and discuss its possible behaviour by drawing comparisons with other marine amniotes possessing forward-pointing teeth. We take this opportunity to make extensive anatomical comparisons among Cretaceous pliosaurids, including previously overlooked cranial features. Bayesian inference of phylogenetic relationships of plesiosaurians reveals that the internal branches in Late Jurassic–Late Cretaceous pliosaurids have generally low rates of morphological evolution, indicating that the recently described Early Cretaceous pliosaurids have effectively bisected the long branch leading to the 'classical' brachaucheniines of the middle Cretaceous (*Brachauchenius, Kronosaurus* and *Megacephalosaurus*). Pliosaurids exhibit low evolutionary rates and a dwindling disparity before their extinction, mirroring the events seen, roughly at the same time, for ichthyosaurians.

ADDITIONAL KEYWORDS: Brachaucheniinae – evolutionary rate – extinction – marine reptiles – Plesiosauria – Sauropterygia.

INTRODUCTION

Pliosauridae are a long-lived clade of sauropterygian marine reptiles that have their first appearances in the fossil record during the Early Jurassic (Storrs & Taylor, 1996; Benson *et al.*, 2011a) or perhaps latest Triassic (Wintrich *et al.*, 2017). Early pliosaurids retained the

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plesiomorphic phenotype of plesiosaurians, with a small body size and an elongated neck (Benson *et al.*, 2012; Fischer *et al.*, 2020). Pliosaurids then evolved a large body size and a suite of predatory adaptations during the Middle Jurassic, with the appearance of the clade Thalassophonea (Ketchum & Benson, 2011a; Benson & Druckenmiller, 2014; Fischer *et al.*, 2020). Many thalassophoneans show craniodental traits associated with macropredators, suggesting that they

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mostly occupied the niche of apex predators of their respective food chains (e.g. Massare, 1987; McHenry, 2009; Fischer *et al.*, 2015, 2020). However, the recent discovery of *Luskhan itilensis* Fischer *et al.*, 2017 from the late Hauterivian (Early Cretaceous) of Russia demonstrated the unexpected iterative evolution of a longirostrine phenotype among pliosaurids, revealing a wider disparity and colonization of multiple trophic roles by the clade (Fischer *et al.*, 2017, 2020).

Despite their relevance to the structure of ancient marine ecosystems, our morphological understanding of pliosaurids is limited, because only a few taxa are represented by complete skeletons (Tutin & Butler, 2017), especially outside of a few well-sampled Lagerstätten of the Jurassic (Benson et al., 2010). Recently, a series of new discoveries from Russia (Fischer et al., 2015, 2017; Zverkov et al., 2018; Zverkov & Pervushov, 2020) and South America (Páramo-Fonseca et al., 2016; Gómez-Pérez & Noè, 2017; Páramo-Fonseca et al., 2018) have expanded knowledge of pliosaurid evolution in the Cretaceous, following the Pliosaurus-dominated assemblages of the Late Jurassic. Luskhan itilensis, from the Early Cretaceous of Russia, is a crucial taxon because it is known by a remarkably complete skeleton (Fig. 1) from a poorly sampled stage (the Hauterivian) and because it illustrates the early stages of the evolution of the last clade of pliosaurids, Brachaucheniinae (Fischer et al., 2017). In this paper, we thoroughly describe the cranial and postcranial anatomy of Luskhan itilensis and assess its phylogenetic position with maximum parsimony and Bayesian inference. We use the Bayesian inference results to discuss the morphological evolutionary rates of pliosaurids from their origin around the Triassic-Jurassic boundary to their extinction during the early Late Cretaceous.

MATERIAL AND METHODS

INSTITUTIONAL ABBREVIATIONS

CAMSM, Museum of Earth Sciences, University of Cambridge, Cambridge, UK; CCNHM, Mace Brown Museum College of Charleston, Charleston, SC, USA; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MNHN, Muséum National d'Histoire Naturelle, Paris, France; **PETM**, Peterborough Museum & Art Gallery, Peterborough, UK; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; OM, Queensland Museum, Hendra, Queensland, Australia; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; YKM, Ulyanovskii Oblastnoi Kraevedcheskii Musei I. A. Goncharova (Ulyanovsk Regional Museum of Local Lore named after I. A. Goncharov), Ulyanovsk, Ulyanovsk Region, Russia.

MATERIAL

We studied the holotype of *Luskhan itilensis*, *YKM* 68344/1_262, a subcomplete, semi-articulated and three-dimensionally preserved skeleton. During the preparation of the remains, several kilograms of the matrix located in the belly region have been sampled and macerated. Only a series of cephalopod hooklets have been recovered, but we consider this evidence as too scant for the unambiguous presence of gut content in the specimen.

TAXONOMY

In a recent paper, Noè & Gómez-Pérez (2022) regarded the type material of the long-known thalassophonean taxon Kronosaurus queenslandicus Longman, 1924 as undiagnostic. However, the current knowledge of this taxon is based on a series of specimens that have been referred to Kronosaurus queenslandicus for decades (White, 1935; Romer & Lewis, 1959; Kear, 2003; McHenry, 2009). Instead of petitioning the International Code of Zoological Nomenclature (ICZN) to propose a neotype and maintain nomenclatural stability, Noè & Gómez-Pérez (2022) restricted the name Kronosaurus queenslandicus to the holotype specimen (QM F1609) and created a new genus and species, Eiectus longmani Noè & Gómez-Pérez, 2021, for reception of the material housed at Harvard University (MCZ) and, 'provisionally' (Noè & Gómez-Pérez, 2022: 6), for all other specimens previously assigned to *Kronosaurus*. We estimate that this course of action conflicts with the recommendations in articles 75.5 and 75.6 of the ICZN and cannot be justified by the (otherwise sensible) possibility of multiple pliosaurid taxa in the Aptian–Albian deposits of Australia (Noè & Gómez-Pérez, 2022). As a result, we will use the name 'Kronosaurus-Eiectus' for the material previously assigned to Kronosaurus queenslandicus in this contribution, pending further progress on this complex taxonomic issue.

THREE-DIMENSIONAL SCANNING AND MODELLING

We scanned the holotype of *Lushkan itilensis* using a hand-held, high-definition structured light scanner (Artec Space Spider). We also scanned a series of important specimens of *Kronosaurus queenslandicus* (also referred to *Eiectus longmani* by Noè & Gómez-Pérez, 2022) from the QM, using a Creaform HandySCAN 300 laser surface scanner. All the three-dimensional (3D) models are deposited in MorphoSource. A 3D model of the symphysis of QM F10113 (0.8 mm resolution; www.morphosource.org/concern/media/000115328) and a 3D model of a cast of the snout tip MCZ 1285 (0.2 mm resolution; www.morphosource.org/



Figure 1. *Lushhan itilensis*, a remarkably complete pliosaurid from the Lower Cretaceous of Russia. A, display of the holotype (*YKM 68344/1_262*) in the YKM. B, C, three-dimensional reconstruction of the skeleton of *Lushhan itilensis* in dorsal (B) and anterolateral (C) views. Please do not use this artistic reconstruction to describe anatomy or score phylogenetic characters.

concern/media/000115329) have already been deposited by Fischer *et al.* (2020) (MorphoSource project 0000C1018). We have also uploaded a 3D model of QM F2446 (0.5 mm resolution; www.morphosource. org/concern/media/000439494) and a 3D model of the 'JCU' specimen (QM F51291) (0.2 mm resolution; www.morphosource.org/concern/media/000439605), in addition to the holotype *Luskhan itilensis*, in several parts (0.25 mm resolution; link to the global project: http://www.morphosource.org/projects/000439440).

PHYLOGENETIC ANALYSES

We used the phylogenetic data matrix of Fischer *et al.* (2020), which is the most recent and most thorough dataset sampling pliosaurids. This matrix stems from the work of Benson & Druckenmiller (2014) and has been updated in various subsequent works (Fischer *et al.*, 2015, 2017, 2018; Madzia *et al.*, 2018; Páramo-Fonseca *et al.*, 2019). We analysed this dataset within a maximum parsimony and a Bayesian framework.

Maximum parsimony analyses were performed in TNT v.1.5 (Goloboff & Catalano, 2016). In order to minimize the impact of homoplasy, we used the implied weighting method to change the weight of each character proportionally to their homoplasy. We used different values of the coefficient k (6, 9 and 12) to test for the influence of different strategies of character weighting; increasing the value of k reduces the penalty applied to homoplastic characters. In a maximum parsimony framework, implied weighting appears to be a method of choice, providing accurate results (Goloboff et al., 2018; Smith, 2019). We raised the maximum number of trees to 100 000 and used the new technology search (ratchet activated: 200 ratchet iterations; drift activated: ten cycles; five hits; ten trees per replication) to identify islands of most parsimonious trees. We applied the tree bisection-reconnection algorithm on the trees recovered by the ratchet analysis to explore these islands fully. We used a symmetric resampling of 33% change probability, which gives the differences in frequency for 10 000 replicates, to analyse the nodal support of our trees in an implied weighting framework. We used the packages ape (Paradis et al., 2004), geoscale (Bell & Lloyd, 2015), paleotree (Bapst, 2012) and strap (Bell & Lloyd, 2015) in the R v.4.0.3 statistical environment (R Core Team, 2016) to timescale the consensus tree a posteriori using the minimum branch length (mbl = 3) method and matrix of taxon ages (or the lower and upper boundaries of the uncertainty window surrounding the first record of each operational taxonomic unit), from the study by Fischer et al. (2020). The matrix, the most parsimonious trees for each value of k, the R script and the taxon age matrix are provided as Supporting Information.

Bayesian inference of topology and clock rates were conducted jointly in MRBAYES (v.3.2.6; Ronquist et al., 2012). Character states were unweighted and unordered, and state frequencies were defined using a symmetrical Dirchlet hyperprior fixed at infinity, which makes all state transitions equally likely. We set four runs of four chains, with a maximum of 200 000 000 generations, sampling at every 1000. We set a stop value at 0.01, considering that convergence is then reached. We applied a burn-in that discards the first 25% generations. We used the Mkv model with gamma rates and an uncorrelated relaxed clock (igr). We modified the clock rate based on the mean rate of character change per million years given by an analysis in maximum parsimony in equal weighting: a lognormal distribution with a mean of -1.82 and a variance of 0.5 and the prior on the variance of the independent gamma rate (igrvarpr) set at exp(1). We also used the fairly neutral fossilized birth-death priors of Motani et al. (2017): fossilization prior (fossilizationpr) as beta (1,150), sampling probability (sampleprob) as 0.1, specification prior (speciationpr) as exp(1) and extinction prior (extinction pr) as beta (1,1). The full matrix with priors and inference protocol, the consensus tree (the. con.tre file), and all the outputs of the Bayesian inference are provided as Supporting Information.

COMPARATIVE DESCRIPTION

Plesiosauria de Blainville, 1835 Pliosauridae Seeley, 1874

THALASSOPHONEA BENSON & DRUCKENMILLER, 2014 BRACHAUCHENIINAE WILLISTON, 1925 (SENSU BENSON & DRUCKENMILLER, 2014)

LUSKHAN ITILENSIS FISCHER, BENSON, ZVERKOV, SOUL, ARKHANGELSKY, LAMBERT, STENSHIN, USPENSKY & DRUCKENMILLER, 2017

(FIGS 1-3, 5-12)

Holotype: YKM 68344/1_262, a subcomplete, semiarticulated and three-dimensionally preserved skeleton.

Locus typicus and stratum typicum: Upper portion of the *Speetoniceras versicolor* Zone, upper Hauterivian, Lower Cretaceous on the right bank of the Volga River, 3 km north of the Slantsevy Rudnik village, western Russia (Fischer *et al.*, 2017).

Note on diagnosis: The diagnosis of Lushhan itilensis remains unchanged compared with that of Fischer $et \ al. \ (2017)$, with the exception that the number of premaxillary teeth is ambiguous, being either six or seven.

Rostrum: The holotype of Luskhan itilensis has longirostrine cranial proportions (Fischer et al., 2017, 2020), with a preorbital rostrum accounting for 59% of the total skull length and a narrow snout (preorbital width/snout length = 0.2), comparable to the proportions of other longirostrine pliosaurids, such as Hauffiosaurus longirostris (Tate & Blake, 1876) (White, 1940; Benson et al., 2011b; Fischer et al., 2020) and Peloneustes Lydekker, 1889 (Ketchum & Benson, 2011b), and some polycotylid plesiosaurians, such as Pahasapasaurus haasi Schumacher, 2007 (Schumacher, 2007; Fischer et al., 2017, 2020) and Polycotylus latipinnis Cope, 1869 (Schumacher & Martin, 2015) (for measurements, see Tables 1 and 2). The rostrum is straight in dorsal view and lacks any mediolateral constriction at the anterior end of the premaxilla-maxilla contact. This is similar to the condition in some longirostrine pliosaurids, such as Marmornectes Ketchum & Benson, 2011 (Ketchum & Benson, 2011a) and Megacephalosaurus eulerti Schumacher, Carpenter & Everhart, 2013 (Schumacher et al., 2013). In contrast, a prominent constriction is seen in most Middle-Late Jurassic pliosaurids (Andrews, 1913; Tarlo, 1960; Ketchum & Benson, 2022) and, to a smaller extent, in Kronosaurus-Eiectus (McHenry, 2009). However, Luskhan itilensis exhibits a minute ventral expansion of the anterior portion of the maxilla, a feature again much more expressed in several latirostrine pliosaurids from the Late Jurassic (e.g. Andrews, 1913; Halstead, 1971; Brown, 1981; Noè et al., 2004; Benson et al., 2013) [it is also possibly present in Marmornectes (Ketchum & Benson, 2011a) and Megacephalosaurus eulerti (Schumacher et al., 2013)]. The dentary is dorsally convex anterior to this region.

Premaxilla: The premaxilla is elongated and slender, tapering anteriorly when seen in dorsal view, without any mediolateral expansion (Figs 2, 3). The premaxilla is slightly thicker dorsoventrally at the level of its second alveoli than at the anterior emergence of the maxilla. Poor preservation of dental alveoli results in an uncertainty regarding the number of premaxillary teeth, which is either six or seven. Most premaxillary teeth are widely separated, with interalveolar spaces that are longer anteroposteriorly than the alveolar lengths. Among thalassophoneans, widely spaced medial alveoli are also found in Pliosaurus westburyensis Benson et al., 2013 (R. Benson, pers. obs. of BRSMG Cc 332). The anteriormost premaxillary alveoli of Luskhan itilensis are small compared with the more posterior alveoli. Nevertheless, they are less reduced than those of *Pliosaurus* and *Acostasaurus* pavachoquensis Gómez-Pérez & Noè, 2017, in which the anteriormost alveolus is half the diameter of the third alveolus or smaller (Benson et al., 2013; Gómez-Pérez & Noè, 2017). As in *Makhaira rossica* Fischer *et al.*, 2015, the anteriormost alveolus is not oriented ventrally but anteroventrally (Fischer *et al.*, 2015). However, this condition is much more strongly developed in *Luskhan itilensis*, resulting in a nearly horizontal, anteriorly projecting first premaxillary tooth. The interalveolar bone between the first and the second alveolus is strongly thickened ventrally, creating a sort of bulbous buttress posterior to the first alveolus. A short, rectangular anteromedian trough is present between the anteriormost alveolus and the thickened interalveolar bone.

The anterolateral portion of the premaxilla-maxilla suture appears slightly crenulated. A crenulated morphology is also present in Stenorhynchosaurus munozi Páramo-Fonseca et al., 2016 (Páramo-Fonseca et al., 2016, 2018), Sachicasaurus vitae Páramo Fonseca et al., 2019 (Páramo-Fonseca et al., 2018) and Liopleurodon ferox Sauvage, 1873 (R.B.J.B., pers. obs. of NHMUK R 2680), but this seemingly differs from the more pronounced zig-zag morphology seen in Pliosaurus spp. (Benson et al., 2013), Simolestes vorax Andrews, 1909 (R.B.J.B., pers. obs. PETMG R.296) and, possibly, Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017). The suture extends in a linear manner posteromedially from the alveolar margin of the jaw, forming the lateral margin of the posteromedian ('facial') process of the premaxilla. The premaxillae appear to be fused medially, lacking a clear interpremaxillary suture. This condition is similar to that of Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2019) and is not observed in younger Cretaceous taxa (in which premaxillae are clearly separated by a straight suture throughout; Williston, 1907; McHenry, 2009; Schumacher et al., 2013). The premaxillae articulate with the parietals via a strongly interdigitating suture that is located directly medially to the external naris. This suture should not be confused with the numerous longitudinal ridges and furrows located further posteriorly, which texture the dorsal surface of the skull roof anterior to the parietal foramen. The anterior location of the premaxilla-parietal contact of Luskhan itilensis is a brachaucheniine synapomorphy (Benson & Druckenmiller, 2014) (which is absent in Acostasaurus pavachoquensis; Gómez-Pérez & Noè, 2017) and differs from the condition of most other pliosaurids, in which the contact is located at the level of the anterior margin of the orbit (Andrews, 1913; Ketchum & Benson, 2011a; Benson et al., 2013) or more posteriorly (Taylor & Cruickshank, 1993).

Maxilla: The anterior part of the maxilla is slightly expanded ventrolaterally (Figs 2, 3), similar to that of *Megacephalosaurus eulerti* (Schumacher *et al.*, 2013). A more prominent ventral expansion of the maxilla is found in many Middle–Late Jurassic pliosaurids



Figure 2. Craniomandiobular osteology of the holotype of *Luskhan itilensis* (*YKM* 68344/1_262). A, B, photograph (A) and interpretation (B) of the skull in dorsal view. C–F, image and interpretation of four cross-sections (locations indicated in A). Uncertain sutures are indicated by a dotted line. The left postorbital bar and temporal arch are present but have not been photographed; they are present in Figure 3.



Figure 3. Craniomandiobular osteology of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*), based on a high-resolution three-dimensional model. A, B, model (A) and interpretation (B) of the skull in left lateral view. C, D, model (C) and interpretation (D) of the skull in ventral view. Uncertain sutures are indicated by a dotted line.

Anteorbital ossification in Kronosaurus queenslandicus/Eiectus longmani



Figure. 4. Cranial osteology of *Kronosaurus–Eiectus* based on high-resolution three-dimensional models. A, C, model (A) and interpretation (C) of QMF 2446 in dorsolateral view. B, D, model (B) and interpretation (D) of QMF 51291 in dorsolateral view. Uncertain sutures are indicated by a dotted line.

(Andrews, 1913; Benson *et al.*, 2013), notably in *Simolestes vorax* (R. Benson, pers. obs. on PETMG R.296; Noè, 2001). In *Acostasaurus pavachoquensis*, the maxillary expansion is only lateral (Gómez-Pérez & Noè, 2017). *Stenorhynchosaurus munozi* seems to lack any marked maxillary expansion (Páramo-Fonseca *et al.*, 2016, 2019). Long longitudinal ridges and furrows texture the lateral surface of the maxilla at its midlength. The contribution of the maxilla to the external naris cannot be assessed because the skull has been dorsoventrally crushed in that region. The maxilla forms a long, transversely compressed posteroventral process, which bears alveoli and underlaps the 'lacrimal' and the anterior part of the jugal. This process extends posteriorly as far as the posterior margin of the orbit, as in *Pliosaurus kevani* Benson *et al.*, 2013 (Benson *et al.*, 2013) and, possibly, *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2016). A series of narrow yet deep depressions are located along the ventral maxilla– lacrimal' suture, but these appear distinct from the longer horizontal series of large foramina texturing the lateral surface of the posterior half of the maxilla



Figure 5. Orbital and postorbital regions of the holotype of *Luskhan itilensis* (*YKM* 68344/1_262). A, orbital and postorbital regions of a high-resolution three-dimensional model, in anterodorsal view. The extent of the orbit and supratemporal fenestra is reconstructed by the dotted lines. B, postorbital region in dorsal view. C–H, photographs and interpretations of the right postorbital and temporal bars in lateral (C, D), ventral (E, F) and medial (G, H) views.

seen in *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2019) and *Kronosaurus–Eiectus* (V. Fischer, pers. obs. on QM F2446 an QM F51291; Fig. 4).

Frontal: The frontals are, in places, difficult to discern owing to imperfect preservation. However, their posteromedial contact with the parietal is obvious, forming an elongated surface with a rugose texture. Although this surface is present and similar on both sides of the skull, the full external exposure

of the frontal cannot be assessed unambiguously (Figs 2, 3). The external exposure of the frontal seems to extend anteriorly up to the premaxillaparietal suture. This condition would be similar to *Megacephalosaurus eulerti*, *Sachicasaurus vitae* and *Stenorhynchosaurus munozi* (Schumacher *et al.*, 2013; Páramo-Fonseca *et al.*, 2018, 2019) and distinct from that of *Brachauchenius lucasi* Williston, 1903 and *Acostasaurus pavachoquensis*, because the premaxillaparietal suture appears to be located more posteriorly



Figure 6. Basicranium of the holotype of *Lushhan itilensis* (*YKM 68344/1_262*). Photographs and interpretations of the basicranium in posterodorsal (A, B), ventral (C, D) and left lateral (E, F) views.



Figure 7. Teeth of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*). A, tip of the snout in left lateral view. B, photograph taken during the preparation stage, showing that the mesialmost dentary teeth possessed at least one carina.

in these taxa (Schumacher et al., 2013; Gómez-Pérez & Noè, 2017). In *Megacephalosaurus eulerti*, the frontal prominently interdigitates in the premaxilla-parietal suture (Schumacher et al., 2013; B. Schumacher, pers. comm. September 2022). Furthermore, the frontal of *Luskhan itilensis* does not contribute to the orbital rim dorsally, unlike the condition in *Acostasaurus pavachoquensis* (Gómez-Pérez & Noè, 2017).

Orbital region: Pliosaurids exhibit a complex osteology in the anterior orbit-narial region, with the presence of numerous bones (Benson et al., 2013), which have in the past been assigned to the nasal, the 'lacrimal', the prefrontal, the palpebral and neomorphic bones (Williston, 1907; Ketchum & Benson, 2011b; Benson et al., 2013). Different interpretations still co-exist among recent papers and remain to some extent unresolved, meaning that the identities of these ossifications remain uncertain (Andrews, 1913; Ketchum & Benson, 2011b; Benson et al., 2013; Schumacher et al., 2013; Páramo-Fonseca et al., 2019). We add to this discussion with observations of specimens referred to Kronosaurus-Eiectus, from the Early Cretaceous of Australia (QMF 2446 and QMF 51291). These specimens clearly show the presence of at least two elements participating in the anteroventral-to-anterodorsal orbit margin (Fig. 4). Element 1 forms the anteroventral orbit margin, including the anterior half of the ventral margin. It is delimited posteriorly by a crenulated suture with the jugal, at about the mid-length of the ventral orbit margin. The existence of this suture has been debated (e.g. Carpenter, 1996; Ketchum & Benson, 2011b; Schumacher et al., 2013), and it is possible that it varies among specimens. However, it is clearly visible on both left and right sides of QMF 51291, where this region is well preserved (Fig. 4). Element 2 forms the entire anterior margin of the orbit. It contacts element 1 via a crenulated suture on both sides of both specimens QMF 2446 and QMF 51291. Most

contact between these two elements is < 50 mm long (Fig. 4). Element 2 is extensive; it forms the posterior margin of the external narial aperture and extends dorsally and posteromedially, contacting, anteriorly to posteriorly, the posterodorsal extremity of the maxilla, the frontal and the postfrontal; the last of these sutures is crenulated distally. Element 2 is thick and pillar-like at the orbital margin. It is textured with numerous small circular foramina in between the orbit and the narial aperture, at least in the specimen QMF 51291 (Fig. 4). Slightly above the level of mid-orbit, element 2 forms a small dorsoventral ridge at the orbital margin; this process inserts into a furrow and is then separated from the dorsal part of the bone by a depression in specimen QMF 51291 (see Fig. 4). In specimen QMF 2446, the dorsal part of element 2 is indistinguishable from the frontal. Yet, the small ridge dorsal to the pillar-like morphology is also visible in that specimen (Fig. 4). Accordingly, element 2 might constitute either a single element or two separate elements (see prefrontal/'palpebral' in Fig. 4). However, aside from the pillar and furrow structure, the rest of the 'palpebral'-prefrontal suture (if present) is indiscernible in these specimens (QMF 2446 and QMF 51291), and it is possible that both these bones instead constitute a large prefrontal, with varying bone textures. We use a 'two bones' colour scheme on our interpretation of Kronosaurus-Eiectus in Figure 4 ('lacrimal' in brown and prefrontal in light green) and Luskhan itilensis (Figs 2, 3).

of the suture is situated inside the orbit; the lateral

'Lacrimal': The 'lacrimal' is a neomorphic bone (but see Noè, 2001) that excludes the maxilla from the anteroventral margin of the orbit and has been identified by some authors in pliosaurids (Williston, 1907; Andrews, 1913; Benson *et al.*, 2011b, 2013; Ketchum & Benson, 2011b; Gómez-Pérez & Noè, 2017; Páramo-Fonseca *et al.*, 2019). Other authors regard this as a long anterior extension of the jugal (Taylor



Figure 8. Cervical region and centrum proportions of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*). A, B, photographs and interpretation of the atlas–axis complex in left lateral view. C, D, photographs and interpretation of the cervical and pectoral regions, in dorsal view. E, evolution of the height-to-length ratio along the entire preserved vertebral column. Abbreviations: c, cervical; p, pectoral.



Figure 9. Axial skeleton of the holotype of *Luskhan itilensis* (*YKM* 68344/1_262) based on high-resolution threedimensional models. A, B anterior cervical vertebrae in left lateral (A) and ventral (B) views. C–G, dorsal centra in dorsal (C), left lateral (D), anterior (E), right lateral (F) and ventral (G) views. H–M, right cervical rib in anterior (H), proximal (I), ventral (J), distal (K), posterior (L) and dorsal (M) views. N–R, cervical neural arch in right lateral (N), anterior (O), dorsal (P), left lateral (Q) and posterior (R) views. S–W, dorsal neural arch in anterior (S), ventral (T), left lateral (U), dorsal (V) and posterior (W) views. X–Z, caudal centra in dorsal (X), left lateral (Y) and ventral (Z) views. AA–AE, more posterior dorsal neural arch in anterior (AA), ventral (AB), left lateral (AC), dorsal (AD) and posterior (AE) views. AF–AH, dorsal rib in anterior (AF), proximal (AG) and posterior (AH) views.

Measurement	Length (anteroposterior)	Height (dorsoventral)	Width (mediolateral
Mandible	1585	78*	_
Symphysis	535	_	_
Splenial, contribution to the symphysis	265	_	_
Preorbital	940	_	130
Retroarticular process	125	_	_
Supratemporal fenestra	183	_	_
Interquadrate distance	420	_	_
Inter-retroarticular distance	435	_	_
Third dentary tooth basal diameter	22	_	_
Neck length (with atlas-axis, without cartilage)	764	_	_
Minimum trunk length (without cartilage)	1930	_	_
Scapula	284	_	_
Scapula, dorsal process	_	178	_
Scapula, posterior (glenoid) process	_	_	147
Scapula, glenoid contribution	105	_	_
Scapula–coracoid facet	73	_	_
Coracoid	650	90 [†]	615
Right forefin	_	_	1495
Right humerus, distally	165	_	645
Right humerus, mid-shaft	295	_	_
Left humerus, distally	307	_	625
Left humerus, mid-shaft	160	_	_
Radius	100	_	69
Ulna	_	_	65
Intermedium	93	_	57
Ischium	615	_	330
Ilium	_	240	_
Pubis	515	_	620
Left femur, distal	285 [‡]	_	802
Left femur, mid-shaft	165	_	_
Right femur, mid-shaft	177	_	805
Tibia	102	_	81
Fibula	137	_	87
Intermedium	90	_	58
Proximal phalange	52	_	69

Table 1. Cranial and appendicular measurements (in millimetres) from the holotype of Luskhan itilensis (YKM68344/1_262)

*Taken at mid-snout.

[†]Maximum height of the intercoracoid facet.

*Minimum value.

& Cruickshank, 1993; Carpenter, 1996; O'Keefe, 2001; Schumacher *et al.*, 2013). This disagreement probably results from typically poor preservation of the suborbital bar in many pliosaurids, resulting in difficulties in identifying the presence of a 'lacrimal'jugal suture (see above in the specimen QMF 51291, *Kronosaurus-Eiectus*). In *Luskhan itilensis*, the jugal is clearly overlapped anterodorsally by a 'lacrimal' (Fig. 5). The 'lacrimal' is a low triangular bone, with a long transversely compressed and dorsally tapering process contacting the posterior process of the maxilla (Figs 2, 3). The 'lacrimal' also forms a long, transversely compressed anterior process contacting the lateral surface of the maxilla, as in *Kronosaurus-Eiectus* (McHenry, 2009). This process appears much shorter in *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2019). The suture between the 'lacrimal' and prefrontal/palpebral is located ventral to mid-orbit height, as is usually the case in thalassophoneans (Ketchum & Benson, 2011b; Benson *et al.*, 2013; Madzia *et al.*, 2018).

Prefrontal: The prefrontal is a large triangular bone with a long transversely compressed anteroventral process (Figs 2, 3). Owing to poor preservation, it is difficult to determine whether the prefrontal extends to

Measurement	$Length \ (anteroposterior)$	Height (dorsoventral)	Width (mediolateral)	Height/width	Height/length
Atlas	55	103	108	0.95	1.87
Atlantal	55	NA	NA	NA	NA
intercentrum					
Axis	43	95	107	0.89	2.21
Axial	37	NA	NA	_	NA
intercentrum					
Cervical 3	47	117	107	1.09	2.49
Cervical 4	42	100	103	0.97	2.38
Cervical 5	43	86	100	0.86	2.00
Cervical 6	46	92	102	0.90	2.00
Cervical 7	45	90	112	0.80	2.00
Cervical 8	46	90	111	0.81	1.96
Cervical 9	51	93	117	0.79	1.82
Cervical 10	52	93	115	0.81	1.79
Cervical 11	48	90	118	0.76	1.88
Cervical 12	47	93	113	0.82	1.00
Cervical 12	48	93	115	0.81	1.94
Cervical 14	50	95	107	0.89	1 90
Cervical 15	47	90	110	0.82	1.00
Poctoral 1	54	97	115	0.84	1.01
Pectoral 2	56	95	117	0.81	1.00
Pectoral 3	55	93	114	0.82	1.70
Dorgal 1	61	90	119	0.80	1.05
Dorsal 2	67	92	103	0.89	1.40
Dorsal 3	70	98	109	0.85	1.57
Dorgal 4	70	03	110	0.50	1.40
Dorsal 5	85	101	105	0.05	1.20
Dorsal 6	90	106	119	0.95	1.10
Dorsal 7	90 86	105	112	0.95	1.10
Dorsal 8	80	95	02	1.03	1.22
Dorgal 0	79	100	08	1.00	1.15
Dorgal 10	78	100	119	0.80	1.20
Dorsal 10	80	100	112	0.87	1.20
Dorgal 12	80	100	110	0.07	1.20
Dorgal 12	82	102	110	0.95	1.24
Dorsal 15	00	109	100	1.00	1.24
Dorgal 15	80	102	107	0.96	1.17
Dorsal 15	80	100	107	0.90	1.29
Dorsal 10	81	100	107	0.95	1.20
Dorsal 17	84	100	107	0.95	1.19
Dorsal 10	80 01	100	107	0.94	1.20
Dorsal 19	01 NA	100	107	0.95	1.20 NA
Dorsal 20		104	115 NA	0.90	1.90
Dorsal 21/	70	90	NA	_	1.20
sacral I	00	0.0	100	0.00	1.10
Dorsal 22/	80	93	100	0.93	1.10
sacral 2					
Dorsal 23/	80	92	100	0.92	1.15
sacral 3					
Dorsal 24/	77	92	115	0.80	1.19
sacral 4					
Caudal 1	82	95	115	0.83	1.16
Caudal 2	75	95	112	0.85	1.27
Caudal 3	74	87	115	0.76	1.18
Caudal 4	70	85	110	0.77	1.21
Caudal 5	53	NA	NA	NA	NA

 Table 2. Axial skeleton measurements (in millimetres) of the holotype of Luskhan itilensis (YKM 68344/1_262)

Abbreviation: NA, not available.

contact the posterior margin of the external naris, but it is likely to be the case given the length of the anterior process. Brachauchenius lucasi, Megacephalosaurus eulerti and Stenorhynchosaurus munozi also possess an anterior process of the prefrontal that contacts the external naris (Schumacher et al., 2013; Páramo-Fonseca et al., 2019). This contact is absent in some earlier thalassophoneans, including Peloneustes and *Pliosaurus*, because the frontal extends anteroventrally to contact the maxilla in these forms, excluding the prefrontal from the posterior margin of the external naris: this condition is supposedly the plesiomorphic one (e.g. Taylor & Cruickshank, 1993; Ketchum & Benson, 2011b; Benson et al., 2013). The lateral surface of the prefrontal appears slightly concave in Luskhan itlensis. The prefrontal contacts the frontal dorsally, and the right prefrontal seems to contact the parietal too, but the absence of well-preserved postfrontals makes this interpretation ambiguous. In its posterodorsal region, the prefrontal forms a small convexity that projects into the dorsal orbit margin. This also occurs in various other thalassophoneans, in which a prominent convexity of the prefrontal projects into the anterodorsal or dorsal orbit margin [e.g. Andrews, 1913; Ketchum & Benson, 2011b; Gómez-Pérez & Noè, 2017 (where is it termed 'orbital flange')].

Jugal: The jugal is transversely compressed, with a dorsoventrally oval cross-section and a limited lateral exposure; the medial exposure is larger (Figs 2, 3, 5). The anterior portion of the jugal is anterolaterally overlapped by the sheet-like posterior processes of the 'lacrimal'. This condition differs from Pliosaurus kevani, Megacephalosaurus eulerti and Kronosaurus-*Eiectus*, where the 'lacrimal' does not overlap the jugal extensively (Benson et al., 2013; Madzia et al., 2018; present study). The jugal-squamosal suture is crenulated, and the jugal projects a small and flat medioventral posterior process underlapping the anterior part of the squamosal (Fig. 5). This condition appears similar to that of *Pliosaurus kevani*, although the posterior process of the jugal of Luskhan itilensis is located medioventrally rather than strictly ventrally in Pliosaurus kevani (Benson et al., 2013).

Postfrontal: Only a posteroventral fragment of the right postfrontal is preserved, forming the dorsal portion of the postorbital bar and contacting the postorbital ventrally in a ventrally convex suture (Fig. 5). The cross-section of lateral process, which contacts the postorbital, is thick and pillar-like.

Postorbital: The postorbital is mediolaterally thin and has a concave anterior margin that forms the posteroventral portion of the posterior orbit margin and a straight, posterodorsally facing posterior surface that forms part of the margin of the temporal fenestra (Fig. 5). The ventral surface of the postorbital contacts the jugal anteriorly and the squamosal posteriorly, meaning that the jugal is excluded from participation in the margin of the temporal fenestra. This condition is present in most plesiosaurians, but is unlike the condition in the Late Cretaceous pliosaurids *Megacephalosaurus eulerti* and *Brachauchenius lucasi*, in which a postorbital–squamosal contact is absent (McHenry, 2009; Schumacher *et al.*, 2013). The lateral surface of the postorbital is smooth and slightly concave, and the posterior part of the postorbital is strongly thickened, with a squared cross-section. The medial surface of the postorbital is rugose.

Parietal: The anterior process of the parietal extends far anteriorly, reaching the level of the external naris (Fig. 2), as in *Brachauchenius lucasi* and *Megacephalosaurus* eulerti (Williston, 1907; Schumacher et al., 2013), and thus slightly more anteriorly than in Kronosaurus-*Eiectus* and *Stenorhynchosaurus munozi* (McHenry, 2009; Páramo-Fonseca et al., 2019) and much more anteriorly than in Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017). The dorsal surface of the parietal anterior to the parietal foramen is textured by deep ridges and furrows, as are commonly present in thalassophoneans (e.g. Ketchum & Benson, 2011b). Some ridges converge posteromedially near the parietal foramen, while the anterior ridges at the level of the premaxilla-parietal suture are longitudinal. A large parietal foramen is present; its dorsal edge is also textured by fine ridges; its position is slightly anterior to the level of the postorbital bar; these two structures are aligned in Kronosaurus-Eiectus, Pliosaurus patagonicus Gasparini & O'Gorman, 2014 and Stenorhynchosaurus munozi (McHenry, 2009; Gasparini & O'Gorman, 2014; Páramo-Fonseca et al., 2019). The parietal crest is tall along its entire length (113 mm), extending dorsal to the more anterior portions of the skull roof as a sharp ridge. Its dorsal margin is straight and oriented anteroventrally. The parietal crest reaches the squamosal arch posteriorly, as in Pliosaurus kevani and unlike in Acostasaurus pavachoquensis, where it is short and convex (Benson et al., 2013; Gómez-Pérez & Noè, 2017). The parietal crest is also short and convex in *Megacephalosaurus* eulerti, but it does reach the squamosal (Schumacher et al., 2013). The ventral surface of the parietal vault is partly broken, but a deep concave posterior portion receiving the brain and the supraoccipital is present. The parietal-squamosal suture is obliterated by bony fusion.

Squamosal: The dorsal processes of the squamosals contact medially posterior to the parietals. The squamosals extend anteriorly and posteriorly at this

contact, forming a prominent and rugose 'squamosal bulb' (Figs 2, 5), a widespread feature among early plesiosaurians and pliosaurids (O'Keefe, 2001: character 55). However, it is especially prominent in Luskhan itilensis [e.g. more so than in Acostasaurus pavachoquensis, Megacephalosaurus eulerti and Pliosaurus patagonicus (Schumacher et al., 2013; Gasparini & O'Gorman, 2014; Gómez-Pérez & Noè, 2017)]. This process seems to disappear in some derived brachaucheniines [Brachauchenius lucasi and, possibly, Kronosaurus-Eiectus (McHenry, 2009)]. Likewise, Luskhan itilensis retains a mediolaterally oriented squamosal crest, as in Jurassic thalassophoneans and unlike the condition in Acostasaurus pavachoguensis (Gómez-Pérez & Noè, 2017) and more derived brachaucheniines (Benson & Druckenmiller, 2014: character 54). The posterior surface of each dorsal process is concave, giving the squamosal arch a marked bow shape in dorsal view. The medial half of the squamosal crest even points anterolaterally in Luskhan *itilensis*; this orientation and shape is similar to polycotylids, such as Dolichorhynchops Williston, 1902 (Sato, 2005; Sato et al., 2011), but differs from other pliosaurids, in which the squamosals extend laterally or posterolaterally from their median contact (Andrews, 1913; Benson et al., 2013; Schumacher et al., 2013; Gómez-Pérez & Noè, 2017). The posterior surface of the squamosal extends posteroventrally at the squamosalquadrate suture to form a recurved, hook-like process bearing a broad, rugose posterolateral bulge (Figs 2, 5). This is likely to be homologous with the rugose eminences seen on the posterior surface of the squamosal in some other pliosaurids, including Hauffiosaurus spp. (Benson et al., 2011b) and many species of Pliosaurus (Benson et al., 2013). Such a rugose eminence appears absent in Pliosaurus patagonicus (Gasparini & O'Gorman, 2014). Laterally, the squamosal is mediolaterally thin and sheet-like, forming the ventral process that covers the lateral surface of the quadrate, and the anterior process, which forms the temporal bar and contacts the jugal and the postorbital anteriorly. This squamosalpostorbital contact excludes the jugal from the temporal fenestra, unlike the condition in Brachauchenius lucasi and Megacephalosaurus eulerti (Albright, Gillette & Titus, 2007; Schumacher et al., 2013). The temporal bar is straight, transversely compressed and expands posteriorly. Its lateral surface becomes slightly concave posterior to the mid-length of the temporal fenestra. The posterior portion of squamosal-parietal vault is mediolaterally broad, equal to approximately half the width of the cranium, as in Pliosaurus spp. (Benson et al., 2013).

Quadrate: Both quadrates are complete but fractured (Figs 2, 3, 5). The dorsal part of the quadrate is rectangular in cross-section, with a mediolateral

long axis. The ventral (articular) end is expanded posteriorly, medially and anteriorly and possesses a squared cross-section with a concave posterior surface. A shallow groove borders the posterodorsal margin of the glenoid surface. The squamosal and quadrate appear partly fused, making it difficult to determine the exact location of the squamosal-quadrate suture.

Basioccipital: The basioccipital is only exposed in part; articulation with the atlas-axis complex covers its posteroventral portion (Fig. 6). The basioccipital condyle is rounded (81 mm in horizontal diameter), as in Peloneustes philarchus Seeley, 1869 and Acostasaurus pavachoquensis (Ketchum & Benson, 2011b; Gómez-Pérez & Noè, 2017) and unlike the condition in Pliosaurus almanzaensis Gasparini, Spalleti & O'Gorman, 2018 and Kronosaurus-Eiectus, in which it is markedly oval (White, 1935; O'Gorman et al., 2018). The basioccipital bears a large notochordal pit, unlike the condition in Pliosaurus and Kronosaurus-Eiectus, which lack such a feature (White, 1935; Benson et al., 2013; O'Gorman et al., 2018). The extracondylar area, comprising the basal tubera, merges continuously with the occipital condyle; a condylar peripheral groove is absent at least dorsally and laterally; the ventral region cannot be observed. The basal tubera expand laterally below the level of the notochordal pit/central point of the condyle, as in *Pliosaurus almanzaensis* and Kronosaurus-Eiectus (White, 1935; O'Gorman et al., 2018); this lateral expansion starts dorsal to the notochordal pit in Peloneustes philarchus (Ketchum & Benson, 2011b).

Exoccipital-opisthotic: The ventral 'feet' of the exoccipitals, which articulate ventrally with the basioccipital, are strongly expanded medially, contacting each other on the midline and thereby excluding the basioccipital from the floor of the foramen magnum (Fig. 6). This is unlike the situation in other plesiosaurians, including pliosaurids such as Peloneustes philarchus (Andrews, 1913), Liopleurodon ferox (Andrews, 1913), Pliosaurus almanzaensis (O'Gorman et al., 2018), Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017) and, probably, Kronosaurus-Eiectus (White, 1935). The foramen for cranial nerve XII is present on the medial surface, but the presence of other exoccipital foramina cannot be assessed owing to imperfect preservation and incomplete removal of the matrix. The exoccipital expands dorsomedially to form the supraoccipital facet. The cross-section of the paroccipital process is dorsoventrally compressed as in *Pliosaurus* (Benson et al., 2013) and, presumably, Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017), but unlike the condition in Peloneustes philarchus (Ketchum & Benson, 2011b). The anterolateral

edge of the paroccipital process is straight, while its posteromedial edge is concave in dorsal view; its dorsal surface is also concave, when seen in posterior view. The ventral surface of the paraoccipital process is in close contact with the dorsal surface of the quadrate ramus of the pterygoid along its entire length. This is unlike the situation in most other plesiosaurians, including the pliosaurids Peloneustes philarchus (Ketchum & Benson, 2011b) and Kronosaurus-Eiectus (White, 1935), in which only the distal end of the paraoccipital process contacts the posterior surface of the ptervgoid on the occipital surface of the skull. Such a continuous contact between the paraoccipital process and quadrate ramus of the pterygoid is found only in Luskhan itilensis and Pliosaurus westburyensis (R. Benson, pers. obs. on BRSMG Cc332).

Supraoccipital: The supraoccipital has been crushed and rotated anteroventrally, such that its originally vertical axis is now horizontal (Fig. 6). It lies on the dorsal surface of the basicranium and is covered anteriorly by a fragment of the ventral surface of the parietal and by the dorsal extremity of the dorsal lamella of the posterior ramus of the pterygoid. Unlike the situation in other thalassophoneans, including Peloneustes philarchus (Andrews, 1913; Ketchum & Benson, 2011b), Kronosaurus-Eiectus (White, 1935) and Pliosaurus kevani (Benson et al., 2013), the ventral margin of the supraoccipital is strongly embayed by the foramen magnum, resulting in a teardrop-shaped foramen magnum. A strongly embayed ventral margin is also present in the supraoccipital of Pliosaurus westburyensis (R. Benson, pers. obs. on BRSMG Cc332).

Parabasisphenoid: The posterior portion of the basicranium is preserved, including most of the posterior interpterygoid vacuity. This cavity is divided on the midline by the parabasisphenoid, which is mediolaterally convex in that region (Fig. 6). A shallow keel is present ventrally (thus perhaps similar to Pliosaurus almanzaensis, which possesses a triangular cross-section of the parasphenoid; O'Gorman et al., 2018). The parasphenoid becomes transversely thicker posteriorly, where its ventral surface becomes rugose and textured by small ridges and furrows. The parasphenoid of Luskhan itilensis appears much more robust than that of Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016, 2019). The rounded ventral surface of the parabasisphenoid is similar to the conditions seen in Brachauchenius lucasi (McHenry, 2009; Schumacher et al., 2013), Megacephalosaurus eulerti (Schumacher et al., 2013), Kronosaurus–Eiectus (White, 1935), Gallardosaurus iturradlei Gasparini, 2009 (Gasparini, 2009), Pliosaurus westburyensis (Taylor & Cruickshank, 1993) and, probably, Stenorhynchosaurus munozi (Páramo-Fonseca et al.,

2016), but is unlike the sharp midline keels seen in Middle Jurassic thalassophoneans (Andrews, 1913; Ketchum & Benson, 2011b, 2022) and some species of Pliosaurus (Benson et al., 2013). In the middle-Cretaceous brachaucheniines Brachauchenius lucasi (Williston, 1907; McHenry, 2009; Schumacher et al., 2013), Megacephalosaurus eulerti (Schumacher et al., 2013) and Kronosaurus-Eiectus (White, 1935), the contact between the parabasisphenoid and basioccipital is visible posteriorly, on the ventral surface of the basicranium. However, in Luskhan *itilensis*, this contact is not visible and is, presumably, covered by the pterygoids posteriorly to the posterior interpterygoid vacuity. This condition is similar to that seen in earlier thalassophoneans (Andrews, 1913: Taylor & Cruickshank, 1993; Ketchum & Benson, 2011b; Gómez-Pérez & Noè, 2017; O'Gorman et al., 2018).

Pterygoid: The posterior parts of both pterygoids are preserved in anatomical connection and articulated with the basicranium (Fig. 6). The pterygoids contact each other on the midline posterior to the posterior interpterygoid vacuity, in a long median contact that obscures the entire ventral surface of the basioccipital and the posterior portion of the parabasisphenoid. The posterior interpterygoid vacuity is anteroposteriorly long (preserved portion = 106.6 mm) compared with its mediolateral width (50.8 mm), yielding a minimum length-to-width ratio of 2.1, which is high compared with that of *Liopleurodon ferox* (Andrews, 1913) but in the range of that of other pliosaurids, such as Peloneustes philarchus (Ketchum & Benson, 2011b), Eardasaurus powelli Ketchum & Benson, 2022 (Ketchum & Benson, 2022), Pliosaurus alamanzaensis (O'Gorman et al., 2018), Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016, 2019), Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017), Sachicasaurus vitae (Páramo-Fonseca et al., 2018) and Kronosaurus-Eiectus (White, 1935). The preserved portion of the posterior interpterygoid vacuity clearly extends anteriorly past the anterior margin of the subtemporal fossa (i.e. the posterior margin of the main portion of the palate), indicating that the original mid-length of the posterior interpterygoid vacuity was located approximately level with-or anterior to-the anterior margin of the subtemporal fossa, as seen in thalassophoneans in the clade comprising Simolestes vorax, Liopleurodon ferox, Gallardosaurus iturraldei, Pliosaurus spp. and brachaucheniines (Williston, 1907; Andrews, 1913; White, 1935; Taylor & Cruickshank, 1993; Gasparini, 2009; Páramo-Fonseca et al., 2016), and in leptocleidids (Smith & Dyke, 2008: character 43).

Laterally, and posteriorly to the posterior interpterygoid vacuity, the ventral surface of the pterygoid bears a broad, curved and ventrolaterally oriented flange, which extends posteromedially from the base of the lateral process of the pterygoid (Fig. 6D). This flange is present in all thalassophoneans (Williston, 1907; Andrews, 1913; Ketchum & Benson, 2011b) and in *Microcleidus* Watson, 1909 (Brown *et al.*, 2013). In *Luskhan itilensis* and most other thalassophoneans (Ketchum & Benson, 2011b; Schumacher *et al.*, 2013; Páramo-Fonseca *et al.*, 2018), the flanges on each pterygoid contact each other on the midline posterior to the interpterygoid vacuity. This is unlike the condition in *Brachauchenius lucasi*, in which the flanges are separated across the midline by a wide gap (Williston, 1907).

The quadrate ramus of the pterygoid is L-shaped in cross-section, forming a high and transversely thick dorsal lamella covering the lateral and laterodorsal surfaces of the basicranium anterior to the exoccipital and buttressing the paroccipital process of the opisthotic posterolaterally (Fig. 6F). We find no evidence for a fossa between the dorsal lamella of the pterygoid and the exoccipital-opisthotic, as in *Pliosaurus westburyensis* (R. Benson, pers. obs. of BRSMG Cc 332). A deep anteroposterior sulcus is present laterally, at the base of the dorsal lamella of the posterior pterygoid ramus.

Mandible: Pyrite has damaged the medial surface of the mandible anteriorly, and the lateral part of the palate is crushed onto the dorsomedial surface of the mandible: it is thus impossible to describe the medial morphology of the mandible. The lateral surface of the mandible is not markedly bowed (Fig. 3), as in Pliosaurus patagonicus (Gasparini & O'Gorman, 2014) and Pliosaurus almanzaensis (O'Gorman et al., 2018) and brachaucheniines in general (Williston, 1907; McHenry, 2009; Angst & Bardet, 2016; Holland, 2018; Páramo-Fonseca et al., 2019; Noè & Gómez-Pérez, 2022), with the exception of Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017). The relative symphysial length is proportionally longer than in any other pliosaurid, with a proportional length of 0.337 of the total mandible length [it is 0.3 in Marmornectes candrewi (Ketchum & Benson, 2011a), 0.28 in Peloneustes philarchus (GPIT03182; see Fischer et al., 2017, 2020), 0.27 in Pliosaurus brachyspondylus (Owen, 1840) (CAMSM J35991; Tarlo, 1959a) and < 0.25 in all other pliosaurids (Fischer *et al.*, 2020)]. The number of dentary alveoli encompassed by the symphysis is difficult to count because of pyrite filling and the general fragility of the material but appears well above ten and probably close to 15, which would be similar to Marmornectes candrewi Ketchum & Benson, 2011, Peloneustes philarchus and Pliosaurus kevani (Ketchum & Benson, 2011a, b; Benson et al., 2013). However, as in the premaxilla, the symphysial

dentary teeth are widely spaced, with interalveolar spaces that are greater in length than the alveolar diameters (Fig. 3). As a result, even with a estimation of 15 symphysial teeth, *Luskhan itilensis* would have a low density of symphysial teeth (0.28 teeth per centimetre); such a value is otherwise found only in taxa with a few large teeth: *Pliosaurus carpenteri* Benson *et al.*, 2013 (0.2) (Knutsen, 2012; Sassoon *et al.*, 2012; Fischer *et al.*, 2017), *Pliosaurus brachydeirus* Owen, 1842 (0.28) (Knutsen, 2012; Fischer *et al.*, 2017), *Pliosaurus brachyspondylus* (0.27) (Tarlo, 1959a, 1960; Knutsen, 2012; Fischer *et al.*, 2017), *Kronosaurus-Eiectus* (0.19) (McHenry, 2009; Fischer *et al.*, 2017, 2020; Holland, 2018) and *Megacephalosaurus eulerti* (0.21) (Fischer *et al.*, 2020).

Dentary: The dentary is elongated. Its anterior portion is not spatulated (Figs 2, 3), unlike the situation in many other thalassophoneans, but similar to the condition in Marmornectes candrewi (Ketchum & Benson, 2011a), Brachauchenius lucasi (Albright et al., 2007), Pliosaurus almanzaensis (O'Gorman et al., 2018), Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2019), Megacephalosaurus eulerti (Schumacher et al., 2013) and, probably, Pliosaurus patagonicus (Gasparini & O'Gorman, 2014). Even if removal of the pyrite incrustation during preparation has destroyed part of the outermost bone layers, the tip of dentary appears rounded and does not form a flat anteroventral surface, unlike the condition in Pliosaurus rossicus Novozhilov, 1948 (Halstead, 1971). Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017) and, to a lesser extent, Kronosaurus-Eiectus (Holland, 2018). A ventral symphysial keel is absent, as in all brachaucheniines (Schumacher et al., 2013; Benson & Druckenmiller, 2014; Fischer et al., 2015; Páramo-Fonseca et al., 2016, 2018). Such a structure is also said to be absent in *Pliosaurus almanzaensis* (O'Gorman et al., 2018), but a raised platform appears present instead, and phylogenetic character 114 was thus scored as present by Fischer et al. (2020). A ventral keel has been described in Kronosaurus-*Eiectus* (Holland, 2018), but this structure appears as faint paired ridges that diverge distally (V.F., pers. obs. on QM F10113), thus possibly not homologous with the keel seen in Middle-Late Jurassic thalassophoneans. The dentary forms a subtle dorsal expansion, with larger teeth at the level of the premaxilla-maxilla suture, where a diastema is present in some Jurassic thalassophoneans (Druckenmiller & Russell, 2008; Ketchum & Benson, 2022). Posteriorly, the dentary becomes transversely compressed to form a sheet that covers the lateral surface of the mandible; its posterior termination is crenulated, forked and located at the level of the coronoid, but clearly not as bifurcated as in Kronosaurus-Eiectus (Holland,

2018). The dentary covers a part of the lateral and dorsal surface of the coronoid eminence, as in early pliosaurids (*Marmornectes candrewi* and *Peloneustes philarchus*) (Ketchum & Benson, 2011a, b) and unlike in *Megacephalosaurus eulerti*, *Acostasaurus pavachoquensis* and *Kronosaurus-Eiectus* (Schumacher *et al.*, 2013; Gómez-Pérez & Noè, 2017; Holland, 2018).

Splenial: The splenial makes an extensive contribution to the symphysis, tapering anteriorly over 265 mm from the posterior end of the symphysis, reaching to the level of the eighth or ninth dental alveolus, thus 49.5% of the total symphysial length (Fig. 3). This is a much larger contribution than in other thalassophoneans (Noè, 2001; Gómez-Pérez & Noè, 2017; Holland, 2018; Páramo-Fonseca et al., 2019). The ventral surface of the splenial in the symphysial region is mediolaterally broad, with a rounded crosssection. The ventral exposure of the splenial extends posteriorly way past mid-mandible, up to the level of the orbit. This exposure is thus much more extensive than in Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017) and Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2019), in which the ventral exposure of the splenial ends anterior to mid-mandible length. The ventral exposure of the splenial reaches mid-mandible length in Kronosaurus–Eiectus (Holland, 2018).

Angular: The angular is visible in lateral view (Figs 2, 3). It emerges laterally from under the posteroventral ramus of the dentary, at the level of the anterior margin of the orbit, thus much more posteriorly than in *Stenorhynchosaurus munozi* and *Sachisaurus vitae* (Páramo-Fonseca *et al.*, 2018, 2019). The angular otherwise forms the ventral portion of the posterior half of the mandible and participates in the retroarticular process. Its sutures with the surangular and articular are obscured by preparation and pyrite incrustation.

Surangular: Deep longitudinal ridges and furrows texture the surangular on its dorsal and dorsomedial surfaces, where it forms a major portion of the coronoid eminence (Fig. 3). This eminence is low in comparison to many Jurassic thalassophoneans, such as Pliosaurus kevani (Benson et al., 2013), and resembles the condition seen in other brachaucheniines (Holland, 2018; Páramo-Fonseca et al., 2019), with the possible exception of Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017). The dorsal surface of the surangular is mediolaterally expanded posterior to the coronoid eminence (Ketchum & Benson, 2010, 2011b), as in other thalassophoneans. As in some species of *Pliosaurus* and possibly *Kronosaurus–Eiectus*, this plateau faces slightly dorsolaterally (Benson et al., 2013; Holland, 2018). The surangular fossa faces dorsolaterally, another similarity with some species of *Pliosaurus* (Benson *et al.*, 2013), which might also be present in *Kronosaurus–Eiectus* (Holland, 2018).

Retroarticular process and glenoid: The retroarticular process is formed by the fused angular, articular and surangular. Its median anteroposterior length is 85 mm and subequal to the length of the glenoid, unlike the condition in *Pliosaurus brachyspondylus* (Taylor & Cruickshank, 1993) and Anguanax zignoi Cau & Fanti, 2015 (Cau & Fanti, 2014), in which the glenoid appears much shorter anteroposteriorly than the retroarticular process. The long axis of the retroarticular process is posteromedially inturned relative to the long axis of the mandible (Fig. 3), a brachaucheniine feature (Williston, 1907; Schumacher & Martin, 2015; Gómez-Pérez & Noè, 2017; Noè & Gómez-Pérez, 2022) that is also possibly present but in a less conspicuous manner in *Pliosaurus almanzaensis* (O'Gorman et al., 2018). In lateral view, it is clear that the retroarticular process extends in an approximately horizontal direction. The dorsal surface of the retroarticular process is dorsomedially inclined and saddle shaped. The posterior end of the retroarticular process is not expanded mediolaterally, unlike the situation in Pliosaurus kevani (Benson et al., 2013) and, possibly, Acostasaurus pavachoquensis (Gómez-Pérez & Noè, 2017). As in other thalassophoneans, the glenoid is inclined to face dorsomedially (Andrews, 1913; Taylor & Cruickshank, 1993; Benson et al., 2013; Gómez-Pérez & Noè. 2017: O'Gorman et al., 2018). A broad sulcus separates the ventral margin of the angular from the ventral part of the glenoid.

Articular: The articular forms a saddle covering the dorsomedian surface of the mandible posterior to the coronoid plateau (Fig. 3). The articular cannot be described thoroughly because of imperfect preservation and anatomical connection with the quadrate. The articular forms a short anterior process, embaying the posterior part of the prearticular.

Dentition: The teeth of Luskhan itilensis are small for a pliosaurid of that size (basal diameter of the third dentary tooth crown = 22 mm, in comparison to a skull length of 1585 mm). A slight variation in tooth size is present along the jaw. The largest teeth of the upper jaw are located on the anterior part of the maxilla, where the maxilla slightly expands ventrally. The largest dentary teeth are present at the level of the anteroventral end of the premaxilla–maxilla suture, where the dentary is slightly raised dorsally. However, there is no evidence for expanded caniniform teeth in Luskhan itilensis, unlike the situation in many other pliosaurids, such as Peloneustes philarchus (Ketchum & Benson, 2011b), Liopleurodon ferox (Andrews, 1913), Pliosaurus spp. (Sassoon et al., 2012; Benson et al., 2013; Gasparini & O'Gorman, 2014), Sachicasaurus vitae (Páramo-Fonseca et al., 2018), Kronosaurus–Eiectus (White, 1935; McHenry, 2009; Holland, 2018), Monquirasaurus boyacensis (Hampe, 1992) (Noè & Gómez-Pérez, 2022) and, possibly, Acostasaurus pavachoquensis (based on the variation in the diameter of tooth alveoli along the dentary; Gómez-Pérez & Noè, 2017). This condition is thus similar to Marmornectes candrewi (Ketchum & Benson, 2011a), Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016, 2019), Brachauchenius lucasi (Albright et al., 2007; Schumacher et al., 2013) and Megacephalosaurus eulerti (Schumacher et al., 2013; Madzia et al., 2018).

All teeth were damaged during extraction and preparation, but the first right dentary tooth shows a somewhat rounded but still trihedral cross-section. Photographs taken during preparation of the specimen indicate that carinae were present at least on the labial surface (Fig. 7). Makhaira rossica and many species of Pliosaurus (Benson et al., 2013; Arkhangelsky & Zverkov, 2015; Fischer et al., 2015; Madzia et al., 2018; O'Gorman et al., 2018; Zverkov et al., 2018) have trihedral teeth, whereas subtrihedral teeth have been described in Pliosaurus kevani (Benson et al., 2013) and Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2019) and conical ones in Acostasaurus pavachoquensis, Monguirasaurus boyacensis, Sachicasaurus vitae, and middle Cretaceous (Aptian-Turonian) brachaucheniines (Madzia, 2016; Gómez-Pérez & Noè, 2017; Páramo-Fonseca et al., 2018; Zverkov et al., 2018; Noè & Gómez-Pérez, 2022). Fine, widely spaced, longitudinal ridges also ornament the distal and labial surfaces of the mesial-most crowns. The thinness and wide space between these ridges contrast with the condition seen in Acostasaurus pavachoguensis and middle Cretaceous brachaucheniines, such as Megacephalosaurus eulerti, Kronosaurus-Eiectus and the nomen dubium 'Polyptychodon interruptus' (Owen, 1841; Fischer et al., 2016; Madzia, 2016; Gómez-Pérez & Noè, 2017; Madzia et al., 2018; Zverkov et al., 2018; McCurry et al., 2019; Noè & Gómez-Pérez, 2022).

Atlas-axis: The atlas-axis is preserved in articulation with the skull (Figs 1, 6, 8). It is anteroposteriorly short (98 mm) relative to its mediolateral width (108 mm) and dorsoventral height (103 mm), similar to the situation in some thalassophoneans, such as *Liopleurodon ferox*, *Simolestes vorax*, *Pliosaurus* spp., *Kronosaurus-Eiectus* and *Eardasaurus powelli* (Andrews, 1913; McHenry, 2009; Ketchum & Benson, 2022) and unlike the situation in *Peloneustes philarchus*, '*Pliosaurus' andrewsi* and *Stenorhynchosaurus munozi* (Andrews, 1913; Páramo-Fonseca *et al.*, 2019), in which the atlasaxis is anteroposteriorly longer. The bases of the atlantal neural arches are preserved. They expand significantly

both ventromedially and posteroventrally, possibly contacting one another on the ventral floor of the neural canal, excluding or at least strongly reducing the contribution of the odontoid (= atlantal centrum) to the neural canal. This does not occur in other pliosaurids, such as Marmornectes candrewi and Peloneustes philarchus (Linder, 1913; Ketchum & Benson, 2011a), and is at present autapomophic for Luskhan itilensis within pliosaurids; a similar condition is, however, seen in the early xenopsarian Brancasaurus brancai Wegner, 1914 (Wegner, 1914; Sachs et al., 2016). The atlantal intercentrum is large, longer than the axis (55 vs. 43 mm) in anteroposterior length. This is similar to that of *Eardasaurus powelli* (Ketchum & Benson, 2022) and unlike the situation in many other plesiosaurians, including Peloneustes philarchus (Linder, 1913) and Marmornectes candrewi (Ketchum & Benson, 2011a), in which the anteroposterior length of the atlantal intercentrum is similar to that of the axis or shorter. The ventral and anteroventral surfaces of the atlantal intercentrum are strongly convex, and the anterior portion of a narrow, triangular ventral keel is present on the ventral surface posteriorly. Facets on the lateral surface of the odontoid that are continuous with the posteroventral edge of the atlantal intercentrum suggest that the atlantal and axial intercentra contacted each other ventrally, excluding the odontoid from the ventral surface of the atlas-axis complex, as in Marmornectes candrewi (Ketchum & Benson, 2011a) and Jurassic thalassophoneans (Andrews, 1913; Ketchum & Benson, 2011a). The axial intercentrum is absent, but its gross morphology can be inferred from the extensive facets on the other elements of the atlas-axis. The axial intercentrum is also strongly developed, reducing the posteroventral exposure of the axis to a thin, transversely oriented ridge, 11 mm in anteroposterior thickness. The axial intercentrum extends far dorsally, indenting the anteroventral margin of the axial rib facet and giving it a 'V'-shaped outline in lateral view (Fig. 8).

There is no evidence for a rib-like posteroventral process on the odontoid, which has a smooth, concave lateral surface. The axial centrum possesses a single-headed rib facet (Fig. 8), which is a character common to all known brachaucheniines (Benson & Druckenmiller, 2014: character 143; Páramo-Fonseca *et al.*, 2018). A thin but prominent ridge extends in an approximately dorsal direction from the rib facet, along the lateral surface of the axial centrum. This ridge is oriented dorsoventrally on the right side and is slightly inclined anteroventrally on the left side. A similar dorsoventral ridge is present in *Pliosaurus irgisensis* (N. Zverkov, pers. obs. on the holotype, *PIN No 426*).

Cervical vertebrae: The neck and first three pectorals are preserved in near anatomical connection (Fig. 8). The

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cervical series is complete, and its total count (including the atlas and the axis) is 15, which is intermediate between that seen in *Pliosaurus* (18 cervicals; Tarlo, 1959b) and that seen in *Brachauchenius* (12 cervicals; Williston, 1907). The first centrum in which the transverse process contributes to at least one-quarter of the rib facet was considered to be the first pectoral centrum (sensu Seeley, 1869). The transverse process of the preceding vertebra to the first pectoral slightly contacts the rib facet, and this centrum thus counted as a cervical. A narrow and prominent ridge, similar to that of the axis, extends dorsally from the rib facet to the neural arch facet on the lateral surface of the centrum. This ridge is most prominent in the four anteriormost centra after the atlas-axis complex. Unlike the situation in the axis, this ridge is oriented in a strictly vertical manner on both sides. This ridge become broader and less prominent in more posterior centra but is present on all cervicals. The cervical rib facets are located slightly ventral to mid-height (Fig. 9), similar to those in *Stenorhynchosaurus munozi* (Páramo-Fonseca et al., 2016), Brachauchenius lucasi (Albright et al., 2007) and Kronosaurus-Eiectus (Benson & Druckenmiller, 2014); this differs from the ventromedially located cervical rib facets of other plesiosaurians and was found to be a synapomorphy of Brachaucheniinae by Benson & Druckenmiller (2014). The cervical rib facets of *Luskhan itilensis* differ from those of Brachauchenius lucasi (Albright et al., 2007) in being strongly concave and only weakly raised from the lateral surface of the centrum. These facets are single (i.e. not divided into two facets by a horizontal groove), as in other brachaucheniines (Benson & Druckenmiller, 2014) with the possible exception of Acostasaurus pavachoquensis (Gómez-Pérez, 2008). Well-developed, paired foramina are present on the ventral surfaces of all cervical centra, unlike the situation in Stenorhynchosaurus munozi, Kronosaurus-Eiectus and Brachauchenius lucasi (Williston, 1907; McHenry, 2009; Páramo-Fonseca et al., 2016). Cervical centra possess a broad and prominent ventral lip extending from their anterior margin (Fig. 9), as in many pliosaurids (Tarlo, 1960). However, in Luskhan itilensis, this lip protrudes far anteroventrally in anterior cervicals, giving the cervical a wave-like shape in ventral view, unlike the situation in other pliosaurids (Williston, 1907; Albright et al., 2007; Ketchum & Benson, 2011a). This condition is most prominent in the third cervical centrum, in which the lip is developed as a long concavoconvex tonguelike process that extends anteriorly to the mid-length of the axis. The anterodorsal surface of the tonguelike process of the third cervical centrum is strongly concave, perhaps engulfing a small intercentrum.

The cervical neural arches are dorsoventrally tall and disarticulated from their corresponding centra. We interpret a small, disarticulated neural arch as belonging to an anterior cervical vertebra. This neural spine is transversely compressed and with a slight transverse constriction at its base, as seen in anterior or posterior view. The ventral articular surface for the centrum is composed of two oblique flat facets in the anterior cervical neural arch. This gives them a weakly 'V'-shaped outline in lateral view. Mid-cervical neural spines are larger and more robust, forming a straight, thick process that thickens transversely at its dorsal end. This articular surface is gently concave in these more posterior cervical neural arches. The zygapophyseal facets are flat, oriented horizontally and diverge anterolaterally such that they are separated from the midline along their entire lengths, whereas postzygapophyses are located close to each other (Fig. 9), as in Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2019). In Middle to Late Jurassic thalassophonean pliosaurids, the zygapophyseal surfaces are, on the contrary, as wide as the width of the centrum. The neural spines are strongly offset posteriorly, having their mid-point located at the intercentral margin. The dorsal margin of the middle cervical neural spines is also slightly expanded laterally, giving them a rectangular cross-section, with a concave dorsal surface. Mid-cervical neural spines are taller (125-130 mm) than the dorsoventral diameter of the corresponding centrum (~92 mm).

The shape of the centra changes throughout the vertebral column, becoming increasingly long with respect to their dorsoventral height (Figs 8, 9): the third and fourth cervical centra exhibit strong anteroposterior compression, with a ratio as high as 2.49 in the third cervical centrum. The remainder of the cervicals have values slightly > 2.0, and the pectoral and anterior dorsal regions mark a rapid decrease of the height-tolength ratio close to 1.2, which stays stable up to and including the caudal region.

Pectoral, dorsal and sacral vertebrae: Three pectoral, \geq 20 dorsal and at least two (but probably five) sacral vertebrae are preserved. It is difficult to be precise about the exact number of sacrals in the absence of well-preserved neural arches and ribs. The pectoral centra have thick transverse processes with a semicircular cross-section and a posterior concave surface, whereas those on the anterior dorsal vertebrae are elongated, with concave anterior and posterior surfaces. Posterior dorsal transverse processes are dorsoventrally compressed, but only a few are preserved in the holotype of Luskhan itilensis. Paired foramina are present on the ventral surfaces of the third pectoral and all the dorsal centra where this trait is unambiguously assessable (Fig. 9). The floor of the neural canal, on the dorsal surface of the centrum, is pierced by numerous foramina of variable size, from 0.5 to 1 mm in diameter; this feature cannot be evaluated in pectorals owing to the presence of crushed neural arches on that surface. Sacral centra have a slightly hexagonal outline in anteroposterior view; the ventral surface seems flatter than in *Peloneustes philarchus* (Linder, 1913). The lateral margins of the floor of the neural canal have a laterally oriented concavity. Neural arches are not fused to their corresponding centra, which might indicate osteological immaturity (Brown, 1981), although even some large specimens of pliosaurids show evidence of features that have sometimes been linked to osteological immaturity (McHenry, 2009; Noè & Gómez-Pérez, 2022) and might thus not be reliable for pliosaurids (Benson et al., 2013; Zverkov & Pervushov, 2020). Dorsal neural arches are high. The base of the transverse processes is located dorsally to the mid-height of the neural canal [they are level with the neural canal in Jurassic thalassophoneans; (Benson & Druckenmiller, 2014)] (Fig. 9). The prezygapophyses face dorsally and are therefore oriented in a broadly horizontal manner, although their articular surfaces are slightly concave mediolaterally.

Caudal vertebrae: At least five caudal centra are preserved. Anterior caudal centra have a flat ventral surface, with paired subcentral foramina (Fig. 9), possibly similar to the 'triangular' condition described in Sachicasaurus vitae (Páramo-Fonseca et al., 2018). The lateral surface bears a protruding, semi-oval caudal rib facet situated in the top half of the centrum and that is confluent with the neural arch facet, as is seen mostly in pliosaurids and polycotylids (e.g. Andrews, 1913; Sato, 2005). Ventrally to that facet, the lateral surface of the anterior caudals is slightly concave. As in dorsal centra, the floor of the neural canal is pierced by numerous foramina of varying size; the lateral margins of this surface are concave. Posterior caudals are poorly preserved in the holotype of Luskhan itilensis, with only one partial centrum from this region being preserved. It has a squared cross-section, with flattened ventral and lateral surfaces. Large semioval chevron facets are present, contacting the anterior margin of the centrum.

Ribs: Most cervical ribs are single headed (Fig. 9), although at least one cervical rib is bicapitate, as evidenced by the articular surface of a cervical rib still connected to its rib facet in one posterior cervical vertebra. This slight polymorphism along the cervical series provides a potential explanation for the seemingly volatile nature of this character. A double-headed cervical rib is preserved in the holotype of *Megacephalosaurus eulerti* (*FHSM VP-32*; Schumacher *et al.*, 2013) and in the third cervical centrum of the holotype of *Monguirisaurus boyacensis* (Gomez, 2001)

cited in Hampe, 2005), whereas other brachaucheniine specimens except *Acostasaurus pavachoquensis* (Gómez-Pérez, 2008), have single-headed cervical rib facets (Albright *et al.*, 2007; Schumacher *et al.*, 2013; Páramo-Fonseca *et al.*, 2016). Nevertheless, all cervical rib facets are simple and oval in *Luskhan itilensis*, not paired or '8'-shaped. The cervical and pectoral ribs are simple and conical; their long axis is directed posterolaterally. They lack an anterior process, and their diameter decreases rapidly lateral to their articular facet; a feature commonly found in brachaucheniines that differs from the distally expanding cervical ribs seen in more basal pliosaurids (Andrews, 1913). The surface of the cervical ribs is textured by numerous longitudinal ridges.

The proximal portions of the dorsal ribs are rod-like.A small dorsal process is present where the rib initiates its ventral bending. There, the rib shaft becomes strongly flattened and slightly expanded anteroposteriorly, with a deep posteroventral longitudinal sulcus. More distally, the rib again becomes rod-like, thin and anteroposteriorly compressed distally. The dorsal ribs appear slender, as in Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016, 2019) and unlike the situation in Monquirasaurus boyacencis (Hampe, 1992; Noè & Gómez-Pérez, 2022) and Sachicasaurus vitae (Páramo-Fonseca et al., 2018). One proximal portion of a sacral rib is preserved. It possesses two articular facets forming an obtuse angle, one facing dorsomedially for articulation with the neural arch and one facing ventromedially for articulation with the sacral centrum. This shape appears similar to that reported in Peloneustes philarchus by Linder (1913), although it is probably more common among pliosaurids.

Coracoid: The coracoid is large; the coracoid-to-scapula length ratio equals 2.3 (Fig. 10), which is similar to that of *Kronosaurus–Eiectus* (~2.5) but higher than in *Stenorhynchosaurus munozi* (< 2) (McHenry, 2009; Páramo-Fonseca et al., 2016). The anteromedial process of the coracoid is short, triangular and points ventrally, forming an angle of 90° with the main surface of the coracoid. This process is markedly inflected ventrally and is unlikely to have contacted the ventral process of the scapula. Although a strong curvature of the coracoid symphysis is often present in well-preserved specimens (Andrews, 1913) (N. Zverkov, pers. obs. on NHMUK PV R3897 and R2437), Luskhan itilensis appears peculiar in having an anteromedial process that clearly points anteroventrally rather than anteriorly. The median intercoracoid facet is strongly thickened dorsally compared with wellknown Jurassic forms (e.g. Andrews, 1913), but this might be attributable to different taphonomical settings. Ventrally, the symphysis is concave, and no mediolaterally oriented buttress is present, unlike



Figure 10. Scapular girdle of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*). A–E, 3D model of the right scapula in anterior (A), posterior (B), lateral (C), ventral (D) and dorsal (E) views. F, left scapula in dorsal view. G–I, anterior coracoids in dorsal (G), anterior (H) and medial (I) views. J, left coracoid in dorsal view. K, right coracoid in dorsal view.

the situation in the dorsal surface. The coracoids are inclined dorsolaterally from the midline, meaning that their ventral surfaces clearly face ventrolaterally, as in *Peloneustes philarchus* (Andrews, 1913). The shape of the posterior part of the coracoid suggests the absence of a tight osseous intercoracoid contact posteriorly. The posterolateral cornu extends further laterally than the glenoid, as in Peloneustes philarchus (Andrews, 1913; Ketchum & Benson, 2011a), Simolestes vorax (Andrews, 1913; Ketchum & Benson, 2011a), Brachauchenius lucasi (Albright et al., 2007) and, probably, as in Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016) and unlike the situation in Anguanax zignoi and Sachicasaurus vitae (Cau & Fanti, 2014; Páramo-Fonseca et al., 2018). The posterior margin of the coracoid is straight in dorsal view and oriented posterolaterally.

Scapula: The scapula is triradiate, comprising a dorsal blade and ventral plate made up of a posterior, glenoid ramus and anterior ramus (Fig. 10). The dorsal surface of the ventral plate is smooth and slightly convex, whereas the ventral surface is mostly flat medially. This surface is separated from the base of the dorsal process by a long, strongly thickened lateral ridge that is ventrally and medially bowed. This ridge merges with the lateral edge of the scapula anterolaterally. The posterior process of the scapula is strongly thickened; the glenoid facet is semicircular with a flat ventral margin, and the coracoid facet is triangular. The long axes of these facets form an angle of 120°, similar to what is seen in other pliosaurids (e.g. Andrews, 1913; Noè & Gómez-Pérez, 2022). The anterior ramus is sheet-like and exhibits strong medial expansion giving it a fan shape; it does not contact the anteromedial part of the coracoid. The dorsal blade is longer than the ventral process and is not posteriorly inclined. Therefore, it forms an angle of 90° with the ventral surface of the scapula when seen in lateral view, as in *Pliosaurus* and unlike the situation in earlier pliosaurids, where it is posterodorsally inclined (Andrews, 1913; Tarlo, 1960). The shaft of the dorsal blade has a teardrop-shaped cross-section, with a thickened posterior edge. The dorsal process is fan shaped, with a dorsal end that is strongly expanded anteroposteriorly. In other thalassophoneans, the dorsal process is either fan, shaped but less so than in Luskhan itilensis, such as in Pliosaurus rossicus (Halstead, 1971), or expands in anteroposterior length dorsally without creating a fan shape, as in Peloneustes philarchus, Liopleurodon ferox, Simolestes vorax and Sachicasaurus vitae (Andrews, 1913; Tarlo, 1960; Páramo-Fonseca et al., 2018).

Forefin: The right forefin, including the humerus, is 1495 mm long proximodistally, only 10 cm shorter

than the mandible. This is likely to be similar to *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2016), and this condition seems to contrast with the absolutely and relatively larger skull of *Monquisaurus boyacensis* (Hampe, 1992; Noè & Gómez-Pérez, 2022), although the forefin of the only known specimen might not be complete.

Humerus: The humerus is shorter proximodistally than the femur, as in other pliosaurids (e.g. Andrews, 1913; Hampe, 1992, 2005; McHenry, 2009; O'Gorman et al., 2018). The humerus is robust (proximodistal length/anteroposterior length at mid-shaft = 3.9) and distally expanded (anteroposterior distal length/ anteroposterior shaft length = 1.78-1.90; this is similar in proportions to those of *Liopleurodon ferox* and Sachicasaurus vitae (Andrews, 1913; Páramo-Fonseca et al., 2018) and differs from the narrower shaft seen in Monquirasaurus boyacensis (Noè & Gómez-Pérez, 2022) and from the thicker shaft with less marked distal expansion of *Pliosaurus* spp. (Tarlo, 1960; O'Gorman et al., 2018). The distal expansion is present both anteriorly and posteriorly and starts slightly distal to mid-length; the posterior expansion forms an extensive sheet-like flange demarcated from the body of the humerus by dorsal and ventral longitudinal concavities (Fig. 10), unlike the situation in other pliosaurids (Andrews, 1913; O'Gorman et al., 2018; Páramo-Fonseca et al., 2018; Noè & Gómez-Pérez, 2022). The humerus is straight. Its capitulum and its shaft are not deflected posteriorly, as seen in some Early Jurassic plesiosaurians (Smith & Dyke, 2008), or anteriorly to form the 'sigmoid' humerus that is seen in some xenopsarians (e.g. Welles, 1962; Schumacher, 2007). Both the anterior and posterior edges are flat to slightly concave medially and gently convex more distally. Unusually, the dorsal tuberosity is well developed, being higher than the ventral expansion of the humeral head. Extensive muscle scars are present on the dorsal surface of the left humerus, > 10 cm distal to the capitulum, and on the anterior surface, at mid-length. Long, slightly convex and marginally tapering facets are present; their long axes are oblique to one another, forming an angle of ~150°. There are no supernumerary epipodial facets.

Epipodium and autopodium: The proximal elements are polygonal and tightly fitting (Fig. 11). The epipodial row appears proximodistally short (radius length/width = 1.42), as in derived polycotylids, and unlike the situation in other pliosaurids (Ketchum & Benson, 2011a) with the possible exception of *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2016) and *Pliosaurus* spp. (Tarlo, 1960; O'Gorman *et al.*, 2018). The radius of the holotype of *Luskhan itilensis* is incompletely preserved, but its straight



Figure 11. Limbs of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*). A, left forefin in dorsal view. B, C, right humerus in proximal (B) and distal (C) views. D, right forefin in dorsal view. E, F, right hind fin in ventral (E) and proximal (F) views. G, H, photographs and interpretation of the right hind fin in dorsal view.

and dorsoventrally thin anterior surface suggests that no anterior accessory epipodial element was present. The preserved left intermedium indicates that a small intermedium facet was present on the radius. The facets on the humerus and the proximal shape of the intermedium indicate that the ulna was 1.17 times longer than the radius. The ulna is strongly waisted in posterior view, and the spatium interosseum is absent, unlike the situation in Middle and Late Jurassic pliosaurids (Andrews, 1913; Tarlo, 1960). The intermedium is also proximodistally short (length/width = 1.63). Its ulnar facet is long and faces nearly proximally. The radiale possesses a facet for the distal carpal II + III, and this latter element is wider and nearly as long as the intermedium. No evidence for a metacarpal V contact is found on the posterior facet of the distal carpal IV. Additionally, the fifth digit appears completely absent in both forefins; it is unclear whether this absence is an additional genuine feature of *Luskhan itilensis* or is taphonomic, given the fact that the fifth digit can be slender and reduced in derived thalassophoneans (Schumacher & Everhart, 2005; see also Páramo-Fonseca *et al.*, 2016 for potential preservation bias of a fifth digit in thalassophoneans). The distal carpal I possesses a small facet for the metacarpal II, and the distal carpal IV possesses a minute facet for metacarpal III. Phalanges (even the distalmost ones) are proximodistally short, being only 1.28 to 1.59 times as wide as they are long; only some phalanges of the fourth digit reach a slightly higher ratio of 1.78. The longest digit preserved (digit III of the right forefin) possesses 12 phalanges and appears complete. Eleven phalanges are recorded in *Stenorhynchosaurus munozi* (Páramo-Fonseca *et al.*, 2016).

Pubis: Pubes are poorly preserved and have been fragmented into dozens of centimetric elements, and most of the bone margins appear to be missing. The pubis becomes sheet-like immediately anteromedial to the acetabulum (Fig. 12).

Ischium: The right ischium is preserved. It is elongated (length/width = 615/330 = 1.86). Its symphysis is wave shaped in medial view, with a dorsal expansion (Fig. 12), although less conspicuous than in the coracoid. The anterior edge is weakly embayed in dorsal view, and the anteromedial process appears small. Although its anterior extent cannot be determined precisely, its lateral edge suggests that a 'median pelvic bar' was absent, unlike the situation in Simolestes vorax (Andrews, 1913). The pubic facet is semicircular and faces ventroanterolaterally.

Ilium: The right ilium is preserved, but its dorsal blade is incomplete. The anterior margin of its dorsal

extremity forms an angle of ~50° with the long axis of the pelvic shaft end, giving the ilium a markedly expanded dorsal process (this is inferred from broken preserved morphology; Fig. 12). The dorsal process of the ilium appears anteroposteriorly shorter in *Peloneustes philarchus*, *Simolestes vorax* (Andrews, 1913) and slightly shorter in *Pliosaurus* cf. *kevani* (Tarlo, 1958, described as a scapula; 1959b; Benson *et al.*, 2013). The shaft is oval in cross-section. The ischial facet is triangular, oblique to the long axis of the ilium, and appears larger than the acetabular facet. The anterior surface of the ilium is strongly curved in lateral view, becoming parallel with the acetabular facet.

Femur: The femur is proximodistally longer than the humerus (mean femur proximodistal length/ mean humerus proximodistal length = 1.27) (Fig. 11), as is often the case in pliosaurids that are more derived than *Hauffiosaurus* (e.g. see data provided by Fischer *et al.*, 2020). Its shape is also different: it is proportionally longer in comparison to its width than is the humerus, but with a slightly smaller distal expansion (proximodistal length/anteroposterior shaft length = 4.54-4.86; anteroposterior distal length/ anteroposterior shaft length ≥ 1.72 ; none of the distal ends of the femora are complete, but the shape of the femur can be estimated by combining the left and right femora). This condition resembles that of



Figure 12. Pelvic girdle of the holotype of *Luskhan itilensis* (*YKM 68344/1_262*). A–D, left ilium in dorsal (A), medial (B), ventral (C) and lateral (D) views, along with a reconstruction of the possible extent of the dorsal blade (dotted line). E, F, right ilium in dorsal (E) and anterolateral (F) views.

Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016). On the contrary, the femur exhibits a more pronounced distal expansion than the humerus in Sachicasaurus vitae and Monguirasaurus boyacensis (Páramo-Fonseca et al., 2018; Noè & Gómez-Pérez, 2022). Contrary to the humerus, the distal portion of the femur seemingly lacks a sheet-like posterior lamella. The femur is straight. Its capitulum and its shaft are not deflected anteriorly or posteriorly. Medially, the anterior surface is concave and the posterior surface saddle shaped. The dorsal trochanter is semioval in cross-section and slightly shorter anteroposteriorly than the capitulum as a whole. The femur forms two distal facets, forming an angle of ~160°. As in the humerus, the distal end of the femur extends further posteriorly than the epipodium, but we found no evidence for an extrazeugopodial element, because the posterior surface of the fibula is thin and edge-like.

Epipodium and autopodium: The fibula is 1.34 times anteroposteriorly longer than the tibia. The epipodial elements are proximodistally shortened (tibia length/ width = 1.26; fibula length/width = 1.57; intermedium length/width = 1.55) and polygonal, forming a tightly fitting mosaic. A spatium interosseum between the tibia and the fibula is absent, unlike the situation in other pliosaurids for which this part of the anatomy is adequately known (Andrews, 1913; Tarlo, 1960). Unusually, the intermedium is located directly distal to the fibula and thus possesses only one flat proximal surface, giving this element a rectangular shape (Fig. 11). The tibiale is trapezoidal and articulates distally solely with the distal tarsal I; this condition is also seen in Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016). The intermedium articulates distally with the distal tarsal II + III; a small posterodistal facet is present for the distal tarsal IV, unlike the situation in other pliosaurids, where the distal facets of the intermedium are subequal in length (Andrews, 1913; Tarlo, 1960). The distal tarsal II + III is anteroposteriorly enlarged, which has a size similar to that of the intermedium, as in Stenorhynchosaurus munozi (Páramo-Fonseca et al., 2016). A single complete proximal hind-fin phalanx is preserved; its proximodistal length-toanteroposterior length ratio is 1.32.

RESULTS

MAXIMUM PARSIMONY INFERENCE OF PHYLOGENY

Fischer *et al.* (2020) used implied weighting to generate a phylogenetic hypothesis for analyses of evolutionary convergence. However, a single concavity

constant was used (k = 3). Here, we test for changes in topology by using increasing values of k (6, 9 and 12), thereby progressively reducing the penalty applied on homoplastic features. This results in a slight loss of resolution within *Pliosaurus*, in addition to the inclusion of Gallardosaurus iturraldei in the clade of Pliosaurus, where it groups with Pliosaurus kevani in k = 9 and k = 12 iterations (Fig. 13; Supporting Information, Figs S1–S3). Brachaucheniines form a large polytomy in all our maximum parsimony analyses and systematically incorporate the Late Jurassic taxon Pliosaurus patagonicus, which is recovered as closely related to Luskhan itilensis (Fig. 13; Supporting Information, Figs S1–S3). The Early Cretaceous taxa from Columbia, Sachicasaurus vitae and Stenorhynchosaurus munozi, also form a clade, and Acostasaurus pavachoquensis is systematically recovered as the most basal brachaucheniine, as in the Bayesian inference produced by Madzia & Cau (2020).

BAYESIAN INFERENCE OF TOPOLOGY AND RATES OF MORPHOLOGICAL EVOLUTION

The general topology is similar to previous maximum parsimony analyses of the dataset from the paper by Benson & Druckenmiller (2014), where the radiation of Thalassophonea is initially marked by stepwise evolution (Peloneustes philarchus, 'Pliosaurus' andrewsi, Simolestes vorax, Liopleurodon ferox and Gallardosaurus iturraldei) that then leads to a split: the '*Pliosaurus* clade' (here recovered as large polytomy) and Brachaucheniinae (Benson & Druckenmiller, 2014; Fischer et al., 2015, 2017; O'Gorman et al., 2018; Morgan & O'Keefe, 2019; Páramo-Fonseca et al., 2019; Madzia & Cau, 2020; Fig. 14; Supporting Information, Fig. S4). However, we recover *Pliosaurus patagonicus* as the sister lineage to all Cretaceous pliosaurids. By definition (see Benson & Druckenmiller, 2014), both maximum parsimony and Bayesian inference recover this late Jurassic taxon as a brachaucheniine pliosaurid, although in a more basal position than in the maximum parsimony framework. Luskhan *itilensis*, then *Makhaira* rossica + Stenorhynchosaurus munozi are recovered as early brachaucheniines, while Acostasaurus pavachoquensis and Sachicasaurus vitae are the successive sister lineages to the 'traditional', middle Cretaceous brachaucheniines (Monquirasaurus, Kronosaurus, Brachauchenius, Megacephalosaurus and 'Polyptychodon'). This differs slightly from the results of our maximum parsimony analyses and those of Madzia & Cau (2020), where Acostasaurus pavachoquensis is the most basal brachaucheniine.

The early radiation of Thalassophonea and the nodes directly leading to it are marked by clearly elevated



Figure 13. Phylogenetic relationships among Pliosauridae. A–C, temporally scaled strict consensus trees depicting the phylogenetic relationships of Pliosauridae in an implied weighting maximum parsimony framework, with increasing concavity constants (k), which progressively reduce the penality applied to homoplasic characters. A, k = 6. B, k = 9. C, k = 12.

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rates of morphological evolution (Fig. 14); these high rates are sustained during the entire Middle Jurassic, a period marked by rapid turnovers among marine reptiles (Fischer et al., 2021). Both the radiation of Pliosaurus during the Late Jurassic and the diversification of Brachaucheniinae during the Cretaceous are characterized by slow rates of morphological evolution, corroborating the results of a previous attempt (Madzia & Cau, 2020). This suggests that the recently described Early Cretaceous brachaucheniines (Acostasaurus pavachoquensis, Luskhan itlensis, Makhaira rossica, Sachicasaurus vitae and Stenorhynchosaurus munozi) have effectively bisected the long branch that previously connected Liopleurodon-like forms of the Middle Jurassic to the Middle Cretaceous brachaucheniines. One exception is the lineage of Sachicasaurus vitae, which briefly exhibits the highest rates of evolution among Pliosauridae. The morphological differences between Acostasaurus pavachoguensis, Sachicasaurus vitae and Kronosaurus-Eiectus might explain the poor resolution in Brachaucheniinae (and the basal placement of Acostasaurus) in a maximum parsimony framework, while a relaxed morphological clock considers Sachicasaurus vitae as an exception in an otherwise slowly evolving grade. In the work of Madzia & Cau (2020), high rates were briefly recorded at a similar time (earliest Cretaceous), but slightly closer to the origin of Brachaucheniinae

(more specifically, the branches leading to *Luskhan itilensis* and *Stenorhynchosaurus munozi*). This difference might be explained by alteration of some brachaucheniine character scores by Fischer *et al.* (2020), incorporated in the present analyses. The evolution of middle Cretaceous brachaucheniines is marked by a sustained period of slow rates of morphological innovation (see also Madzia & Cau, 2020), up to their extinction at the end of the Turonian (Schumacher, 2011).

DISCUSSION

Luskhan itilensis is characterized notably by a unique combination of plesiomorphic and derived features within thalassophoneans, bisecting the long temporal and morphological branch separating mid-Cretaceous brachaucheniines from Late Jurassic pliosaurids. Far more unexpected are the several autapomorphic features of Luskhan itilensis, which depart significantly from the morphology of thalassophoneans (Fischer *et al.*, 2017). One of the most striking of these features is the forward-pointing first premaxillary teeth that appear to be supported posteriorly by thickened interalveolar bone of the premaxilla, forcing the presence of a thickened diastema between the first and the second premaxillary alveoli (Figs 2, 3, 7). We reject the



Figure 14. Phylogenetic relationships among Pliosauridae. Extended majority consensus tree ('allcompat') obtained by a relaxed morphological clock Bayesian inference. Each branch is coloured according to its medial clock rate from the posterior distribution. Abbreviation: J: Jurassic.

hypothesis that this feature is an artefact of taphonomic deformation, given the excellent state of preservation of the holotype specimen. The hypothesis of a pathology appears difficult to assess in a population of one individual, besides the fact that this trait is fully symmetrical and did seemingly not modify the dorsal and lateral parts of the rostrum. The absence of a similar structure on the dentary probably precludes a direct involvement in food procurement and processing, unlike the situation in the several marine and terrestrial taxa bearing procumbent teeth that probably permit easier catch of small prey items (e.g. Chatterjee & Small, 1989). '[F]orwardly oriented' mesial dentary teeth have been described in another pliosaurid, Pliosaurus patagonicus (Gasparini & O'Gorman, 2014: 276). However, these alveoli are broken off; because plesiosaurian alveoli are internally curved (e.g. Sassoon et al., 2015), it is presently impossible to conclude whether Pliosaurus patagonicus had forwardpointing teeth or not. The mesialmost teeth of the mosasaurid Prognathodon solvayi Dollo, 1889 and the ophthalmosaurid ichthyosaurian Pervushovisaurus campylodon (Carter, 1846) can be slightly oriented anteriorly (Lingham-Soliar & Nolf, 1989; Fischer, 2016, respectively; Fig. 15) but, again, this condition does not resemble that of Luskhan itilensis.

Some tusked ziphiid cetaceans (beaked whales) have some similarities to Luskhan itilensis, having procumbent mesial teeth (Fig. 15) and thickened rostral bones (e.g. Bianucci et al., 2016). The ziphiid Tasmacetus Oliver, 1937 is especially interesting, possessing two forward-pointing mesialmost teeth (albeit on the dentary), which are positioned anterior to an elongated diastema. Gut content suggests that this dental adaptation is not linked to a particular diet (Best et al., 2014), hence it is a poor predictor of ecological niche. However, these supplementary bone deposits in the anterior part of the rostrum are hypothesized to play a role in absorbing stresses resulting from use of the anteriorly oriented tusks during male fights (Lambert et al., 2010). Squalodontid odontocetes also have forward-pointing mesial tooth crowns that are supported by elongated, horizontally inclined roots (e.g. Fordyce, 1994; Fig. 15), yet lack the thickened interalveolar bone and the diastema seen in Luskhan itilensis (e.g. Rothausen, 1968). In both ziphiids and squalodontids, these features are thought to be associated with visual display and, for some extant ziphiids, male fights, leaving a series of scars on the bodies of old adult males (Heyning, 1984). The 'tusks' of Luskhan itilensis could thus have served a similar function, given the morphological similarity. However, caution is advisable, because evidence for visual display and male-male behavioural interactions is exceedingly rare among Mesozoic marine reptiles (Zammit & Kear, 2011).

The enlarged atlantal and axis intercentra and the broad atlas-axis neural arch of Luskhan itilensis together form a thick layer of bone almost completely wrapping the odontoid and the axis. Moreover, the cervical centra of Luskhan itilensis possess an elongated anteroventral processes inserting into a wide groove situated in the anterior centrum. This process is large on the third cervical centrum and progressively decreases in size in more posterior centra. Such a feature (the cervical 'lip') is present in other pliosaurids (Tarlo, 1960), but much smaller. Mechanically, all these cervical features would probably lock the anterior part of the neck, preventing movement in this region and, possibly, helping to absorb shocks and pressure. Neck stiffening has evolved several times in marine amniotes, being found in ichthyosaurians [through fusion (Broili, 1907; McGowan & Motani, 2003; Maxwell & Kear, 2010) and/or undulating margins (Fischer et al., 2012)] and cetaceans [through extensive fusion (e.g. VanBuren & Evans, 2016)] and is interpreted, in pelagic taxa, as an adaptation to high-speed swimming (Fish, 2000; McGowan & Motani, 2003; VanBuren & Evans, 2016). The long skull of *Luskhan itilensis* is clearly convergent with the supposedly fast-swimming (Adams, 1997) polycotylid plesiosaurians (Fischer et al., 2017, 2020). Luskhan itilensis also departs from the large-headed morphology seen in all other thalassophoneans, having a mandibular-to-femur length ratio of 1.81, whereas other thalassophoneans (bar Peloneustes philarchus and Simolestes vorax) have values ranging from 2.0 to 2.73 (Fischer et al., 2020). All these lines of evidence suggest that both the morphology and the probable niche and behaviour of Luskhan itilensis differed greatly from those of other pliosaurids.

Nevertheless, our Bayesian inference results indicate that internal branches among Late Jurassic-Late Cretaceous pliosaurids have generally low rates of morphological evolution overall (Fig. 14). These rates represent the transition frequencies of cladistic characters rather than specifically the most functionally or ecologically relevant traits of species. Furthermore, they do not consider the multiple autapomorphies of Luskhan itilensis or other species. These low rates indicate, in general, that the recently described Early Cretaceous pliosaurids from Russia and Colombia have populated the gap that previously separated *Pliosaurus* from Kronosaurus, Brachauchenius and Megacephalosaurus, presenting somewhat 'intermediate' combinations of character states, with only minimal occurrence of new character states. The last pliosaurids exhibit low evolutionary rates (see also Madzia & Cau, 2020), large to very large sizes (Longman, 1930; Benson et al., 2013; Zverkov & Pervushov, 2020) and a reduced range of craniodental morphologies (Fischer et al., 2020) before their extinction, which presumably occurred at



Figure 15. Comparative cranial anatomy of raptorial marine amniotes with procumbent mesialmost teeth. All are high-resolution three-dimensional models. A, *Luskhan itilensis (YKM 68344/1_262)*. B, *Pervushovisaurus campylodon* (CAMSM B20671). C, *Prognathodon solvayi (IRSNB R33b)*. D, *Ninoziphius platyrostris (MNHN SAS 941)*. E, *Tasmacetus shepherdi* (USNM 484878). F, *Ziphius cavirostris* (NHMUK 1915.7.20.1). G, *Ankylorhiza tiedemanni* (CCNHM 103). H, *Prosqualodon davidis* (USNM 467596). Silhouettes: *Ziphius* by Chris Huh, from Phylopic (http://phylopic.org/image/7c1d06fb-2d6e-454d-b57b-a859d5dbdb9f/); *Squalodon* by Craig Hylke, from Phylopic (http://phylopic.org/image/95a73c63-e7c7-4e81-8e6d-592f647b07bc/).

the end of the Turonian (Schumacher, 2011). This combination of selective extinctions strongly recalls the events associated with the Cenomanian extinction of ichthyosaurians (Fischer, 2016; Fischer *et al.*, 2016) and might be indicative of global restructuring of marine trophic webs at the beginning of the Late Cretaceous.

CONCLUSIONS

 $Luskhan \ itilensis$ is an unusual brachaucheniine thalassophonean from the Hauterivian of western

Russia, documenting the 'Early Cretaceous gap' in pliosaurid evolution. Our detailed comparative description and high-precision 3D surface scans confirm the uniqueness of numerous traits of *Luskhan itilensis*, such as the long, slender rostrum, forward-pointing mesial premaxillary teeth resembling the morphology seen in some ziphiid whales, hook-like processes on the squamosal and ventrally dipping anterior processes of the coracoids. Despite its unique phenotype and possible ecology, *Luskhan itilensis* forms a grade with a series of other Early Cretaceous pliosaurids that bisects the long branch separating middle Cretaceous brachaucheniines from their *Pliosaurus*-like ancestors. This, in turn, results in low morphological evolutionary rates during the entire Cretaceous history of pliosaurids, especially before their extinction in the early Late Cretaceous.

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AUTHOR CONTRIBUTIONS

V.F., R.B.J.B., N.G.Z., and M.S.A. designed the project and wrote the paper. I.M.S., G.N.U., N.G.Z., and M.S.A. prepared the specimen and gathered the stratigraphic and geological data. N.E.P. and V.F. scanned the specimens and processed the 3D data. V.F. ran the analyses. All authors significantly contributed to the manuscript.

DATA AVAILABILITY

All the 3D models are deposited in MorphoSource: a 3D model of the symphysis of QM F10113 (0.8 mm resolution, www.morphosource.org/concern/media/000115328) and a 3D model a cast of the snout tip MCZ 1285 (0.2 mm resolution, www.morphosource.org/concern/media/000115329) have already been deposited by Fischer *et al.* (2020) (MorphoSource project 0000C1018). We have also uploaded a 3D model of QM F2446 (0.5 mm resolution, www.morphosource.org/concern/media/000439494) and a 3D model of the "JCU" specimen (QM F51291) (0.2 mm resolution, www.morphosource.org/concern/media/000439495), as well as the holotype *Luskhan itilensis*, in several parts

(0.25 mm resolution, link to the global project: http:// www.morphosource.org/projects/000439440). The phylogenetic matrix, the most parsimonious trees for each value of k, the R script, and the taxon age matrix are provided as supporting information.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website:

Figure S1. Phylogenetic relationships of Plesiosauria, with strict consensus, implied weighting and maximum parsimony (concavity constant, k = 6).

Figure S2. Phylogenetic relationships of Plesiosauria, with strict consensus, implied weighting and maximum parsimony (concavity constant, k = 9).

Figure S3. Phylogenetic relationships of Plesiosauria, with strict consensus, implied weighting and maximum parsimony (concavity constant, k = 12).

Figure S4. Phylogenetic relationships of Plesiosauria arising from the relaxed morphological clock Bayesian inference, with 'allcompat' majority rule consensus.