

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 characterised as apex predators [2–5], whereas members of the distantly related clade Polycotylidae (middle–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 convergence with closely to 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.

Keywords: Plesiosauria; Thalassophonea; Convergence; Ecomorphology; Morphospace; Jurassic; Cretaceous.

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, 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 *Speetonicerias 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 in supplementary information).

Etymology. The Volga river area is the heart 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/quadrato suture expanding posteriorly into a hook-like, rugose process on the squamosal; 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 3rd 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*); 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 1585 mm. *Luskhan*
itolensis 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
Results, below). Its primitive features include: posteroventral process of jugal underlaps

squamosal anteriorly as in *Pliosaurus* [3]; squamosal contacts the posteroventral process of the postorbital, 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. pers. obs. of BRSMG Cc 332); a deep, U-shaped ventral excavation of supraoccipital, shared with *Pliosaurus westburyensis* (R.B.J.B. pers. obs. of BRSMG Cc 332); 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]); large subcentral 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: 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],

126 *Megacephalosaurus eulerti* [16], *Kronosaurus queenslandicus* [24], and *Gallardosaurus*
127 *iturradlei* [25], and unlike in Middle Jurassic thalassophoneans (it is variable in *Pliosaurus*
128 [3]); the surangular fossa faces dorsolaterally, as some species of in *Pliosaurus* [3] (we cannot
129 yet determine the condition in brachauchenines); the ilium has an anteroposteriorly large
130 dorsal expansion (inferred from broken preserved morphology) [21].

131 Brachauchenine features shown by *Luskhan* are [2,15,16]: preorbital portion of skull is
132 long anteroposteriorly, and temporal region is short; parietal extends anteriorly to
133 approximately the position of the external naris; rostral constriction is absent, although a
134 secondary expansion of the maxilla seems to be present posterior to the premaxilla/maxilla
135 contact, and predominantly expands ventrally (e.g. as in *Megacephalosaurus*); isodont mesial
136 maxillary and distal premaxillary dentitions; posteromedially inturned retroarticular process
137 relative to glenoid; widely spaced premaxillary, and mesial dentary and maxillary alveoli;
138 cervical rib facets located at mid height of cervical centra, as in *Kronosaurus* and
139 *Brachauchenius*, but unlike in Jurassic pliosaurids, in which the facets are located
140 ventrolaterally as is common among plesiosaurs; bases of dorsal transverse process located
141 dorsally to the level of the neural canal (they are level with the neural canal in Jurassic
142 thalassophoneans); coracoid:scapula length ratio shared with *K. queenslandicus* (2.288 in *L.*
143 *itilensis*, ca. 2.5 in *K. queenslandicus*) but higher than in *Stenorhynchosaurus munozi* (<2)
144 [15,22].

145 Despite the presence of this combination of primitive and derived characters, several
146 other morphological features of *Luskhan itilensis* cannot be predicted by a simple sequence of
147 character evolution from Jurassic thalassophoneans to *Kronosaurus*- and *Brachauchenius*-like
148 forms of the middle and Late Cretaceous. We particularly emphasise features shared by
149 *Luskhan* and polycotyloid plesiosauroids such as *Dolichorhynchops* from the Late Cretaceous
150 [e.g. ,6]: its rostrum is markedly slender (Figures 1, 2) compared to other thalassophoneans,

lacking their typical macrophagous features [3,13,18,23,24,26] (i.e. the ventral keel of the symphysis absent, diastema absent, marked lateral expansion of the premaxilla and the maxilla and rostral constriction absent, dentition is essentially isodont, lacking a caniniform 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., pers. obs.], 27% in *Pliosaurus brachyspondylus* [CAMSM J35991; [27] and below 25% in all other pliosaurids), but within the range of polycotylids (from 27.9% in *Edgarosaurus* to 45.2% in *Dolichorhynchops osborni* [28,29]; see supplementary information). Teeth are widely spaced and the tooth row terminates around orbital mid-length, as in polycotylids [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, 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 polycotylids, and *Luskhan* falls closer to polycotylids 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 polycotylids. It lies outside the 99.73% confidence interval (mean \pm 3 standard deviations) for thalassophonean dissimilarity from polycotylids (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 polycotylics (Figure S3), and evidence for convergent evolution towards polycotyloid-like character states is also weaker when combined craniodental and postcranial data are analysed together (Figure S3) than when the craniodental data are analysed alone (Figure 4). This was also found for ecomorphological data (craniodental results described below, and see Figure S4), suggesting that the axial and appendicular morphology of polycotylics 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 polycotylics in terms of craniodental architecture (Figures 4C, 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 polycotylics. *Luskhan itilensis* is the only derived pliosaurid to re-explore that region of the ecomorphospace (Figures 4C, S4).

In the cluster dendrogram analysis of craniodental data (Figure 4D), most polycotylics 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 polycotylic *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*, *Megacephalosaurus*) still suggests a trophic position that is similar to that of earlier, Late Jurassic thalassophoneans, as evidenced by our ecomorphological analyses (Figure 4, Fig 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]. Polycotyliidae 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: polycotyliids 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], *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. While the morphology of *Makhaira rossica* indicates that some early brachauchenines 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 towards that of early pliosaurids and polycotylids. 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 likely occupied by most other thalassophoneans, even though the mesialmost tooth crowns of *Luskhan itilensis* still possess at least one carina and were likely weakly trihedral. This dental morphology has been associated with macropredation [4], but perhaps results from plesiomorphic retention 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 colonisation of a lower trophic level, evolving polycotylid-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 colonisation of a piscivorous/teuthophagous niche through 135 million years of the Jurassic and Cretaceous. Indeed, many of the early members of Pliosauridae, Brachaucheninae, and Polycotylidae seem to cluster within a relatively narrow range of craniodental ecomorphological traits, while more nested members of those clades explored distinct regions of ecomorphospace (macropredatory pliosaurids, later polycotylids), 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 colonisation 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 characterized by frequent and profound convergence ranging from anatomical details to entire body plans.

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. gathered 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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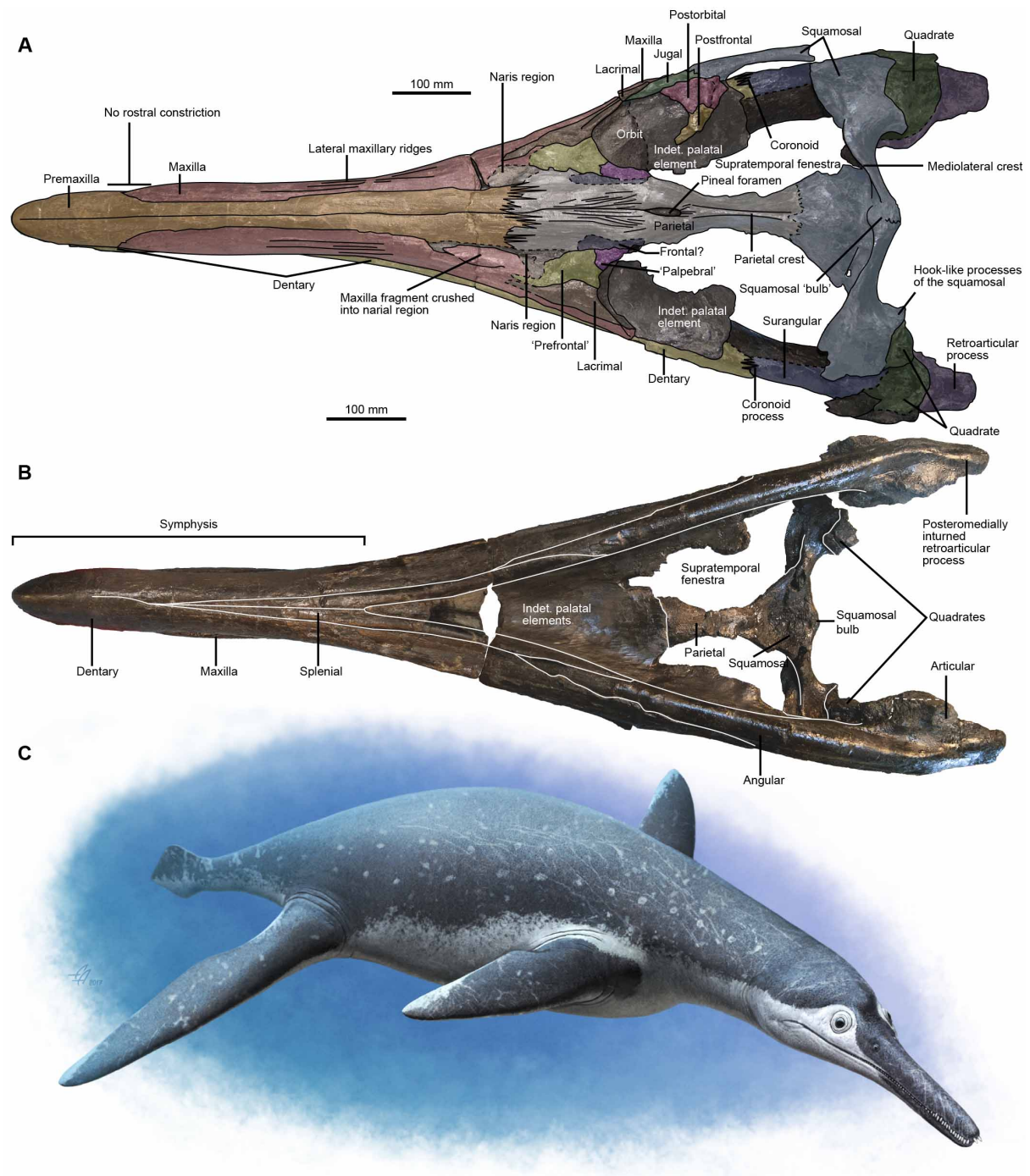
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MAIN-TEXT FIGURE LEGENDS



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475 **Figure 1. Craniodental morphology of *Luskhan itilensis*.**

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

477 Reconstruction by Andrey Atuchin. See also Figure S1.

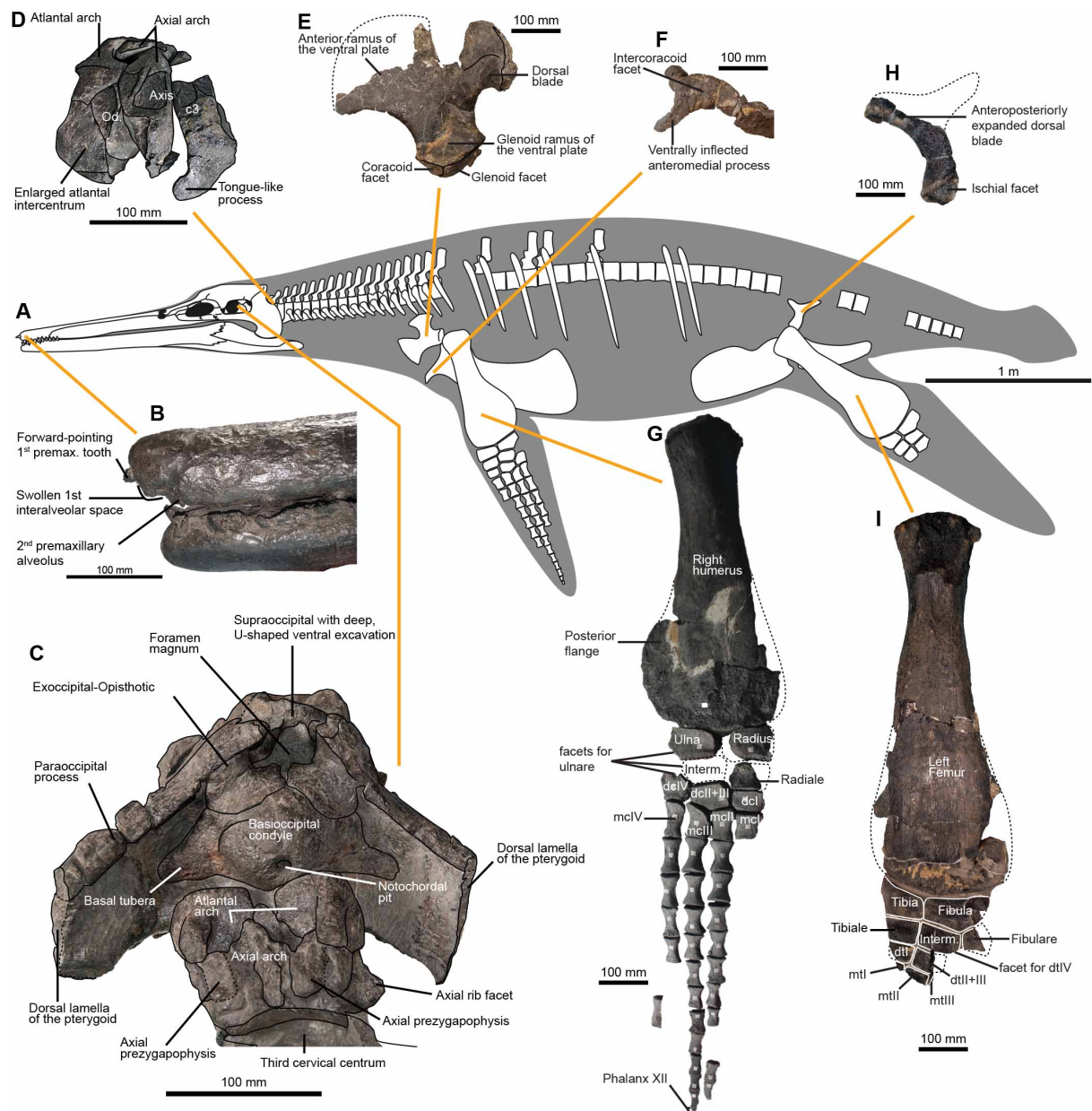


Figure 2. Postcranial morphology of *Luskhan itilensis*.

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. See also Figure S1.

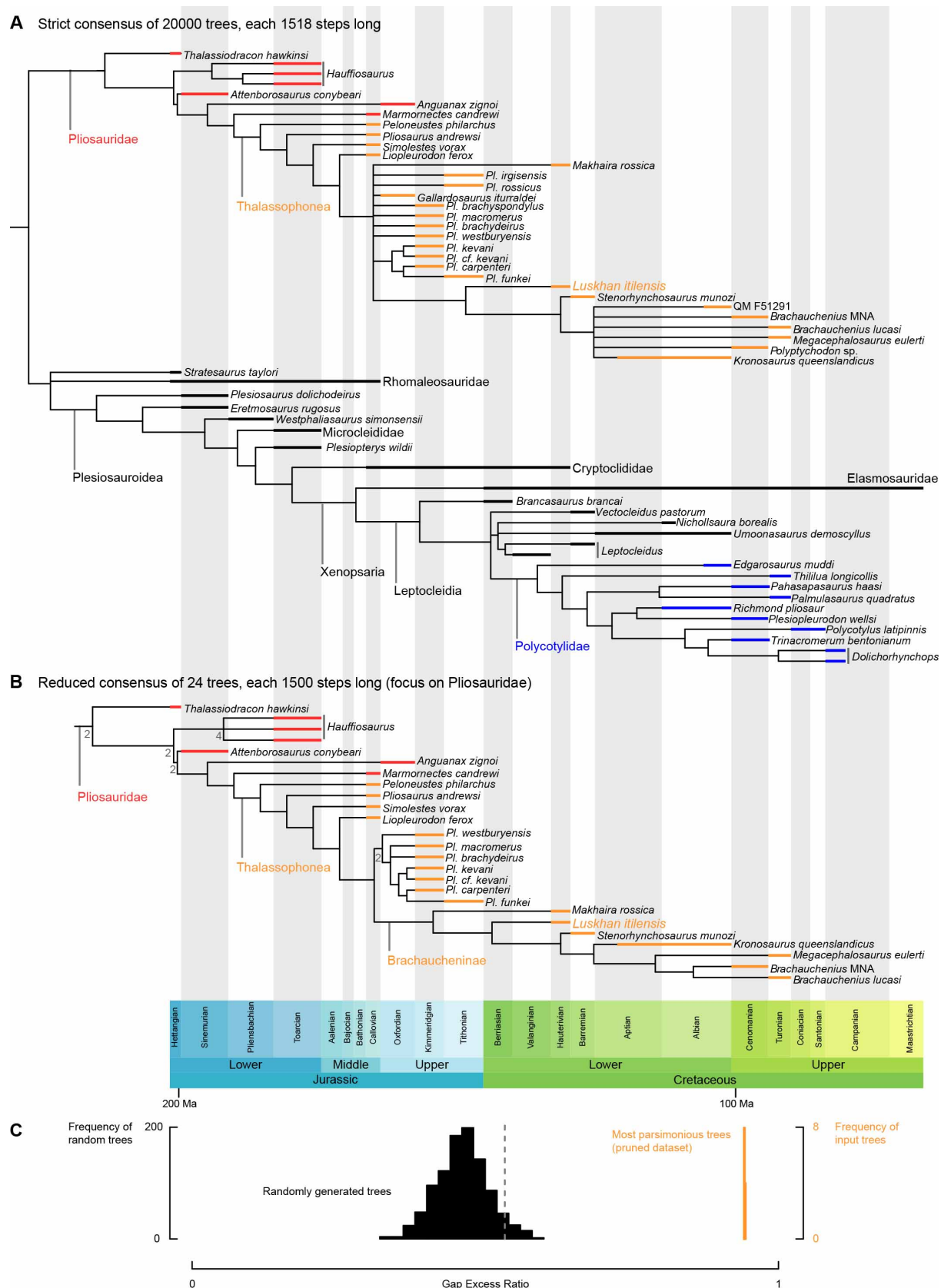


Figure 3. Timescaled phylogeny of plesiosaurs.

487 (A) Timescaled strict consensus of 20000 most parsimonious trees, each with a length of 1518
488 steps arising from the analysis of the Full dataset. In this analysis, all brachauchenines but
489 *Makhaira rossica* form a clade, containing *Luskhan itilensis* as its earliest branching member,
490 followed by *Stenorhynchosaurus munozi*. Aptian–Turonian brachaucheninines form a large
491 polytomy. (B) Timescaled reduced consensus (reduced dataset) of 24 most parsimonious
492 trees, each with a length of 1500 steps (see also Figure S2), with a focus on Pliosauridae. This
493 analysis yielded a nearly fully resolved consensus tree for Pliosauridae, with excellent
494 stratigraphic congruence indexes (C), here represented by the Gap Excess Ratio, compared to
495 a set of 1000 randomly generated trees. *Makhaira rossica*, *Luskhan itilensis*,
496 *Stenorhynchosaurus munozi*, and *Kronosaurus queenslandicus* form a pectinate grade leading
497 to a clade of highly derived pliosaurids containing the last thalassophoneans:
498 *Megacephalosaurus eulerti* and *Brachauchenius*. See supplementary information for
499 additional phylogeny results. See also Figure S2, Data S1, Data S2.

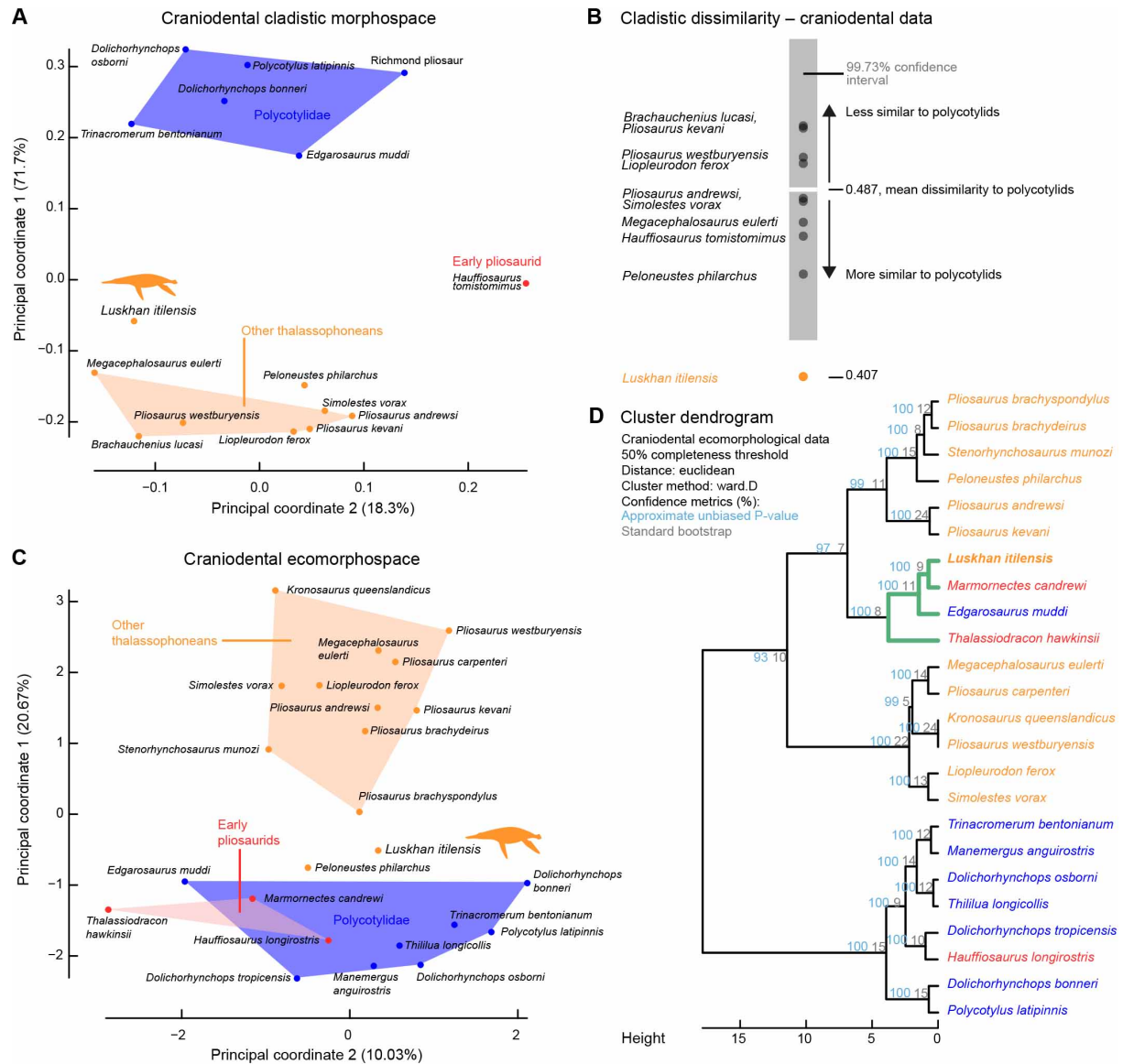


Figure 4. Morphospace occupation and dissimilarity of polycotyliids and pliosaurids.

(A) First two principal coordinates using the craniodental cladistic scores as source. (B) Dissimilarity to Polycotyliidae for each pliosaurid using craniodental cladistic scores as source. (C) First two principal coordinates using the craniodental ecomorphological data as source. (D) cluster dendrogram analysis of the ecomorphological dataset with confidence metrics for each node. The cluster in bold groups *Luskhan*, early pliosaurids and the early polycotyliid *Edgarosaurus*. A 58% completeness threshold was applied to the cladistic data and 50 % completeness threshold was applied to the ecomorphological data beforehand. See also Figures S3, S4, Data S3, Data S4.

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STAR METHODS

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 grey, slightly sandy shales, interbedded with siltites 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. pers. obs. July 2015). The total thickness of this series can reach 50 m and span three ammonite zones: the *Speetoniceras 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 grey shales and siltites of the g-5 ghorizont, in the upper part of the Speetoniceras versicolor Zone; specimens of Speetoniceras 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 polycotylids that were not previously included in the dataset (data sources in brackets): *Palmulasaurus quadratus* [41], *Pahasapasaurus haasi* [29], *Polycotylus latipinnis* ([6,42–46]; FMNH PR 187; H. Ketchum, pers. comm. 2008 on YPM 1125 and USNM 27678; B. Schumacher pers. comm. 2015 on SDSM 23020]), *Thililua longicollis* [47], *Trinacromerum bentonianum* ([43,48,49]; H. Ketchum, pers. comm. 2008 on USNM 10945, 10946, and KUVP 5070), *Dolichorhynchops osborni* ([6,43,48,50]; H. Ketchum pers. comm. 2008 on KUVP 1300, FHSM VP 404, and MCZ 1064; UCMP 35059), *Dolichorhynchops bonneri* ([7]; H. Ketchum pers. comm. 2008 on KUVP 40001 and KUVP 40002).

We used TNT (v1.5; [51]) 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 [52], recently implemented in TNT 1.5 [53], to apply a

strict reduced consensus approach [54]. 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 polycotylids, 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 analysed 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 polycotylid 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 visualise the overall structure of intertaxon dissimilarities (reviewed by [59]).

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586 **Ecomorphospace analysis.** We ran a second morphospace analysis using a series of
587 continuous measurements and ratios that collectively summarise the general ecomorphology
588 of derived short-necked plesiosaurs, i.e. pliosaurids and polycotylids [1]. This analysis has
589 also been realised in the R statistical environment (v3.3.2; [55]) We focused our efforts on
590 single specimens, but in some case, especially for polycotylids, mean values from multiple
591 specimens have been used (see Data S3 and Data S4 for more information). We used absolute
592 and relative measurements, all of which are ecologically relevant: relative snout width
593 (rostrum width anterior to the orbit divided by mandible length), relative symphysis length
594 (symphysis length divided by mandible length), absolute crown height of the largest tooth (a
595 crucial determinant in the diet of odontocete cetaceans [e.g. ,60]), crown shape (crown height
596 divided by the basal diameter of the crown, largest tooth), relative skull size (mandible length
597 divided by trunk length), relative neck length (neck length divided by trunk length),
598 homogeneity of flipper sizes (humerus proximodistal length divided by femur proximodistal
599 length) and flipper size (mandible length divided by femur length). In addition to our own
600 measurements, we used the following references for pliosaurids:
601 [1,6,13,15,16,22,23,26,27,30,31,61–66] and the following references for polycotylids
602 [7,28,29,41,45,47,67,68] (see Data S3 and Data S4 for more information). We then applied a
603 50% completeness threshold to remove the influence of highly incomplete taxa.

604 We submitted this dataset to a cluster dendrogram analysis in the R statistical
605 environment (v3.3.2 [55], stats package) using the Ward method to investigate the
606 phenomenon of ecomorphological convergence between short-necked plesiosaur species.
607 Data were scaled to have equal variances and transformed to a Euclidean distance matrix
608 before clustering. As for the cladistic data, we set a completeness threshold to remove the
609 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 visualised 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 visualise 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 Fig 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 polycotyloid-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 as supplementary files:

- Stratigraphic ages of the taxa used in the phylogenetic analyses, related to Figure 3 and STAR Methods: Data S1.txt
- Cladistic dataset, related to Figure 3 and STAR Methods: Data S2.xlsx; also uploaded as a nexus file on morphobank (<http://morphobank.org/permalink/?P2669>)
- Detailed ecomorphological data with sources and specimens, related to Figure 4 and STAR Methods: Data S3.xls
- Ready-to-use ecomorphological data, related to Figure 4 and STAR Methods: Data S4.txt

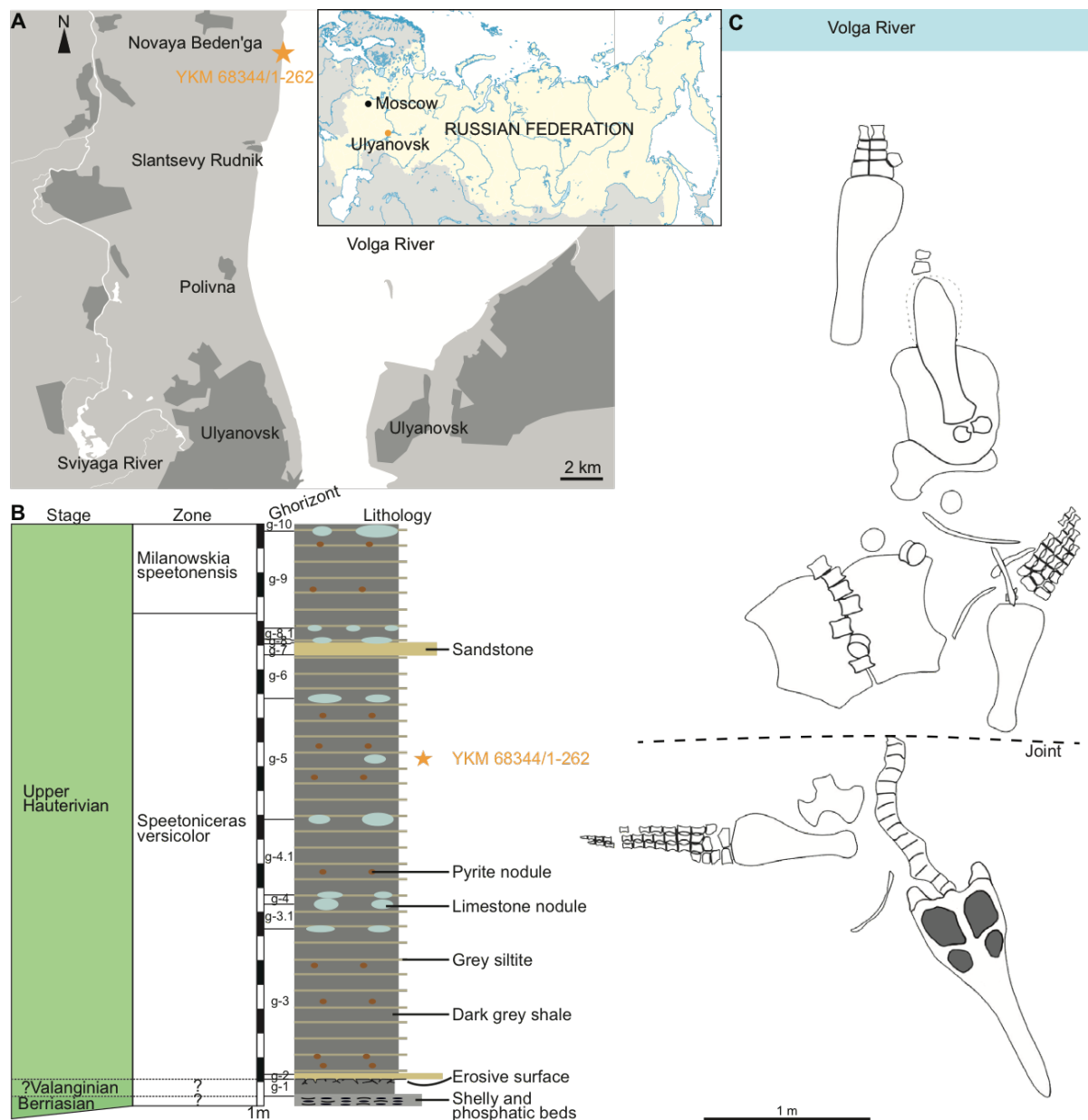


Figure S1. Spatiotemporal setting of the holotype of *Luskhan itilensis* (YKM 68344/1_262). (A). Localisation of the section (inlay map of the Russian Federation modified from TUBS, Wikimedia Commons, 2013). (B) Stratigraphic position. (C) In situ drawing of the holotype of *Luskhan itilensis* (YKM 68344/1_262),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

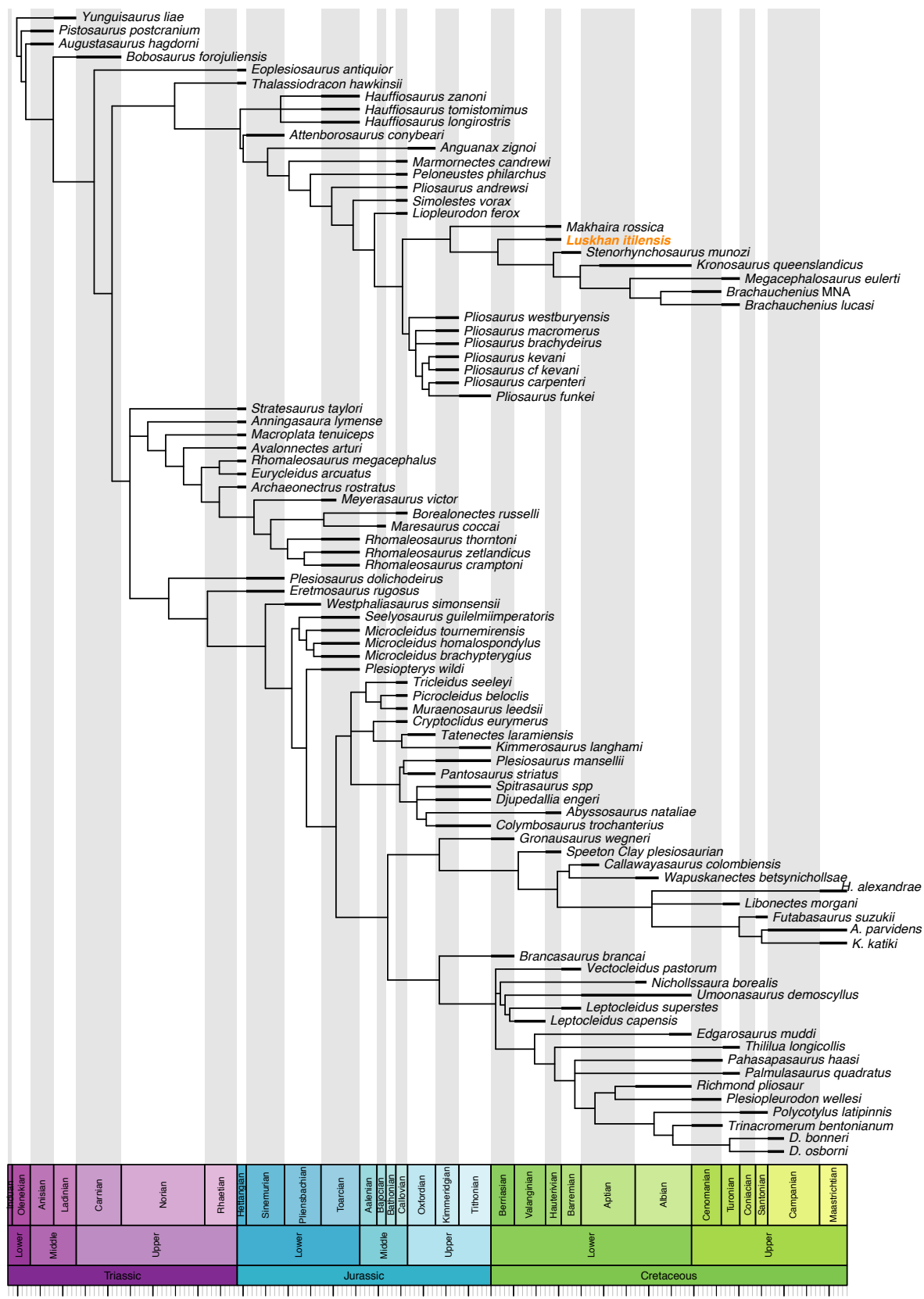


Figure S2. Phylogeny of plesiosaurs. Strict consensus of the 24 most parsimonious trees resulting from the maximum parsimony analysis of the reduced dataset, related to Figure 3 and STAR Methods.

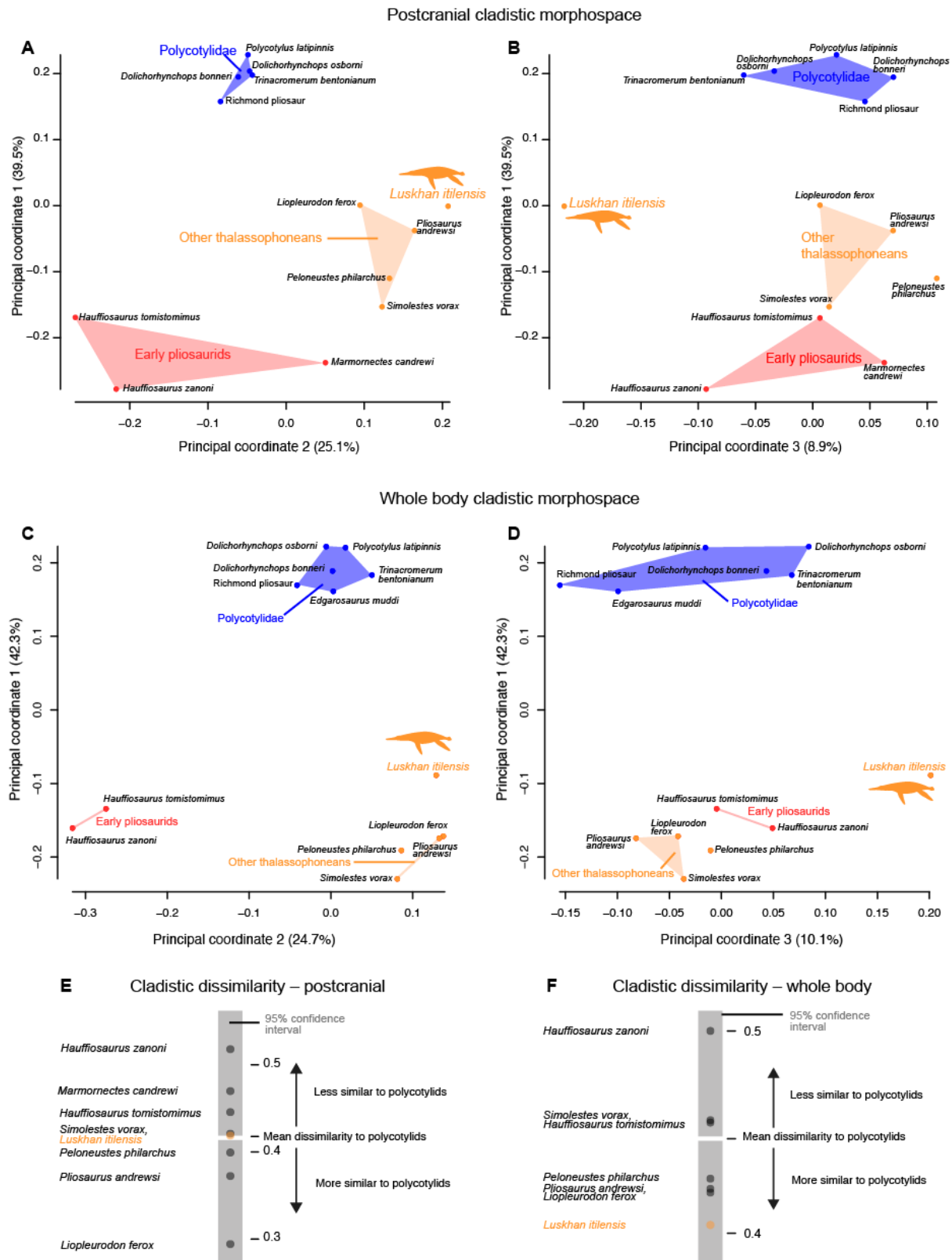


Figure S3. Cladistic morphospace occupation of short-necked plesiosaurs. (A, B) Occupation of the postcranial skeleton morphospace by polycotylids and plesiosaurs, visualised using principal coordinates 1 and 2 (A) and principal coordinates 1 and 3 (B). (C, D) Occupation of the whole skeleton morphospace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

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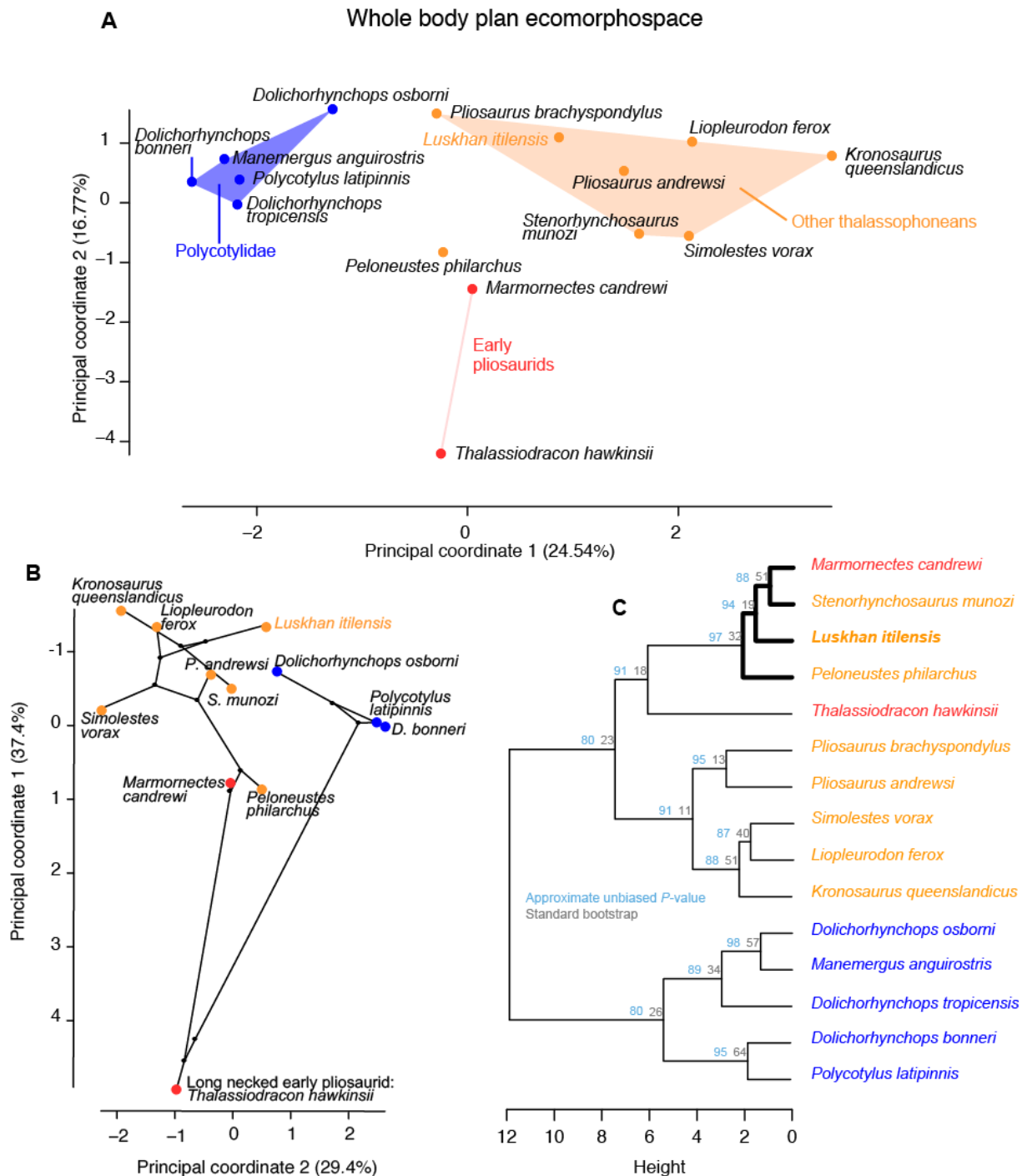


Figure S4. Ecomorphological morphospace occupation of short-necked plesiosaurs. (A) occupation of the whole body ecomorphospace by polycotylids and plesiosaurs. (B) Whole body plan phylomorphospace of plesiosaurs and polycotylids (using a pruned dataset with the species present in both the ecomorphological 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 plesiosaurs *Marmornectes* and *Peloneustes*. All these analyses used ecomorphological data as source data; a 50% completeness threshold was applied to the data beforehand.

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