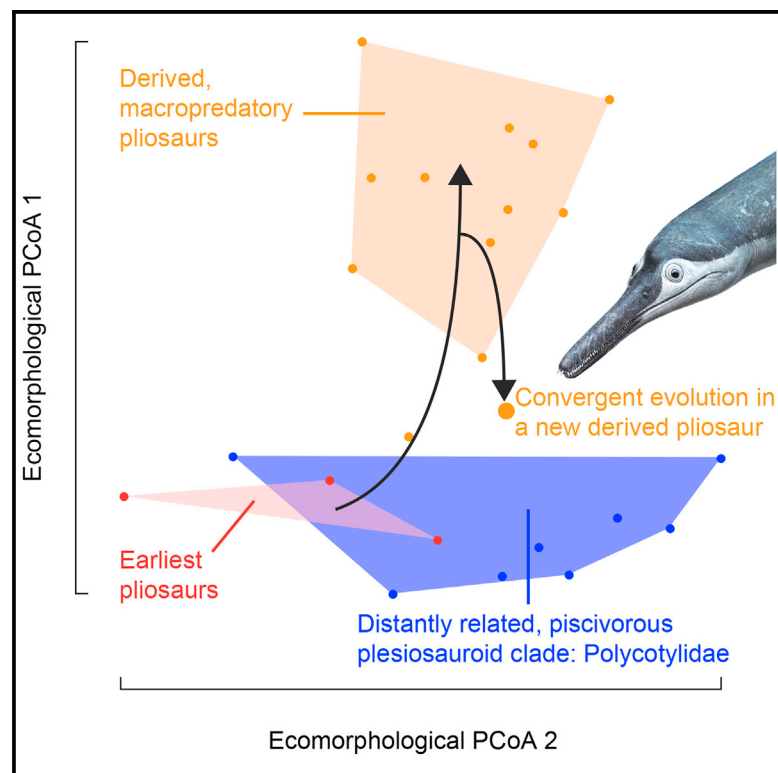


Current Biology

Plasticity and Convergence in the Evolution of Short-Necked Plesiosaurs

Graphical Abstract



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In Brief

Fischer et al. describe a new unusual plesiosaur marine reptile from the Russian Cretaceous. Plesiosaurs repeatedly evolved longirostry and explored novel ecological niches during the final chapter of their long evolution. The amount of convergence characterizing the evolution of plesiosaurs is even larger than previously assumed.

Highlights

- A new unusual plesiosaur marine reptile is described from the Cretaceous of Russia
- Ecomorphological convergence is assessed in short-necked plesiosaurs
- Plesiosaurs repeatedly evolved longirostrine piscivorous forms
- Profound convergence characterizes the evolution of short-necked plesiosaurs

Plasticity and Convergence in the Evolution of Short-Necked Plesiosaurs

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SUMMARY

Plesiosaurs were the longest-surviving group of secondarily marine tetrapods, comparable in diversity to today's cetaceans. During their long evolutionary history, which spanned the Jurassic and the Cretaceous (201 to 66 Ma), plesiosaurs repeatedly evolved long- and short-necked body plans [1, 2]. Despite this postcranial plasticity, short-necked plesiosaur clades have traditionally been regarded as being highly constrained to persistent and clearly distinct ecological niches: advanced members of Pliosauridae (ranging from the Middle Jurassic to the early Late Cretaceous) have been characterized as apex predators [2–5], whereas members of the distantly related clade Polycotylidae (middle to Late Cretaceous) were thought to have been fast-swimming piscivores [1, 5–7]. We report a new, highly unusual pliosaurid from the Early Cretaceous of Russia that shows close convergence with the cranial structure of polycotylids: *Luskhan itilensis* gen. et sp. nov. Using novel cladistic and ecomorphological data, we show that pliosaurids iteratively evolved polycotylid-like cranial morphologies from the Early Jurassic until the Early Cretaceous. This underscores the ecological diversity of derived pliosaurids and reveals a more complex evolutionary history than their iconic representation as gigantic apex predators of Mesozoic marine ecosystems suggests. Collectively, these data demonstrate an even higher degree of morphological plasticity and convergence in the evolution of plesiosaurs than previously thought and suggest the existence of an optimal ecomorphology for short-

necked piscivorous plesiosaurs through time and across phylogeny.

RESULTS AND DISCUSSION

Plesiosauria Blainville, 1835 [8].

Pliosauridae Seeley, 1874 [9].

Thalassophonea Benson & Druckenmiller, 2014 [2].

Brachaucheninae Williston, 1925 [10] sensu Benson & Druckenmiller [2].

Luskhan itilensis gen. et sp. nov.

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Figures 1 and 2.

Holotype, Horizon, and Locality

YKM 68344/1_262, a nearly complete, three-dimensionally preserved skeleton excavated in 2002 by one of us (G.N.U.) in the upper portion of the *Speetonicerus versicolor* Zone, upper Hauterivian, Lower Cretaceous on the right bank of the Volga river, 3 km north of the Slantsevy Rudnik village, western Russia. The horizon is level g-5 in local stratigraphy [11] (Figure S1).

Etymology

The Volga river area is the heartland of Golden Horde from the Mongol Empire. In Mongolian and Turkic mythology, “luuses” are spirits and masters of water, and “khan” means chief. “Itil” is the ancient Turkic name of the Volga.

Diagnosis

Luskhan itilensis is characterized by the following autapomorphies: seven premaxillary teeth (unique within Thalassophonea); procumbent, nearly horizontal first premaxillary tooth; wide and strongly swollen interalveolar space between the first and second premaxillary alveoli; squamosal/quadrate suture expanding posteriorly into a hook-like, rugose process on the squamosal;

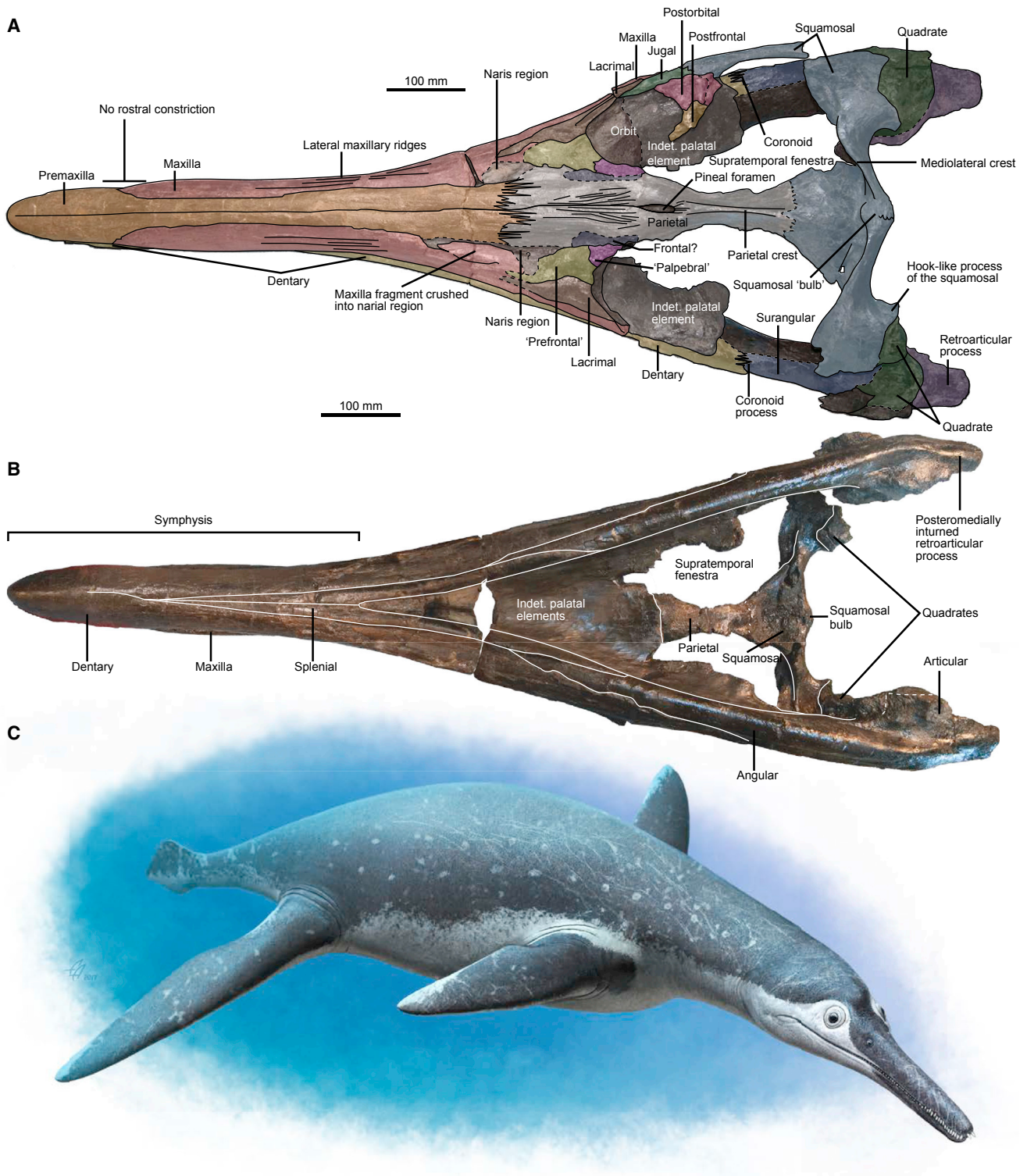


Figure 1. Craniodental Morphology of *Luskhan itilensis*

(A and B) Holotype specimen YKM 68344/1_262 in (A) dorsal and (B) ventral views.

(C) Reconstruction by Andrey Atuchin.

See also [Figure S1](#).

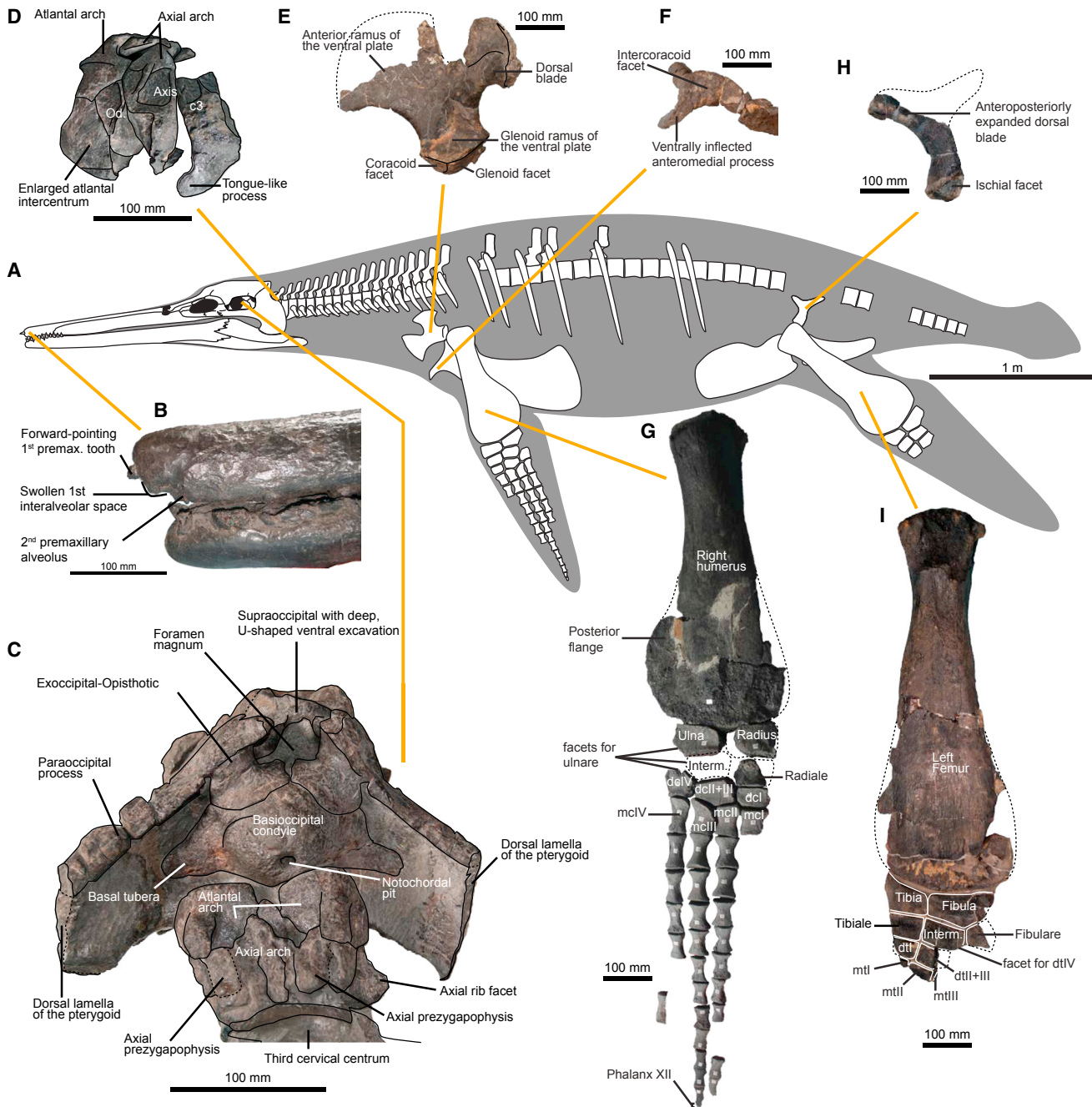


Figure 2. Postcranial Morphology of *Luschan itilensis*

Holotype specimen YKM 68344/1_262.

(A) General reconstruction in left lateral view.

(B) Tip of the rostrum in left lateral view.

(C) Basicranium in posterior view.

(D) Atlas-axis in left lateral view.

(E) Right scapula in dorsal view.

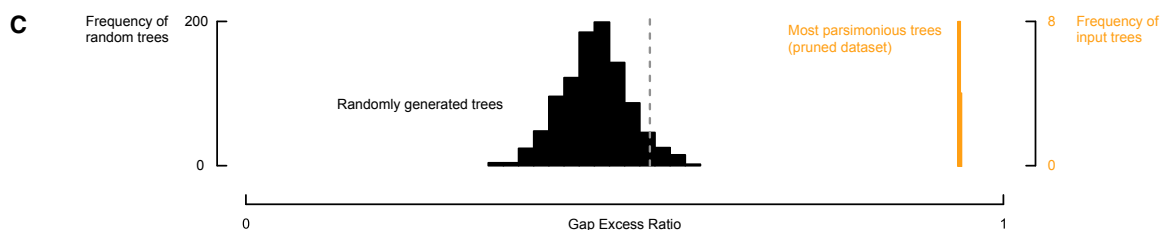
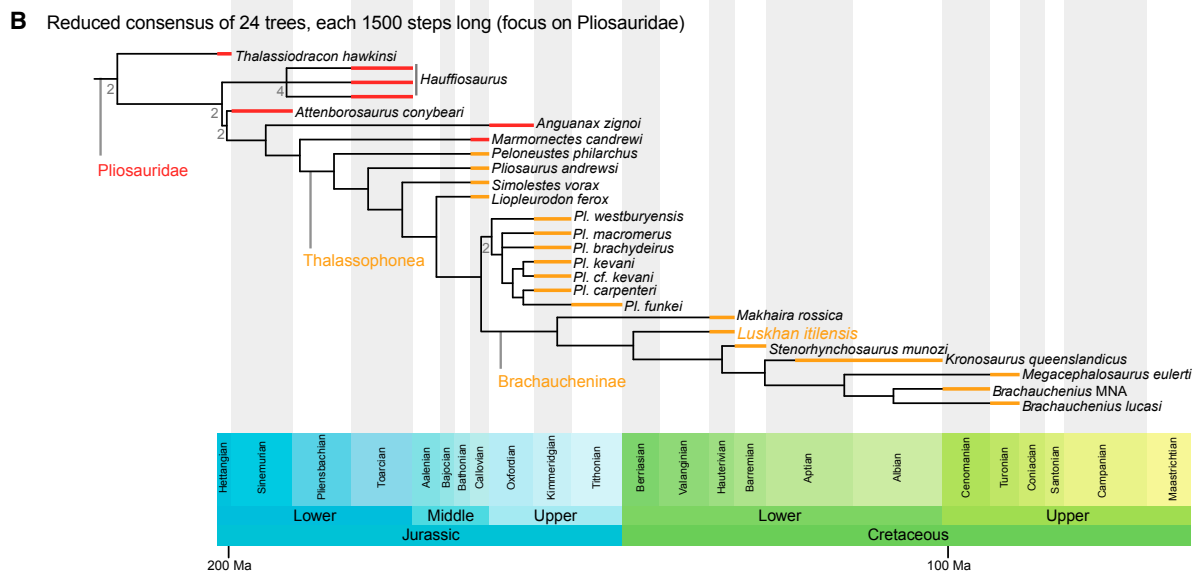
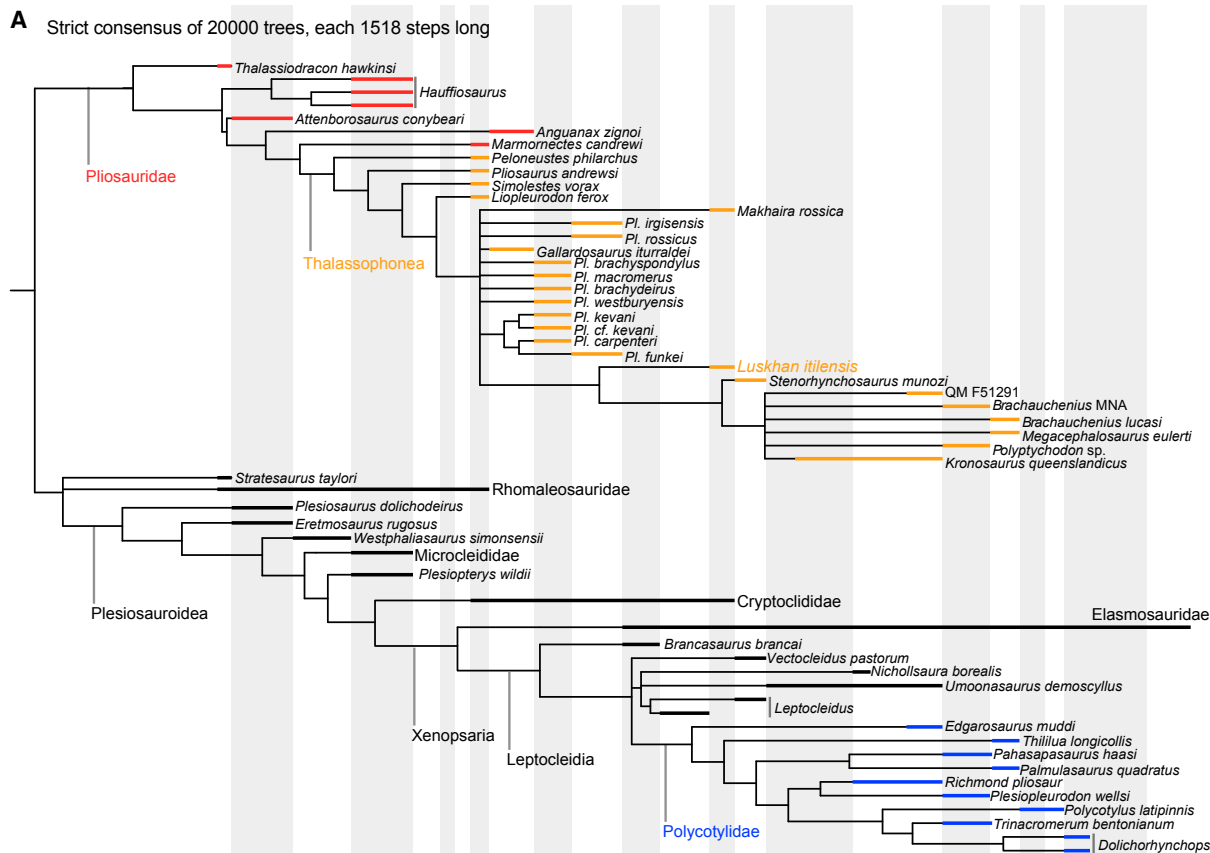
(F) Anterior part of the right coracoid in medial view.

(G) Right forefin in dorsal view.

(H) Right ilium in medial view.

(I) Left hind fin in dorsal view.

c3, third cervical centrum; dc, distal carpal; dt, distal tarsal; interm, intermedium; mc, metacarpal; mt, metatarsal; od, odontoid. See also [Figure S1](#).



(legend on next page)

exoccipitals meet ventromedially and thereby exclude the basioccipital from participating in the floor of the foramen magnum (at least posteriorly); deep lateral sulcus ventrally on the lateral surface of the dorsal lamella of the pterygoid; enlarged atlantal intercentrum swollen posteroventrally, with longitudinal ventral ridge; ventromedially expanded atlantal arches excluding the odontoid from the neural canal; tongue-like ventral process of the third cervical centrum extending far anteroventrally to cover the ventral exposure of the axial centrum; anteromedial process of the coracoid extends ventrally rather than anteriorly, forming a 90° angle with coracoid plate; dorsoventrally short dorsal process of the scapula, extending approximately only as far dorsally as the distance posteriorly from the base of the scapular blade to the scapulocoracoid contact (unique among thalassophoneans; present otherwise in elasmosaurids, e.g., [12]); epipodial elements are reduced, being comparable in size to tarsals; humeral tuberosity higher dorsally than ventral expansion of humeral capitulum; ulna longer than radius; absence of an epipodial foramen (unique among pliosaurids); intermedium contacting only the fibula proximally, and so bearing only a single proximal facet (the distal tarsals are not offset with respect to proximal tarsals in *Marmornectes* + *Thalassophonea* [2, 13, 14], but the intermedia of these species still bear a facet for the tibia, unlike in *Luskhan itilensis*); and fibula much longer anteroposteriorly than tibia.

Description and Comparison

A detailed morphological description of *Luskhan* is in preparation and will be published elsewhere. Key morphological features aside from the autapomorphies are as follows: *Luskhan* is a moderately large thalassophonean estimated from its preserved portions to be 6.5 m long, with a mandible length of 1,585 mm. *Luskhan itilensis* possesses a combination of primitive features of thalassophonean pliosaurids, features shared with *Pliosaurus*, and derived features seen in younger brachauchenines such as *Kronosaurus* and *Brachauchenius*, as does *Stenorhynchosaurus munozi* [15]. This observation is consistent with our finding that *Luskhan* represents an early-diverging brachauchenine (see [Figure 3](#)). Its primitive features include the following: posteroventral process of jugal underlaps squamosal anteriorly as in *Pliosaurus* [3]; squamosal contacts the posteroventral process of the post-orbital, excluding jugal from the temporal fenestra, as in most plesiosaurs, but unlike in *Brachauchenius* and *Megacephalosaurus* [16, 17]; a squamosal “bulb” is present, as in Jurassic pliosaurids (although it is larger and more prominent in *L. itilensis*), but unlike in *Brachauchenius* and *Megacephalosaurus* [16, 17]; a large, thick quadrate process of the pterygoid, which contacts the ventral surface of the paroccipital process along its entire length leaving no foramen between them (shared with *Pliosaurus*

westburyensis; R.B.J.B., personal observation of BRSMG Cc 332); a deep, U-shaped ventral excavation of the supraoccipital, shared with *Pliosaurus westburyensis* (R.B.J.B., personal observation of BRSMG Cc 332); a mediolaterally oriented crest extends dorsally from the posterodorsal surface of squamosals, as in non-brachauchenine thalassophoneans ([2], character 54); ventromedial flanges of the pterygoids contact each other on the midline posteriorly, as in most thalassophoneans ([18, 19], character 69), but unlike in *Brachauchenius*, in which they do not contact ([2], character 101; [16, 20]); cervical vertebral count is 14 (the entire neck and the first three pectorals—which were counted as part of the trunk—are fully articulated), which is intermediate between that seen in *Pliosaurus* (18 cervicals; [21]) and that seen in *Brachauchenius* (12 cervicals; [20]); and large sub-central foramina are present on the ventral surfaces of the cervical centra, as in most plesiosaurs, but unlike in *Kronosaurus* and *Brachauchenius* [22].

Derived features of *Luskhan* shared with *Pliosaurus* [3] + brachauchenines are as follows: teeth with triangular cross-sections and bearing at least one carina (seen in incompletely preserved and damaged teeth—nevertheless, the remaining morphology is consistent with the trihedral condition seen in *Pliosaurus* spp. and early brachauchenines [3, 23], albeit much smaller in size); the posterior portion of the squamosal/parietal vault is mediolaterally broad, equal to approximately half the width of the cranium; the ventral surface of the parabasisphenoid is mediolaterally convex, lacking a sharp ventral keel, as in *Brachauchenius lucasi* [16, 22], *Megacephalosaurus eulerti* [16], *Kronosaurus queenslandicus* [24], and *Gallardosaurus iturradlei* [25], and unlike in Middle Jurassic thalassophoneans (it is variable in *Pliosaurus* [3]); the surangular fossa faces dorsolaterally, as in some species of *Pliosaurus* [3] (we cannot yet determine the condition in brachauchenines); and the ilium has an anteroposteriorly large dorsal expansion (inferred from broken preserved morphology) [21].

Brachauchenine features present in *Luskhan* are as follows [2, 15, 16]: preorbital portion of skull is long anteroposteriorly and temporal region is short; parietal extends anteriorly to approximately the position of the external naris; rostral constriction is absent, although a secondary expansion of the maxilla seems to be present posterior to the premaxilla/maxilla contact, and predominantly expands ventrally (e.g., as in *Megacephalosaurus*); isodont mesial maxillary and distal premaxillary dentitions; post-eromedially inturned retroarticular process relative to glenoid; widely spaced premaxillary, mesial dentary, and maxillary alveoli; cervical rib facets located at mid height of cervical centra, as in *Kronosaurus* and *Brachauchenius*, but unlike in Jurassic pliosaurids, in which the facets are located ventrolaterally as is common

Figure 3. Time-Scaled Phylogeny of Plesiosaurs

(A) Time-scaled strict consensus of the 20,000 most parsimonious trees, each with a length of 1,518 steps arising from the analysis of the full dataset. In this analysis, all brachauchenines except *Makhaira rossica* form a clade, containing *Luskhan itilensis* as its earliest-branching member, followed by *Stenorhynchosaurus munozi*. Aptian-Turonian brachauchenines form a large polytomy.

(B and C) Time-scaled reduced consensus (reduced dataset) of the 24 most parsimonious trees, each with a length of 1,500 steps (see also [Figure S2](#)), with a focus on Pliosauridae (B). This analysis yielded a nearly fully resolved consensus tree for Pliosauridae, with excellent stratigraphic congruence indexes (C), here represented by the gap excess ratio, compared to a set of 1,000 randomly generated trees. *Makhaira rossica*, *Luskhan itilensis*, *Stenorhynchosaurus munozi*, and *Kronosaurus queenslandicus* form a pectinate grade leading to a clade of highly derived pliosaurids containing the last thalassophoneans: *Megacephalosaurus eulerti* and *Brachauchenius*. Bremer support values >1 in the reduced consensus are indicated next to their corresponding node. See [Figure S2](#) for additional phylogeny results.

See also [Figure S2](#) and [Data S1](#) and [S2](#).

among plesiosaurs; bases of dorsal transverse process located dorsally to the level of the neural canal (they are level with the neural canal in Jurassic thalassophoneans); and coracoid:scapula length ratio shared with *K. queenslandicus* (2.288 in *L. itilensis*, ~2.5 in *K. queenslandicus*) but higher than in *Stenorhynchosaurus munozi* (<2) [15, 22].

Despite the presence of this combination of primitive and derived characters, several other morphological features of *Luskhan itilensis* cannot be predicted by a simple sequence of character evolution from Jurassic thalassophoneans to *Kronosaurus*- and *Brachauchenius*-like forms of the middle and Late Cretaceous. We particularly emphasize features shared by *Luskhan* and polycotyloid plesiosauroids such as *Dolichorhynchops* from the Late Cretaceous (e.g., [6]): its rostrum is markedly slender (Figures 1 and 2) compared to other thalassophoneans, lacking their typical macrophagous features [3, 13, 18, 23, 24, 26] (i.e., ventral keel of the symphysis absent; diastema absent; marked lateral expansion of the premaxilla and the maxilla and rostral constriction absent; dentition essentially isodont, lacking a canniniform region). The mandibular symphysis of *Luskhan* measures 33.7% of the total mandible length and is proportionally longer than in other thalassophoneans [28% in *Peloneustes philarchus* (GPIT03182; L.S., personal observation), 27% in *Pliosaurus brachyspondylus* (CAMSM J35991; [27]), and below 25% in all other pliosaurids], but within the range of polycotyloids (from 27.9% in *Edgarosaurus* to 45.2% in *Dolichorhynchops osborni* [28, 29]; see Data S3 and S4). The teeth are widely spaced, and the tooth row terminates around orbital mid-length, as in polycotyloids (e.g., [29]), but unlike in other thalassophoneans, where the teeth are closely spaced and terminate further posteriorly, close to the level of the postorbital bar [16, 25, 30]. The squamosal arch is similar to that of *Dolichorhynchops* (e.g., [6]), with dorsal rami that extend anterolaterally from the median contact of the squamosals, rather than laterally or posterolaterally as in other thalassophoneans [3, 16, 25, 30].

Morphospace Analyses

Cladistic morphospace analyses indicate that *Luskhan itilensis* is dissimilar to other thalassophoneans, both cranially and postcranially (Figures 4, S3, and S4). The first principal coordinates axis (PCo1) of our craniodental data explains a high proportion of the pairwise distances in our dataset (71.7%). This axis separates pliosaurids from polycotyloids, and *Luskhan* falls closer to polycotyloids on this axis than do other thalassophoneans, along with the Early Jurassic non-thalassophonean pliosaurid *Hauffiosaurus* (Figure 4A). Examination of pairwise dissimilarities for craniodental data indicates that *Luskhan itilensis* is the thalassophonean that is the most similar (the least dissimilar) to polycotyloids. It lies outside the 99.73% confidence interval (mean \pm 3 SDs) for thalassophonean dissimilarity to polycotyloids (Figure 4B). *Luskhan itilensis* is thus, by far and most notably in craniodental cladistic characters, the most polycotyloid-like pliosaurid.

In contrast to craniodental data, postcranial cladistic data do not indicate convergence between *Luskhan* and polycotyloids (Figure S3), and evidence for convergent evolution toward polycotyloid-like character states is also weaker when combined craniodental and postcranial data are analyzed together (Figure S3) than when the craniodental data are analyzed alone (Figure 4). This was also found for ecomorphological data (craniodental re-

sults are described below; see Figures 4 and S4), suggesting that the axial and appendicular morphology of polycotyloids is distinct from that of all pliosaurids and that convergent ecomorphological evolution occurred only in the skull.

Ecomorphological data further demonstrate the close similarity of *Luskhan itilensis* and polycotyloids in terms of craniodental architecture (Figures 4C and S4). Non-thalassophonean pliosaurids such as *Hauffiosaurus* from the Early Jurassic [31] and *Marmornectes* from the Middle Jurassic [13], plus the early-diverging thalassophonean *Peloneustes philarchus*, occupy a craniodental ecomorphospace region close or within that of polycotyloids. *Luskhan itilensis* is the only derived pliosaurid to re-explore that region of the ecomorphospace (Figures 4C and S4).

In the cluster dendrogram analysis of craniodental data (Figure 4D), most polycotyloids form a well-defined cluster, which also includes the long snouted early pliosaurid *Hauffiosaurus longirostris*. *Luskhan itilensis* clusters with the early pliosaurids *Marmornectes candrewi* and *Thalassiodracon hawkinsi*, as well as the early polycotyloid *Edgarosaurus muddi*. Remaining thalassophoneans, including the early brachauchenine *Stenorhynchosaurus munozi*, are distributed within two distinct groups containing members with macrophagous adaptations such as short symphyses and large tooth crowns.

Iterative Evolution in Short-Necked Plesiosaurs

Although the earliest pliosaurids were small, gracile, and relatively long-necked [13, 31–33], later pliosaurids—belonging to the clade Thalassophonea—evolved a large robust skull, a short neck, and a suite of cranial and dental features indicating a niche of large top-tier predators in marine ecosystems [2–5]. These short-necked, large-headed body proportions were conserved with relatively few modifications in thalassophoneans, until their extinction during the Turonian (early Late Cretaceous) [22, 23], although the last representatives of the clade lost some features usually functionally correlated to a macrophagous diet, notably carinated tooth crowns, spatulate rostrum (but see [34]), and extensive parietal crests [16, 20, 22, 24]. The large body size and large teeth of the mid-Cretaceous brachauchenines (*Kronosaurus*, *Brachauchenius*, and *Megacephalosaurus*) still suggest a trophic position that is similar to that of earlier, Late Jurassic thalassophoneans, as evidenced by our ecomorphological analyses (Figures 4 and S4). The rare Early Cretaceous pliosaurid remains previously published were initially referred either to *Kronosaurus* (“*Kronosaurus*” *boyacensis* [35]) or *Brachauchenius* (*Brachauchenius* sp. [36]) based on gross similarities. This has suggested that pliosaurids were constrained to a narrow range of ecological niches from the Middle-Late Jurassic up to their final extinction before possibly being replaced ecologically by large mosasaurs [37, 38]. Polycotyloids was a clade of plesiosauroids that convergently attained “pliosauromorph” body proportions from long-necked ancestors [1, 5, 39]. However, aside from their similarity in overall body proportions, evidence for detailed ecomorphological convergence between plesiosauroids and thalassophoneans is scarce, and both clades show important morphological differences, notably in body size, snout and tooth shape, and inferred diet: polycotyloids are regarded as fast-swimming piscivores [5–7] (but see Vincent et al. [40]).

Together with the recently described Early Cretaceous taxa *Makhaira rossica* [23] and *Stenorhynchosaurus munozi* [15],

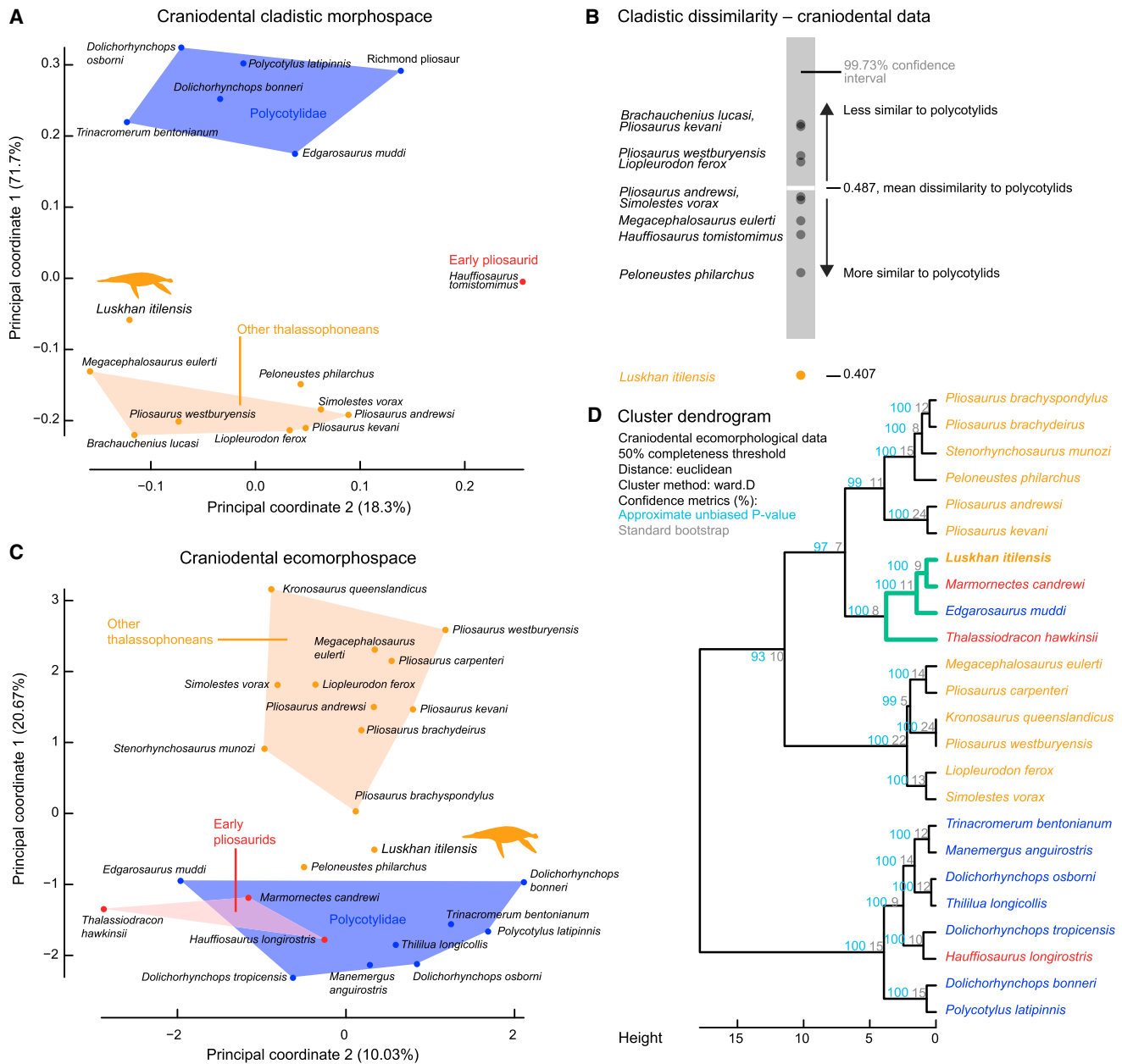


Figure 4. Morphospace Occupation and Dissimilarity of Polycotyliids and Pliosaurids

(A) First two principal coordinates using the craniodental cladistic scores as the source.

(B) Dissimilarity to Polycotyliidae for each pliosaurid using craniodental cladistic scores as the source.

(C) First two principal coordinates using the craniodental ecomorphological data as the source.

(D) Cluster dendrogram analysis of the ecomorphological dataset with confidence metrics for each node. The cluster in green groups *Luskhan*, early pliosaurids, and the early polycotyliid *Edgarosaurus*. A 58% completeness threshold was applied to the cladistic data, and a 50% completeness threshold was applied to the ecomorphological data beforehand.

See also [Figures S3 and S4](#) and [Data S3 and S4](#).

Luskhan itilensis breaks a 40-million-year window of poorly documented pliosaurid evolution. As shown by our cladistic analyses, and contra Páramo-Fonseca et al. [15], these Early Cretaceous pliosaurids form a phylogenetic grade that documents the early evolution of Brachaucheninae. Although the morphology of *Makhaira rossica* indicates that some early bra-

chauchenines most likely retained a macrophagous diet [23], the morphology of *Luskhan itilensis* markedly expands the previously known morphospace occupation of thalassophoneans, because its craniodental morphology converges toward that of early pliosaurids and polycotyliids. This is found both for discrete cladistic characters and ecomorphological metrics (Figure 4).

The long, slender, and straight snout, the long symphysis, the anteroposteriorly shorter parietal crest, the small isodont teeth, and the shorter tooth row (terminating anterior to the level of the orbit) can be functionally correlated with a diet of smaller, softer prey. This indicates an obvious departure from the apex predatory niche most likely occupied by most other thalassophoneans, even though the mesialmost tooth crowns of *Luskhan itilensis* still possess at least one carina and were most likely at least weakly trihedral. This dental morphology has been associated with macropredation [4], but perhaps results from plesiomorphic retention from *Pliosaurus*-like ancestors in *Luskhan* [23]; moreover, the teeth of *Luskhan* are smaller than those of Jurassic pliosaurids and *Makhaira rossica*. *Luskhan* is the first derived pliosaurid to exhibit a clear signal of colonization of a lower trophic level, evolving polycotyloid-like features 10 million years before the appearance of that clade.

Short-necked plesiosaurs iteratively evolved a large bodied, long-snouted morphology, suggesting the iterative colonization of a piscivorous/teuthophagous niche through 135 million years of the Jurassic and Cretaceous. Indeed, many of the early members of Pliosauridae, Brachaucheninae, and Polycotyliidae seem to cluster within a relatively narrow range of craniodental ecomorphological traits, whereas more nested members of those clades explored distinct regions of ecomorphospace (macropredatory pliosaurids and later polycotyliids), this time with little convergent evolution. Our analyses suggest that the emergence of the diverse and long-lived clades of short-necked plesiosaurs was not driven by a precocious colonization of the particular ecological niches proposed for the later branching members of the clades, hence confirming that early pliosaurids were “mesophagous” instead of macrophagous [3, 13]. The evolution of plesiosaurs as a whole appears to be characterized by frequent and profound convergence ranging from anatomical details to entire body plans.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and four data files and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.04.052>.

AUTHOR CONTRIBUTIONS

V.F. and R.B.J.B. wrote the manuscript. M.S.A., I.M.S., G.N.U., and N.G.Z. gathered the stratigraphic and geological data; R.B.J.B., P.S.D., and V.F. gath-

ered the phylogenetic data; and L.C.S., N.G.Z., M.S.A., O.L., and V.F. gathered the ecological data. V.F., R.B.J.B., and L.C.S. designed and ran the analyses. All authors significantly contributed to and revised the manuscript and supplementary information.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Character-taxon cladistic matrix	This paper	Data S2; Morphobank (project 2669, http://morphobank.org/permalink/?P2669)
Ecomorphological data	This paper	Data S3 and S4
Stratigraphic ages of taxa	This paper	Data S1
Software and Algorithms		
TNT1.5	[41]	http://www.lillo.org.ar/phylogeny/tnt/
R	[42]	https://www.r-project.org/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources (cladistic and ecomorphological datasets, R scripts) and should be directed to and will be fulfilled by the Lead Contact, Valentin Fischer (v.fischer@ulg.ac.be).

METHOD DETAILS

Institutional abbreviations

FHSM: Fort Hays Sternberg Museum, Fort Hays, Kansas, USA; **FMNH:** Field Museum of Natural History, Chicago, Illinois, USA; **KUVP:** Kansas Museum of Natural History, Lawrence, Kansas, USA; **MCZ:** Museum of Comparative Zoology, Cambridge, Massachusetts, USA; **UCM:** University of Colorado Museum, Boulder, Colorado, USA; **USNM:** National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; **YKM:** Ulyanovskii Oblastnoi Kraevedcheskii Musei I.A. Goncharova (Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov), Ulyanovsk, Ulyanovsk Region, Russia.

Stratigraphic age and taphonomy of the specimen

In the Ulyanovsk area, only the upper part of the Hauterivian is preserved. It is constituted of monotonous deposits of dark gray, slightly sandy shales, interbedded with siltite beds and containing large carbonate nodules ranging from 0.2 to 1.5 m in length. These nodules occur within well-defined horizons and have a specific external and internal structure; as a result, they serve as stratigraphic markers, within a biostratigraphic framework based on ammonites, which are abundant (I.M.S, G.N.U. M.S.A., N.G.Z., and V.F., personal observation, July 2015). The total thickness of this series can reach 50 m and span three ammonite zones: the *Speetonicer* *versicolor* Zone, the *Milanowskia speetonensis* Zone and the *Craspedodiscus discofalcatus* Zone; the latter is not preserved in the section where YKM 68344/1_262 was excavated (Figure S1) [1–3].

YKM 68344/1_262 was found in the dark gray shales and siltites of the g-5 ghorizont, in the upper part of the *Speetonicer* *versicolor* Zone; specimens of *Speetonicer* *versicolor* were collected a couple of meters to the north of the locality in the beds just overlying the horizon of YKM 68344/1_262, but still within the g5 ghorizont. Some bones were enclosed within carbonate nodules with the specific composition and structure of that layer.

Phylogenetic analyses

We coded YKM 68344/1_262 in a modified version of the dataset of Fischer et al. [23], which was in turn modified from that of Benson & Druckenmiller [2]; the completeness and good preservation of the holotype permits scoring of 74.44% of the characters. In addition to YKM 68344/1_262, we added seven polycotyliids that were not previously included in the dataset (data sources in brackets): *Palmulasaurus quadratus* [43], *Pahasapasaurus haasi* [29], *Polycotylus latipinnis* [6, 44–48] (FMNH PR 187; H. Ketchum, personal communication, 2008, on YPM 1125 and USNM 27678; B. Schumacher personal communication, 2015, on SDSM 23020), *Thililia longicollis* [49], *Trinacromerum bentonianum* [45, 50, 51] (H. Ketchum, personal communication, 2008, on USNM 10945, USNM 10946, and KUVP 5070), *Dolichorhynchops osborni* [6, 45, 50, 52] (H. Ketchum, personal communication, 2008, on KUVP 1300, FHSM VP 404, and MCZ 1064; UCMP 35059), *Dolichorhynchops bonneri* [7] (H. Ketchum, personal communication, 2008, on KUVP 40001 and KUVP 40002).

We used TNT (v1.5; [41]) New Technology search (200 ratchet iterations, drift and tree fusing activated, 20000 trees limit) to recover most parsimonious trees that were used as a basis for a heuristic search using tree branch reconnection. We performed a second analysis pruning unstable taxa, using the a posteriori method “Iterative Positional Congruence Reduced” (IterPCR) of Pol & Escapa [53], recently implemented in TNT 1.5 [54], to apply a strict reduced consensus approach [42]. The following OTUs were identified as unstable and pruned from the second analysis in order to build the reduced consensus: *Pistosaurus*

skull, *Pliosaurus brachyspondylus*, *Pliosaurus rossicus*, *Pliosaurus irgisensis*, *Gallardosaurus itturaldei*, QM F51291, *Polyptychodon* sp., and *Eromangasaurus australis*. We computed Bremer supports on this pruned dataset. See [Data S1](#) and [Data S2](#) for more information.

Cladistic morphospace analysis

We ran a morphospace analysis using discrete characters compiled for our cladistic analysis, in the R statistical environment (v3.3.2; [55]). We set a completeness threshold to remove the influence of highly incomplete taxa for which pairwise dissimilarities cannot be estimated precisely due to abundant missing data. Preliminary tests found that setting this threshold at 58% completeness allowed the inclusion of all reasonably-known pliosaurids and polycotyliids, yielding robust dissimilarity estimates, at the cost of the exclusion of a smaller number of less well-documented taxa from the analysis. In addition to analysis using the entire skeleton (270 characters), we also analyzed cranial (140 characters) and postcranial (130 characters) characters separately, keeping the 58% completeness threshold.

Treating all characters as unordered, we generated a square matrix of pairwise patristic dissimilarities between taxa. This contains the total number of observed character state differences between each taxon pair, as a proportion of the number of characters that were positively scored (i.e., not missing data or inapplicable) in both taxa for each pair [56–58]. We report these pairwise dissimilarities, as well as the mean dissimilarities between individual taxa and groups of taxa (e.g., the mean pairwise dissimilarity between YKM 68344/1_262 and polycotyliid species). Using the *labdsv* package in the R statistical environment, we also used the dissimilarity matrix as the basis of a principal co-ordinates analysis that was used to visualize the overall structure of intertaxon dissimilarities (reviewed by [59]).

Ecomorphospace analysis

We ran a second morphospace analysis using a series of continuous measurements and ratios that collectively summarize the general ecomorphology of short-necked plesiosaurs, i.e., pliosaurids and polycotyliids [1]. This analysis has also been realized in the R statistical environment (v3.3.2; [55]) We focused our efforts on single specimens, but in some case, especially for polycotyliids, mean values from multiple specimens have been used (see [Data S3](#) and [Data S4](#) for more information). We used absolute and relative measurements, all of which are ecologically relevant: relative snout width (rostrum width anterior to the orbit divided by mandible length), relative symphysis length (symphysis length divided by mandible length), absolute crown height of the largest tooth (a crucial determinant in the diet of odontocete cetaceans; e.g. [60]), crown shape (crown height divided by the basal diameter of the crown, largest tooth), relative skull size (mandible length divided by trunk length), relative neck length (neck length divided by trunk length), homogeneity of flipper sizes (humerus proximodistal length divided by femur proximodistal length) and flipper size (mandible length divided by femur length). In addition to our own measurements, we used the following references for pliosaurids: [1, 6, 13, 15, 16, 22, 23, 26, 27, 30, 31, 61–66] and the following references for polycotyliids [7, 28, 29, 43, 47, 49, 67, 68] (see [Data S3](#) and [Data S4](#) for more information). We then applied a 50% completeness threshold to remove the influence of highly incomplete taxa.

We submitted this dataset to a cluster dendrogram analysis in the R statistical environment (v3.3.2 [55], *stats* package) using the Ward method to investigate the phenomenon of ecomorphological convergence between short-necked plesiosaur species. Data were scaled to have equal variances and transformed to a Euclidean distance matrix before clustering. As for the cladistic data, we set a completeness threshold to remove the influence of highly incomplete taxa for which pairwise dissimilarities cannot be estimated precisely due to abundant missing data. This threshold was set at 50%. We also visualized the ecomorphological disparity and convergences of short-necked plesiosaurs via principal coordinate analyses of the same dataset, applying the Cailliez correction for negative eigenvalues and using the *ape* package (v3.5) [69].

Finally, we computed a phylomorphospace, to visualize the evolutionary pathway within ecomorphospace, using the *phytools* (v0.5–64), *zoo* (v1.7–14), *paleotree* (v2.7) and *ape* (v4) packages in R [69–72]. We used the most parsimonious tree from the reduced consensus analysis with the best Gap Excess Ratio score, because the phylomorphospace approach requires a tree with branch lengths, not a consensus tree. We computed the Gap Excess Ratio score using *strap* (v1.4) package in R [73]. However, only 12 taxa from the phylogeny pass the 50% completeness threshold on ecomorphological data, resulting in a new morphospace (computed using principal coordinate analysis on craniodental ecomorphological data) that is based on much less taxa than those presented in [Figure 4](#). It is therefore suboptimal in terms of power, but illustrate the fact that *Luskhan* originate from a node located deeply within the ecomorphological range of thalassophoneans and convergently acquired a polycotyliid-like morphology unlike any other pliosaurid of the dataset ([Figure S4](#)).

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical analyses have only been applied to the cluster dendrogram analyses, to evaluate the robustness of the clusters. Commonly implemented bootstrapping methods were rendered inadequate by the small sample size and substantial proportion of missing values (46.21%) in the dataset, which were a result of the focus on ecologically relevant measurements and high number of single specimen taxa. To resolve this issue, we assessed the statistical support of our resulting cluster dendrogram using the

“Approximately Unbiased P-value” method of the pvclust package (v2.0) [74] in R, following the same procedure as in Fischer et al. [75]: we ran the multiscaled bootstrapping from 0.5 to 5 times the size of the original dataset, at increments of 0.1 and 10,000 bootstraps per increment. Both the standard bootstrap and the approximately unbiased p value are reported in [Figure 4](#) and [Figure S4](#).

DATA AND SOFTWARE AVAILABILITY

All data are provided in [Data S1](#), [Data S2](#) (also uploaded as a Nexus file on Morphobank, <http://morphobank.org/permalink/?P2669>), [Data S3](#), and [Data S4](#).

Current Biology, Volume 27

Supplemental Information

**Plasticity and Convergence in the Evolution
of Short-Necked Plesiosaurs**

Valentin Fischer, Roger B.J. Benson, Nikolay G. Zverkov, Laura C. Soul, Maxim S. Arkhangelsky, Olivier Lambert, Ilya M. Stenshin, Gleb N. Uspensky, and Patrick S. Druckenmiller

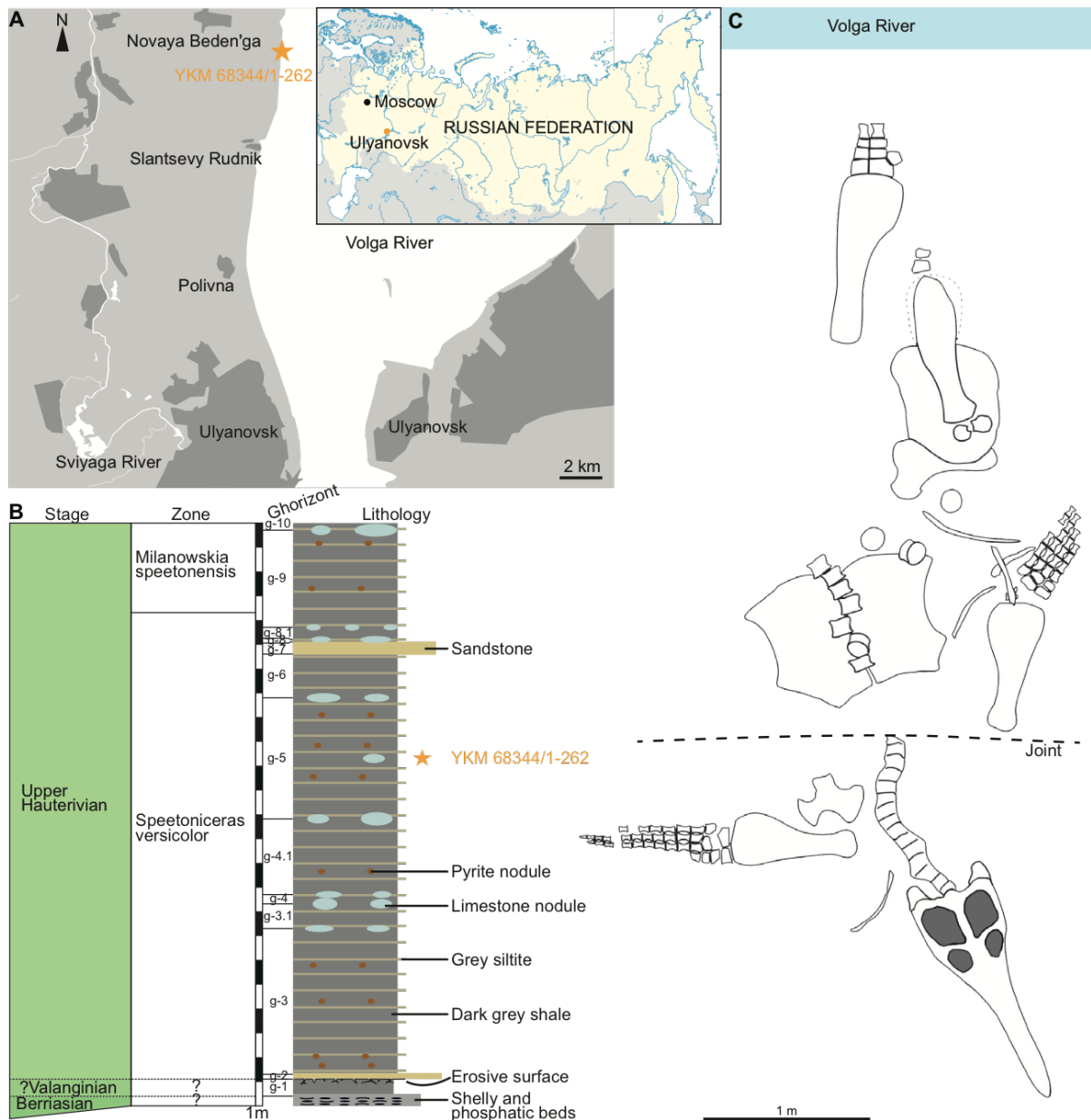


Figure S1. Spatiotemporal setting of the holotype of *Luskhan itilensis* (YKM 68344/1_262). (A). Localisation of the section (inlay map of the Russian Federation modified from TUBS, Wikimedia Commons, 2013). (B) Stratigraphic position. (C) In situ drawing of the holotype of *Luskhan itilensis* (YKM 68344/1_262), related to Figure 1, Figure 2, and STAR Methods.

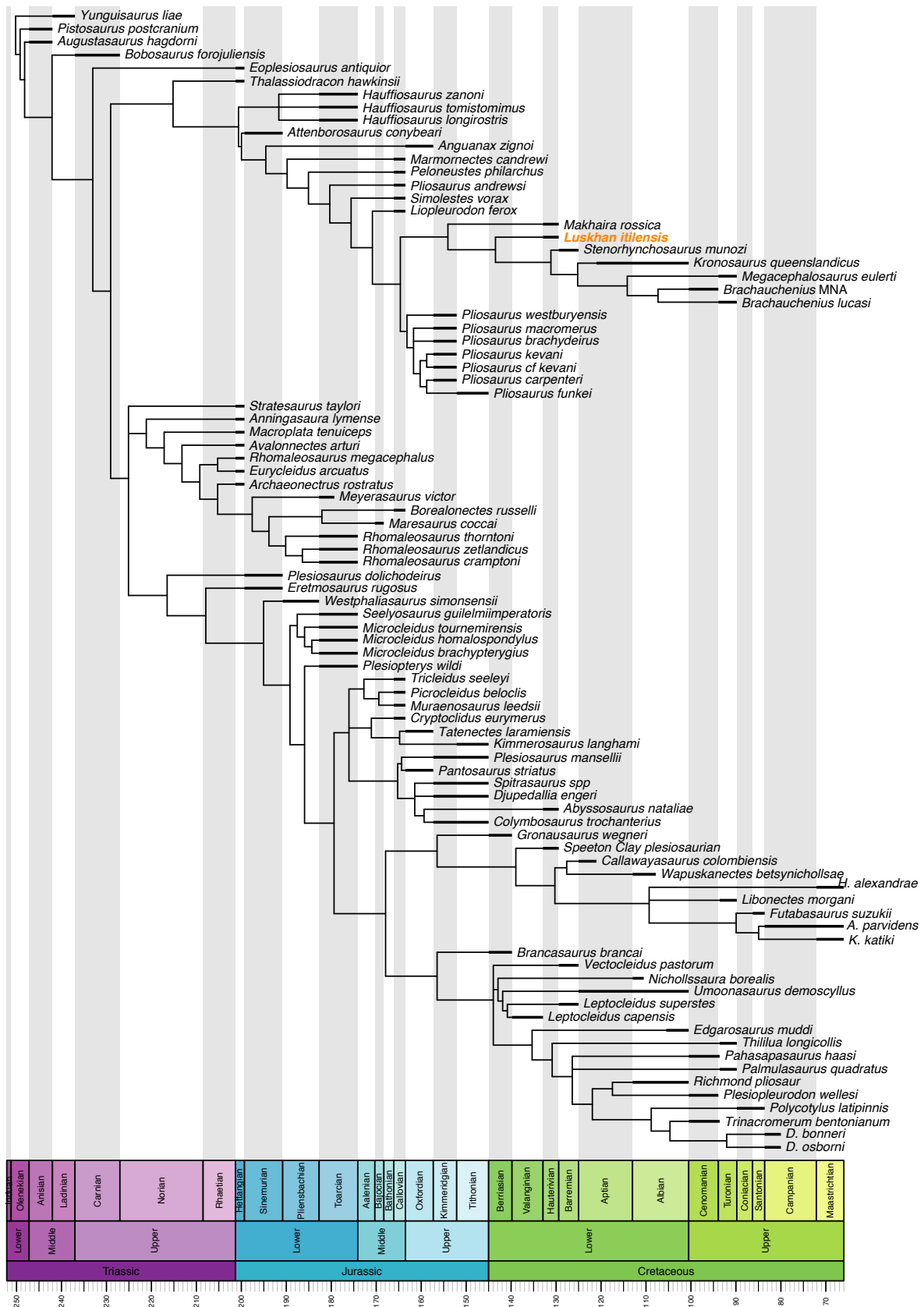


Figure S2. Phylogeny of plesiosaurs. Strict consensus of the 24 most parsimonious trees resulting from the maximum parsimony analysis of the reduced dataset, related to Figure 3 and STAR Methods.

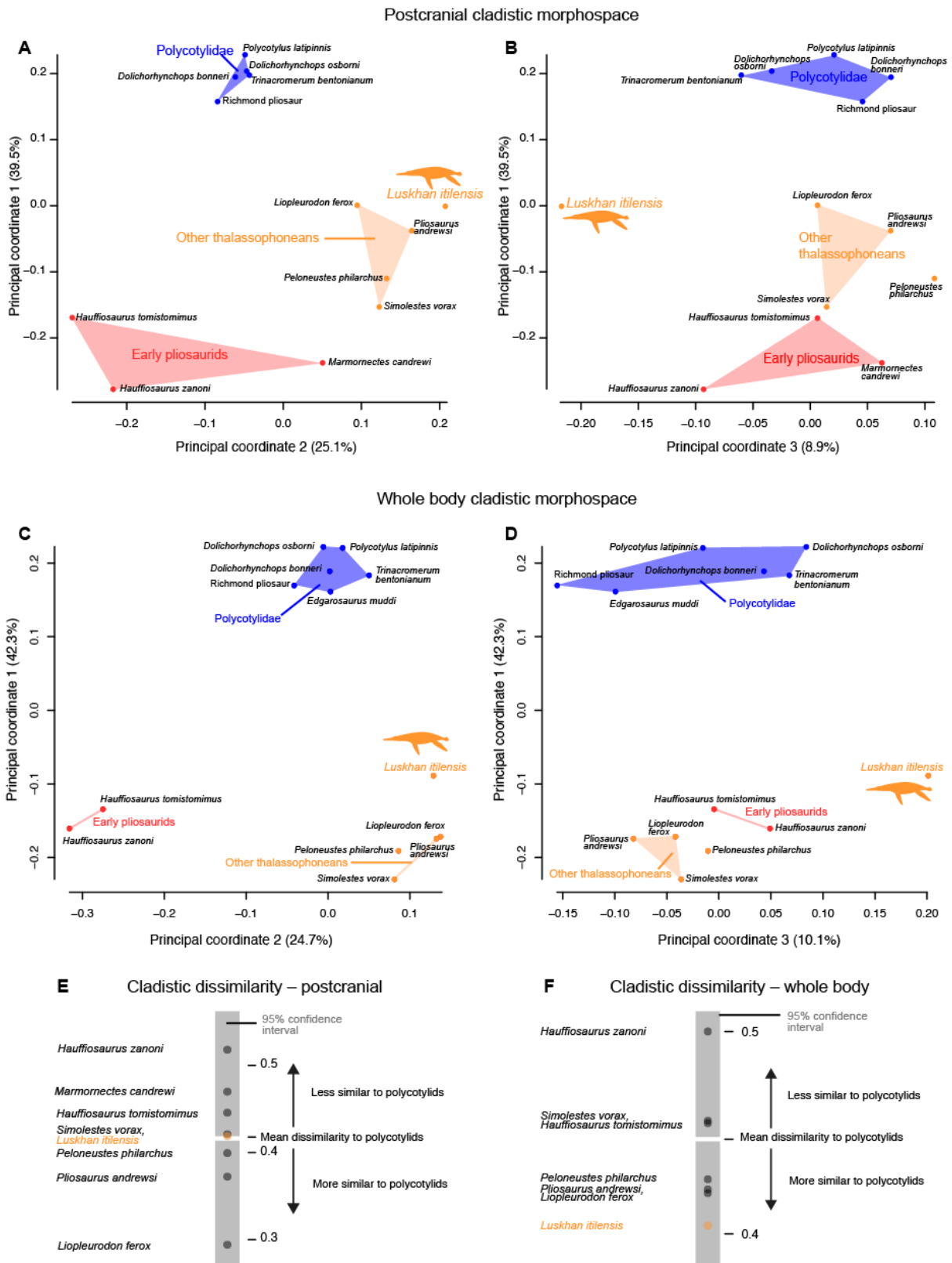


Figure S3. Cladistic morphospace occupation of short-necked plesiosaurs. (A, B) Occupation of the postcranial skeleton morphospace by polycotyliids and pliosaurids, visualised using principal coordinates 1 and 2 (A) and principal coordinates 1 and 3 (B). (C, D) Occupation of the whole skeleton morphospace by polycotyliids and pliosaurids, visualised using principal coordinates 1 and 2 (C) and principal coordinates 1 and 3 (D). (E, F) mean

dissimilarity to Polycotylidae for each pliosaurid taxa, using postcranial (E) and whole body (F) data. All these analyses used cladistic scores as source data; a 58% completeness threshold was applied to the data beforehand. Related to Figure 4 and STAR Methods.

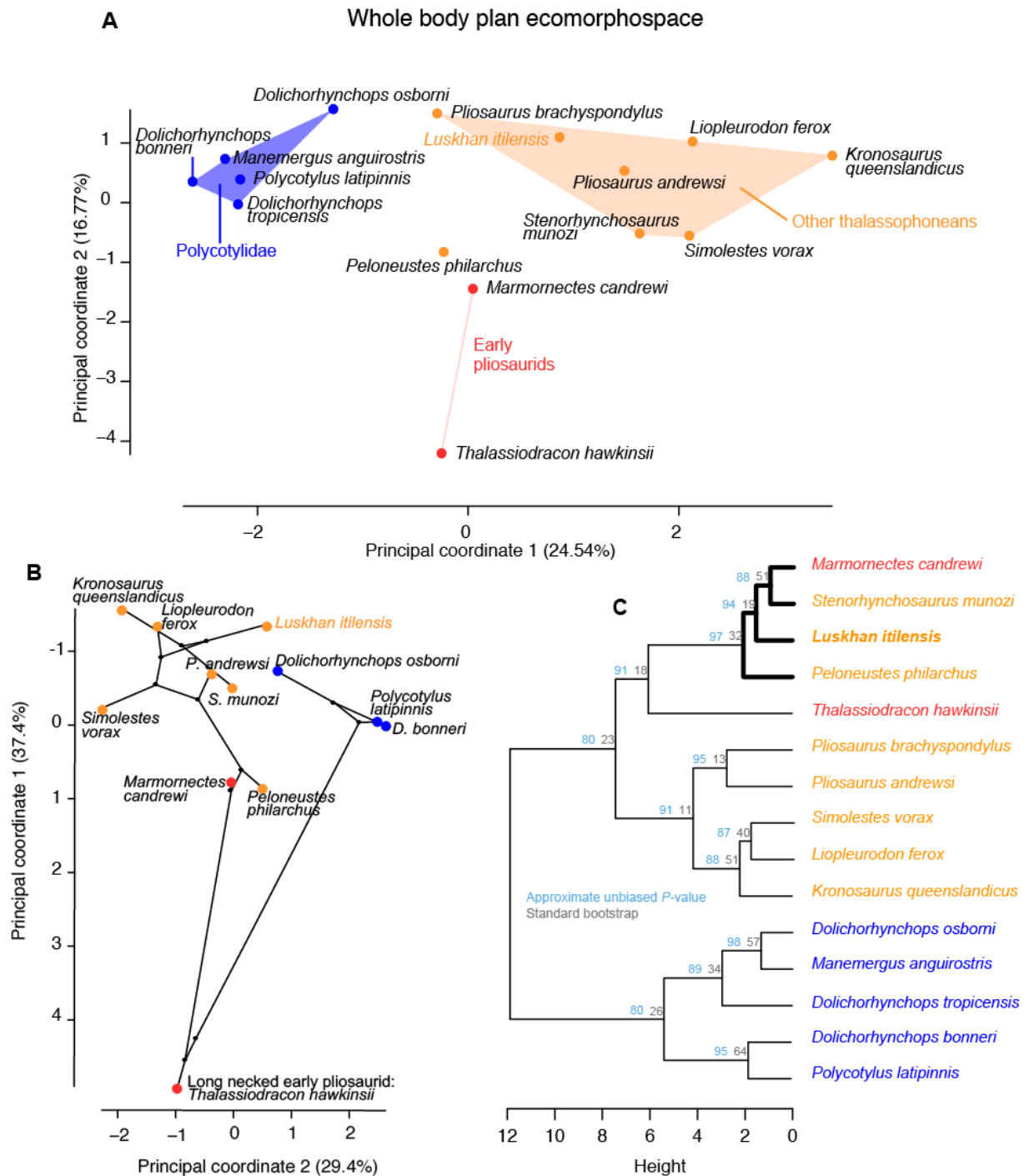


Figure S4. Ecomorphological morphospace occupation of short-necked plesiosaurs. (A) occupation of the whole body ecomorphospace by polycotyliids and pliosaurids. (B) Whole body plan phylomorphospace of pliosaurids and polycotyliids (using a pruned dataset with the species present in both the ecomorphological dataset and the phylogeny). (C) Cluster dendrogram (based on Euclidean distances, using the Ward's D clustering method) of the whole body ecomorphological data; the thick black lines denote a cluster grouping the early brachaucheninines *Luskhan* and *Stenorhynchosaurus* and the early pliosaurids *Marmornectes* and *Peloneustes*. All these analyses used ecomorphological data as source data; a 50% completeness threshold was applied to the data beforehand. Related to Figure 4.

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