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Early-diverging plesiosaurs from the Pliensbachian (Lower Jurassic) of northwestern Germany

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The knowledge of Pliensbachian (Early Jurassic, ~192.9–184.2 Ma) plesiosaurs is notoriously insufficient. Although there have been specimens described from different parts of the world, only three of them could have been established as diagnosable taxa. Here, we describe two previously unreported lower Pliensbachian plesiosaur occurrences that originate from two sites located in North Rhine-Westphalia, Germany. One of the new occurrences is represented by three cervical and three indeterminable vertebrae from Werther, the other includes two associate pectoral or anterior dorsal vertebrae from Bielefeld. Although highly incomplete, the Werther individual, which derived from the *Uptonia jamesoni* Zone, is found to represent the only reliably identified early Pliensbachian pliosaurid known to date. Its material is geographically and stratigraphically proximate to the late Pliensbachian pliosaurid *Arminisaurus schuberti*, found in a clay-pit located in the Bielefeld district of Jöllenbeck. However, even though the Werther plesiosaur and *A. schuberti* show a broadly similar morphology of the preserved cervical section, there are also slight differences indicating that the Werther material most likely represents a hitherto unknown early-diverging pliosaurid taxon, thus increasing the known diversity of pliosaurids in Early Jurassic European epeiric seas.

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Abstract. The knowledge of Pliensbachian (Early Jurassic, ~192.9–184.2 Ma) plesiosaurs is notoriously insufficient. Although there have been specimens described from different parts of the world, only three of them could have been established as diagnosable taxa. Here, we describe two previously unreported lower Pliensbachian plesiosaur occurrences that originate from two sites located in North Rhine-Westphalia, Germany. One of the new occurrences is represented by three cervical and three indeterminable vertebrae from Werther, the other includes two associate pectoral or anterior dorsal vertebrae from Bielefeld. Although highly incomplete, the Werther individual, which derived from the *Uptonia jamesoni* Zone, is found to represent the only reliably identified early Pliensbachian pliosaurid known to date. Its material is geographically and stratigraphically proximate to the late Pliensbachian pliosaurid *Arminisaurus schuberti*, found in a clay-pit located in the Bielefeld district of Jöllenbeck. However, even though the Werther plesiosaur and *A. schuberti* show a broadly similar morphology of the preserved cervical section, there are also slight differences indicating that the Werther material most likely represents a hitherto unknown early-diverging pliosaurid taxon, thus increasing the known diversity of pliosaurids in Early Jurassic European epeiric seas.

Introduction

Plesiosaurs were a diverse clade of aquatic tetrapods whose fossil record spans from the Upper Triassic to the Cretaceous/Paleogene boundary (e.g., Ketchum & Benson 2010; Benson and Druckenmiller 2014; Madzia & Cau 2020). Yet, their stratigraphic distribution is uneven. For instance, with respect to their Lower Jurassic record, rich plesiosaur material is known from Hettangian and Toarcian strata. Notoriously poor, however, is their record dated to the Pliensbachian (~192.9–184.2 Ma). So far, only three plesiosaur taxa have been established from this stage: *Westphaliasaurus simonsensii* from the lower Pliensbachian of Sommersell in western Germany (Schwermann & Sander 2011), *Cryonectes neustriacus* from the upper Pliensbachian of Fresney-le-Puceux in northern France (Vincent et al. 2013), and *Arminisaurus schuberti* from the upper Pliensbachian of Bielefeld in northwestern Germany (Sachs & Kear 2018).

In addition to these taxa there are a number of incomplete and fragmentary specimens known from Germany (e.g., Janensch 1928, Schubert 2007), Spain (Schulz 1858), England (Storrs 1995, Forrest 2006, Bardet et al. 2008, Evans 2012), Denmark (Rees & Bonde 1999, Smith 2008), Greenland (Bendix-Almgreen 1976, Kear et al. 2016), and Australia (Thulborn & Warren 1980, Kear 2004, 2012, 2016, Kear & Hamilton-Bruce 2011).

Here, we describe and illustrate previously unreported historical plesiosaur specimens from the lower Pliensbachian of northwestern Germany (**Figs 1–3**). The material originates from two fossil sites and includes three cervical vertebrae and additional indeterminate vertebrae found at Werther (GZG [unnumbered]), and two associated post-cervical vertebral centra, either pectorals or anterior dorsals, found in the vicinity of Bielefeld (Namu ES/jL-3868).

Institutional abbreviations. GZG, University of Göttingen, Göttingen, Germany; Namu, Naturkunde-Museum Bielefeld, Bielefeld, Germany.

Geological and stratigraphic setting

The studied specimens (GZG [unnumbered] and Namu ES/jL-3868) originate from successions preserved within the Herford Syncline (Herforder Liasmulde, e.g. Schubert, 2007) and its southwestern boundary, the Osning Fault Zone, a multi-phasic normal/reverse/strike-slip fault system (e.g., Drozdzewski & Dölling, 2018; **Fig. 2**). Both structural elements attained their current configuration during the Late Cretaceous and underwent exhumation since the late Paleogene. During the Early Jurassic the area was part of the Central European Archipelago, an array of islands separated by marine straits and local basins. Within the area of the Herford Syncline and its surroundings, marine sedimentation during the Sinemurian and Pliensbachian mostly comprised claystones and marlstones. The discontinuity surface at the base of the Pliensbachian is a notable exception from this rather monotonous succession. Caused by a local regression, it is overlain by a highly condensed section (Rottorf Formation, Mönnig 2023a), representing the lowermost Pliensbachian (*Uptonia jamesoni* Zone). These marginal facies passed basin-wards and upwards into the claystones and marlstones of the Capricornumergel Formation, representing the continuous distal facies of the lower Pliensbachian (*U. jamesoni* to

Tragophylloceras ibex to *Prodactylioceras davoei* Zones, Mönnig 2023b). The fine-grained, clayey-marly lithofacies continue upward into the overlying Amaltheenton Formation (*Amaltheus margaritatus* Zone, upper Pliensbachian; **Fig. 3**).

The material from the former Spilker clay-pit at Werther lacks precise stratigraphic information. However, the lithology and fossil content of the matrix attached to the skeletal remains allow determining their stratigraphic position within the succession that was once exposed at this outcrop. According to Büchner et al. (1986), the clay-pit exposed the Osning Fault Zone, resulting in steep to nearly vertical dip of the beds. By reverse faulting, lower Middle Triassic sandstones (Röt Formation) in the NE were upfaulted against the Lower Jurassic succession in the SW. The latter comprised an upper Sinemurian section of unspecified thickness, overlain by 1.5 m of the condensed Rottorf Formation (lower Pliensbachian, *U. jamesoni* Zone), which is, in turn, overlain by 115 m of dark, partially pyritiferous claystones with calcareous concretions of the Capricornumergel Formation (lower Pliensbachian, *T. ibex* and *P. davoei* zones; Meyer, 1907; Büchner et al., 1986).

The Rottorf Formation consists of bioclastic clay- and marlstones with high amounts of dispersed Fe-hydroxide („iron stones"), causing a distinct pink to reddish color on the weathered surface, and in many layers contain Fe-ooids or interbedded Fe-oolites. According to Büchner et al. (1986), there are also common calcareous pebbles that are often altered by bioerosion (borings) and wood fragments.

The plesiosaur remains from the Spilker clay-pit are associated with pinkish, bioclastic, particle-bearing claystones and well-rounded calcareous pebbles, with a Fe-hydroxide coating. Accompanying invertebrate fossils include shell debris (identifiable are the bivalves *Oxytoma* sp. and *Eopecten*? sp., and a pleurotomariid gastropod), indeterminate belemnites, as well as the ammonites *Phricodoceras* cf. *taylori* (Sowerby, 1829), *Platypleuroceras* cf. *caprarium* (Quenstedt, 1856), and *Platypleuroceras* sp.. Consequently, the GZG (unnumbered) plesiosaur material can stratigraphically be unambiguously referred to the Rottorf Formation. The accompanying ammonites indicate the *taylori* Subzone of the *jamesoni* Zone (Hoffmann 1982). It is worth noting that Büchner et al. (1986) have previously reported the *brevispina* Subzone as the lowermost section of the Rottorf Formation. If the identification of the *taylori* Subzone is correct, the 1.5 m thick Rottorf Formation at the Spilker clay-pit represents condensed section of three subzones (*taylori*, *polymorphus*, and *brevispina*) of the *jamesoni* Zone.

In any case, the plesiosaur specimens from the *jamesoni* zone of the Spilker clay-pit represent the stratigraphically oldest of the specimens under consideration herein, followed by the material (Namu ES/jL-3868) from the Bielefeld-Sudbrack locality (*P. davoei* Zone, Capricornumergel Formation, lower Pliensbachian), and the type horizon of *Arminisaurus schuberti* (*Amaltheus subnodosus* Subzone, *Amaltheus margaritatus* Zone, Amaltheenton Formation, upper Pliensbachian; Sachs & Kear 2018).

Methods

Phylogenetic analyses

The Werther plesiosaur (GZG [unnumbered]) is geographically and stratigraphically proximate to the late Pliensbachian pliosaurid *Arminisaurus schuberti* from the Beukenhorst II clay-pit that is located in the Bielefeld district of Jöllenbeck, with which it also shares the majority of character states (see Discussion for detailed information). In order to assess the phylogenetic significance of these similarities, we explore the placement of GZG (unnumbered) among plesiosaurs using the dataset of Sachs et al. (2024), which represents a substantially modified version of the matrix originally assembled by Benson and Druckenmiller (2014), and includes first-hand scores of *Arminisaurus schuberti* obtained from Sachs et al. (2023). The final version of the matrix, which differs from that of Sachs et al. (2024) only in the addition of the Werther plesiosaur, includes 131 operational taxonomic units (OTUs) and 270 characters; 67 of which were set as 'additive' (= 'ordered') following Madzia et al. (2019).

Our analyses were performed using maximum parsimony as the optimality criterion and through TNT 1.6 (Goloboff and Morales, 2023). We have conducted four runs. The first run wase based on equal weights; the other three runs used the implied weighting function, with the concavity parameter (*K*) set to 6, 9, and 12. In all our analyses, we used *Neusticosaurus pusillus* as the outgroup. For each of the phylogenetic analyses, we fixed the maximum number of most parsimonious trees to 200,000 (command "hold 200000"). Then, we ran the 'New Technology' (NT) search which involved 500 addition sequences and default settings for sectorial searches, ratchet, drift, and tree fusing (all activated). Following the NT search, we performed a 'Traditional Search' with tree bisection-reconnection (TBR) branch-swapping on trees saved to RAM. For the phylogenetic analysis using equal weights, we nodal support was assessed through the Bremer support values (with TBR and retaining sub-optimal trees incorporating up to 3

additional steps). Nodal support for the parsimony analyses with implied weighting was assessed through Symmetric Resampling, using a 'Traditional Search', 1,000 replicates, a default change probability (set at 33), and output expressed as frequency differences (GC).
See Supplementary Information 1 for the character list and a TNT-executable code.

Systematic paleontology

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Pliosauridae Seeley, 1874
Pliosauridae indet.

Material. GZG (unnumbered), three cervical vertebrae and three indeterminable vertebrae (**Figs 4, 5**).
Locality and horizon. Former Spilker clay-pit, Werther (Westfalen), Gütersloh district, North Rhine-Westphalia, Germany; lower Pliensbachian (*Uptonia jamesoni* Zone), Lower Jurassic, of the Rottorf Formation.
Remarks. GZG (unnumbered) lacks detailed documentation, including information regarding its discovery.

Description and comparisons

Six incomplete vertebrae are preserved; three of them can be identified as cervicals, shown by the lateroventrally placed rib facets (**Fig. 4**). The remaining three are not preserved well enough to be identified with certainty (**Fig. 5**). One of the cervicals (**Fig. 4K–O**) is considerably larger and shows more prominent rib facets. Consequently, this vertebra likely derives from the posterior section of the neck. The size of the two other cervicals (**Fig. 4A–J**) indicates that they likely originate from the anterior or middle section of the neck.
The articular faces of the centra are exposed in all three cervicals and in one of the indeterminable vertebrae (**Fig. 5B**). In the other specimens they are either damaged or obscured by matrix.

All cervical centra are wider and higher than long, a condition found in several early-diverging plesiosaurs, including *Rhaeticosaurus mertensi* and the pliosaurids *Arminisaurus schuberti* and *Cryonectes neustriacus* (Vincent et al. 2013; Wintrich et al. 2017; Sachs & Kear 2018). As visible, the articular facets are amphicoelous and surrounded by a thickened rim. Anteroventrally, a prominent lip is present in two vertebrae (**Fig. 4C, D, H**). A similar prominent lip is found in the pliosaurid *Arminisaurus schuberti* (Sachs & Kear 2018). The posterior articular face is preserved in one of the vertebrae (**Fig. 5E**) and here a ventral lip is absent. The lateral sides of the cervical centra are anteroposteriorly concave. In the best preserved cervical (**Fig. 4D**), there is a circular lateral depression present dorsal to the rib facet on both sides. Dorsal to this concavity, there is a structure resembling a lateral keel. However, neither of these structures is present in the other cervicals. Therefore, these structures might be a taphonomic artefact or possibly a pathology. A similar circular depression can be found in some cervicals of *Brancasaurus brancai* (S. Sachs, pers. obs. 2013). In one of the cervicals, remnants of the cervical ribs are still fused to the centrum (**Fig. 4A–E**). The rib facets in all cervicals are placed lateroventrally and slightly more posterior to the mid-length of the centrum. In all cervicals, the morphology of the rib facets is somewhat obscured by either the cervical ribs or by matrix. However, a slight depression in the anterior margin of the cervical ribs indicates that two co-joined rib facets were formed (**Fig. 4E**). This condition is found in most pliosaurids and rhomaleosaurids, but also in some Early Jurassic plesiosauroids, such as microcleidids or *Westphaliasaurus simonsensii* (Benson & Druckenmiller 2014: Appendix 2, character 160). The dorsolaterally-placed neural arches are fused to the centra but a semicircular neurocentral suture is still indicated in the cervical vertebrae. A circular neural canal is visible in two cervicals (**Fig. 4A, F**) and one of the indeterminate vertebrae (**Fig. 5B**). The zygapophyses are poorly assessable; they are either largely broken off or otherwise damaged. One right postzygapophysis is reasonably well preserved (**Fig. 4B, D, E**). It exceeds the level of the centrum posteriorly with most of its length. Laterally, the postzygapophyses are subequal to the width of the centrum and the articular faces are planar. The neural spines are broken off in all vertebrae, preserving only their base in one distal cervical (**Fig. 4B**). In ventral view, the anterior and posterior edges of the articular surface rims are transversely widened and form a triangular-shaped bulge. In the anterior articular face this bulge extends further ventrally and forms the lip like protrusion described above. Both, the anterior and posterior articular surface bulges extend towards the mid-length of the centrum where they merge with a thickened and rounded midline keel (**Fig. 4C, H**). This condition is also present in the geographically and stratigraphically proximal Pliensbachian pliosaurid *Arminisaurus schuberti.* A similar rounded ventral midline keel is also present in the cervicals of later-diverging pliosaurids; e.g., *Peloneustes philarchus* and *Eardasaurus powelli* (Linder 1913, Ketchum & Benson 2022). There are two subcentral foramina.

Plesiosauria indet.

Material. Namu ES/jL-3868, two associate pectoral or anterior dorsal vertebrae (**Fig. 6**)
Locality and horizon. Former Klarhorst clay-pit, Sudbrackgebiet, Bielefeld, North Rhine-Westphalia, Germany; lower Pliensbachian (*Prodactylioceras davoei* Zone), Lower Jurassic, of the Formation.
Remarks. Namu ES/jL-3868 was found in the early 1930s in association with skeletal remains of a giant specimen of the ichthyosaur *Temnodontosaurus*. Hungerbühler & Sachs (1996) assigned the vertebrae to the ichthyosaur specimen.

Description and comparisons

Two associated centra with attached neural arch pedicles are preserved. These vertebrae resemble the pectoral vertebrae of *Rhomaleosaurus thorntoni* (see Smith & Benson 2014: pl. 13, Fig. 2). However, given that the rib facet and/or dorsal process are not preserved, it remains unclear whether they are indeed pectoral vertebrae (*sensu* Sachs et al. 2013) or rather anterior dorsal vertebrae. Both centra are wider than long and high and higher than long. The articular faces of the centra are mostly obscured but they appear only slightly amphicoelous (**Fig. 6**), being surrounded by flattened articular surface rims. Laterally, both centra are largely occupied by the broken rib facets/transverse processes, which are placed dorsally, adjacent to neural canal. Transverse ~~process~~ of dorsal vertebrae being placed adjacent to the neural canal is a common condition in plesiosaurs (Benson & Druckenmiller 2014: Appendix 2, character 181). This differs, however, from the dorsal vertebrae of *Arminisaurus schuberti* where the transverse processes are placed dorsal to the neural canal (Sachs & Kear 2018: Fig. 5A). Ventral to the remnants of the rib facets/transverse processes, a transverse buttress is indicated. This buttress likewise resembles the condition observable in *R. thorntoni* (see Smith & Benson 2014, pl. 13, fig. 2). Adjacent to the buttress, a subdiapophyseal fossa (*sensu* Hampe 2013) is formed on each side (**Fig. 6B**). In *A. schuberti*, the ventral sides of the transverse processes of the dorsal vertebrae show a transverse buttress and an associated anterior fossa (Sachs & Kear 2018). A circular neural canal is visible in the anterior of the two vertebrae (**Fig. 6A**). The prezygapophyses are preserved in the posterior vertebra (**Fig. 6**). They are lobate in lateral view and extend over the level of the centrum with about half of their length. The postzygapophyses of the anterior-more vertebra articulate with the prezygapophyses of the second vertebrae and are thus only partly visible. They extend over the level of the centrum with most of their length. The postzygapophyses of the posterior-more vertebra are largely damaged. The articular faces are not visible in any of the zygopophyses. The neural spines are broken off in both vertebrae. The ventrolateral and ventral sides of the centra are concave and lack foramina subcentralia (**Fig. 6**).

Results of phylogenetic analyses

See Table 1 for the numerical results of our phylogenetic analyses, **Figure 7** for reduced tree topologies focusing on the pliosaurid segments of the trees that are relevant for the assessment of the phylogenetic placement of the Werther plesiosaur, and Supplementary Information 2 for full tree topologies and nodal support values.

The parsimony analysis using equal weights has produced a very poorly resolved strict consensus tree, failing to reconstruct a monophyletic Pliosauridae. However, inspection of the most parsimonious trees (MPTs) has shown that the basal topological instability was mainly caused by the nesting of *Thalassiodracon hawkinsii* that was alternatively inferred as either, an early-diverging pliosaurid or an early-diverging plesiosauroid, and *Rhaeticosaurus mertensi* that was found either as an early-diverging pliosaurid or to lie outside the basal branching of Pliosauridae, Rhomaleosauridae, and Plesiosauroidea. The Werther plesiosaur (GZG [unnumbered]) operational taxonomic unit (OTU) has been inferred as a pliosaurid in all MPTs though its precise placement could not be found due to the fragmentary nature of the material. In contrast, all analyses using the implied weighting inferred a monophyletic Pliosauridae (including *Thalassiodracon* that was found at the base of the clade but excluding *Rhaeticosaurus* that ~~lied~~ outside the basal branching of the three major plesiosaur clades). All these runs also reconstructed the Werther plesiosaur among pliosaurids though, again, the runs did not found a stable placement for the OTU.

Discussion and conclusions

We describe previously unreported occurrences of Pliensbachian plesiosaurs from two sites located in North Rhine-Westphalia, Germany. One of the new records, originating from the *Uptonia jamesoni* Zone at Werther, represents the only reliably identified early Pliensbachian pliosaurid described to date. It is geographically and stratigraphically proximate to the late Pliensbachian pliosaurid *Arminisaurus schuberti* with which it shares a number of characters, including dorsoventrally facing cervical zygapophyses that are about as wide as the centrum, a rounded neurocentral suture, the presence of a prominent semicircular lip that extends ventrally from the anterior articular surface, triangular-shaped ventral bulge on the anterior and posterior articular facet, and a pronounced rounded ventral midline keel. A key character of *Arminisaurus*, the presence of parazygapophyseal processes between the pre- and postzygapophyses (Sachs & Kear 2018: Fig. 4G), is not preserved in the Werther specimen. However, apparent similarities in the cervical anatomy can also be observed in *Cryonectes*, the only other currently known Pliensbachian pliosaurid, which slightly differs from the Werther plesiosaur in the morphology of the ventral surface of its cervical centra that do not show the ventral keel and lack a ventrally-projecting lip.

Owing to the lack of Pliensbachian plesiosaurs in general, which is manifested by an incomplete knowledge of the anatomy of their cervical region, it is currently difficult to infer the phylogenetic affinities of the Werther individual. Its character state combination clearly indicates that it represents an early-diverging pliosaurid that was likely very similar, or perhaps even closely related, to *Arminisaurus schuberti*. Nevertheless, its slight morphological differences combined with its older age suggest the Werther taxon most likely represents a distinct and hitherto unknown pliosaurid taxon. As such, its recognition increases the known diversity of pliosaurids in Early Jurassic European epeiric seas.

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Figure captions

Figure 1. Map showing the localities at Werther (1) and Bielefeld Sudbrack (2), as well as the type locality of *Arminisaurus schuberti* in Bielefeld Jöllenbeck (3) with their position within the map of Germany.

Figure 2. (A) Geological sketch-map of the Herford Syncline and the Bielefeld Section of the Osning Fault Zone with the plesiosaur fossil sites discussed in this paper, indicated by numbers (1 to 3, corresponding to Figure 1). From Drozdzewski & Dölling (2018) and GeoPortalNRW (2023), modified and simplified. (B) Geological cross-section of the Osning Fault Zone at the line a-a' (Fig. 1A), showing the approximate position of the former Spilker clay-pit (locality 1), slightly projected to the SE. From Drozdzewski & Dölling (2018), modified and simplified.

Figure 3. (A) Paleogeography and lithofacies of what is today northwestern Germany during the early Pliensbachian. From Büchner et al. (1986), modified. (B) Chrono-, bio- and lithostratigraphy of the lower Pliensbachian in the Herford Syncline and adjacent regions. After Hoffmann (1982), Deutsche Stratigraphische Kommission (2016), and Mönnig (2023a, b), modified. Locations of the plesiosaur fossil sites discussed in this paper are indicated by numbers (1 to 3, corresponding to Figure 1).

Figure 4. GZG (unnumbered), cervical vertebrae. (A–E) Anterior cervical vertebra in (A) anterior, (B) dorsal, (C) ventral, (D) lateral, and (E) posterior view. (F–J) Supposed mid-cervical vertebra in (F) anterior, (G) dorsal, (H) ventral, (I) lateral, and (J) posterior view. (K–O) Supposed posterior cervical vertebra in (K) anterior, (L) dorsal, (M) ventral, (N) lateral, and (O) posterior view. Scale bars equal 5 cm. Abbreviations: cr, cervical rib; crd, posterior depression at cervical rib; lp, lip-like projection; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; rf, rib facet; zyg, zygapophysis.

Figure 5. GZG (unnumbered), indeterminate vertebrae. (A) A damaged vertebra, (B–C) a centrum in (B) articular and (C) damaged lateral view, (D–E) a damaged centrum in (D) articular and (E) lateral view. Scale equals 5 cm. Abbreviation: nc, neural canal.

Figure 6. Namu ES/jL-3868, pectoral or anterior dorsal vertebrae. (A) Anterior, (B) right lateral, (C) dorsal, (D) posterior, (E) left lateral, and (F) ventral view. Scale bar equals 5 cm. Abbreviations: bt, broken rib facet or transverse process; nc, neural canal; poz, postzygapophysis; prz, prezygapophysis; sdf, subdiapophyseal fossa.

Figure 7. The phylogenetic placement of the Werther plesiosaur (GZG [unnumbered]) showed on the pliosaurid segment of Plesiosauria. (A) Reduced majority rule consensus tree reconstructed through parsimony analysis using equal weights (numbers at nodes indicate the percentage of the most parsimonious trees that found the nodes) and reduced strict consensus trees reconstructed through weighted parsimony analyses with *K* set to (B) 6, (C) 9, and (D) 12. The full topologies resulting from particular parsimony analyses, the Bremer support values for particular nodes inferred through the analysis using equal weights, and the results of Symmetric Resampling are provided in Supplementary Information 2.

Table 1 (on next page)

Numerical results of the parsimony analyses.

BS, best score (tree length); CI, Consistency Index; EW, parsimony analysis using equal weighting; IW, parsimony analysis using implied weighting; MPT, number of most parsimonious trees; NT, ‘New Technology’ search; RI, Retention Index; TS, ‘Traditional Search’.

Table 1. Numerical results of the parsimony analyses. BS, best score (tree length); CI, Consistency Index; EW, parsimony analysis using equal weighting; IW, parsimony analysis using implied weighting; MPT, number of most parsimonious trees; NT, 'New Technology' search; RI, Retention Index; TS, 'Traditional Search'.

Run	**MPT (NT)**	**BS**	**MPT (TS)**	**CI**	**RI**
EW	57	2088	200,000	0.191	0.684
IW (*K* = 6)	26	137.11275	113,967	0.190	0.681
IW (*K* = 9)	23	109.07487	32,319	0.190	0.682
IW (*K* = 12)	45	90.80995	4,617	0.191	0.683

Figure 1

Locality map

Map showing the localities at Werther (1) and Bielefeld Sudbrack (2), as well as the type locality of *Arminisaurus schuberti* in Bielefeld Jöllenbeck (3) with their position within the map of Germany.

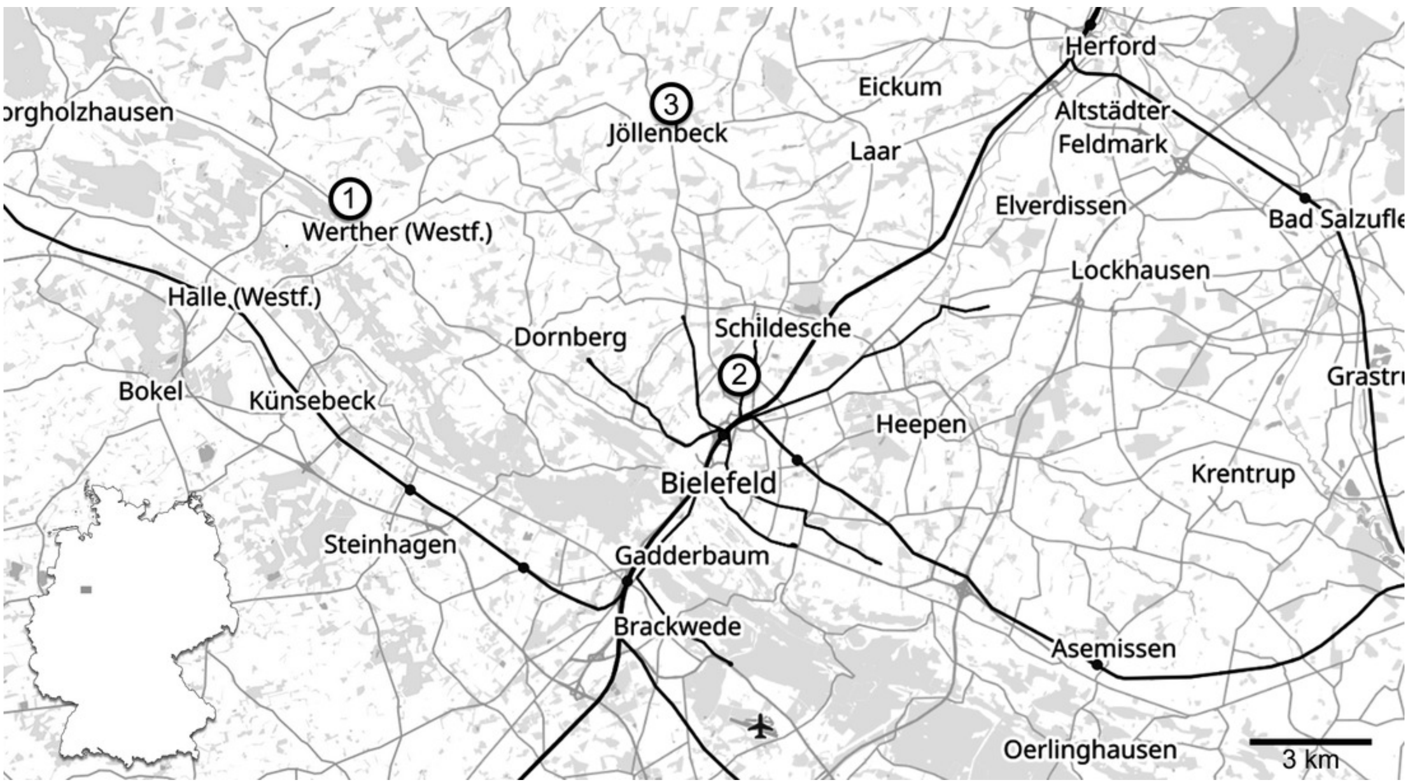

Figure 2

Regional geological situation

(A) Geological sketch-map of the Herford Syncline and the Bielefeld Section of the Osning Fault Zone with the plesiosaur fossil sites discussed in this paper, indicated by numbers (1 to 3, corresponding to Figure 1). From Drozdzewski & Dölling (2018) and GeoPortalNRW (2023), modified and simplified. (B) Geological cross-section of the Osning Fault Zone at the line a-a’ (Fig. 1A), showing the approximate position of the former Spilker clay-pit (locality 1), slightly projected to the SE. From Drozdzewski & Dölling (2018), modified and simplified.

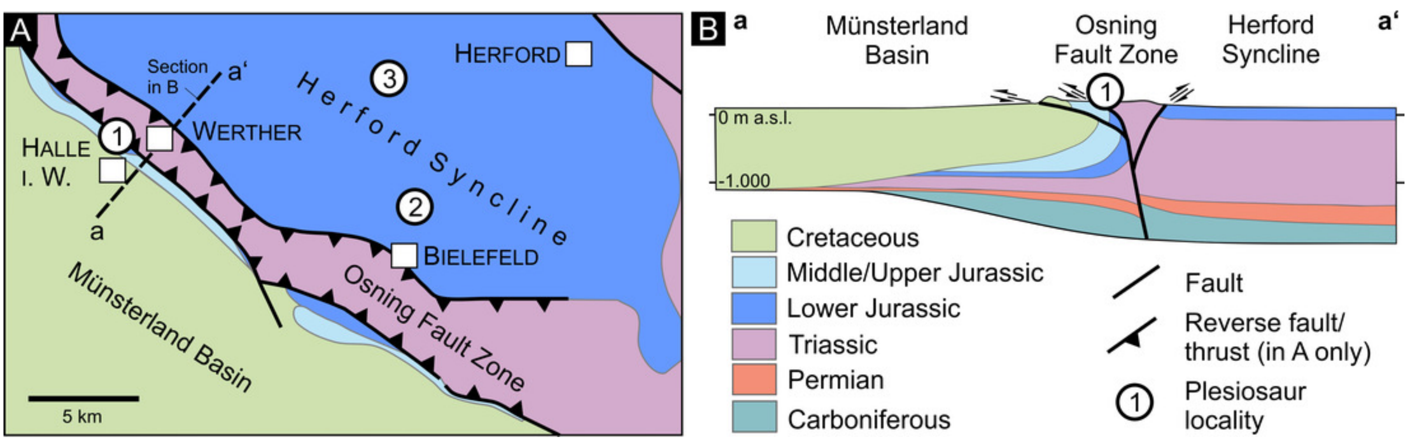

Figure 3

Geology and stratigraphy

(A) Paleogeography and lithofacies of what is today northwestern Germany during the early Pliensbachian. From Büchner et al. (1986), modified. (B) Chrono-, bio- and lithostratigraphy of the lower Pliensbachian in the Herford Syncline and adjacent regions. After Hoffmann (1982), Deutsche Stratigraphische Kommission (2016), and Mönnig (2023a, b), modified. Locations of the plesiosaur fossil sites discussed in this paper are indicated by numbers (1 to 3, corresponding to Figure 1).

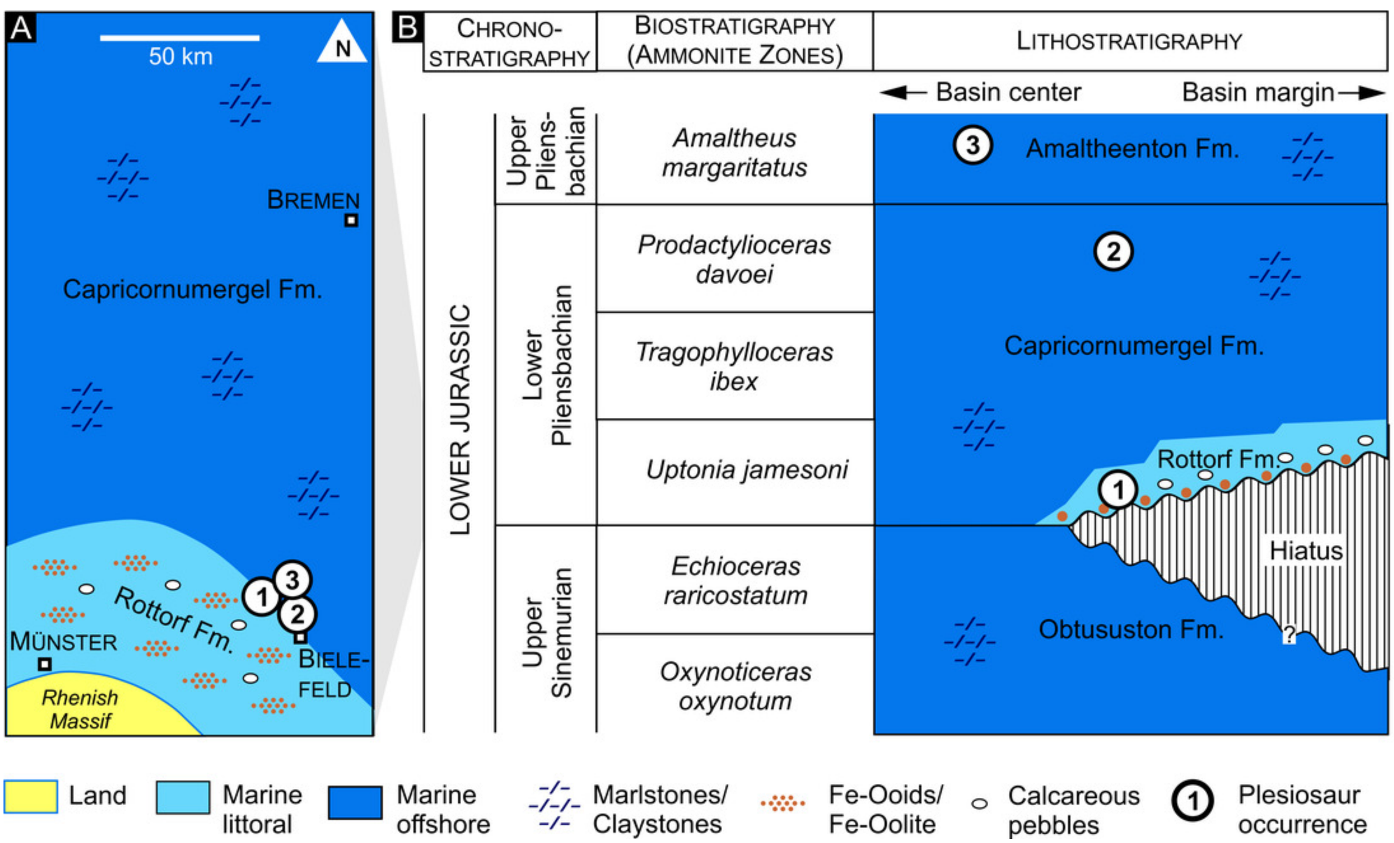

Figure 4

GZG (unnumbered), cervical vertebrae

(A–E) Anterior cervical vertebra in (A) anterior, (B) dorsal, (C) ventral, (D) lateral, and (E) posterior view. (F–J) Supposed mid-cervical vertebra in (F) anterior, (G) dorsal, (H) ventral, (I) lateral, and (J) posterior view. (K–O) Supposed posterior cervical vertebra in (K) anterior, (L) dorsal, (M) ventral, (N) lateral, and (O) posterior view. Scale bars equal 5 cm. Abbreviations: cr, cervical rib; crd, posterior depression at cervical rib; lp, lip-like projection; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; rf, rib facet; zyg, zygapophysis.

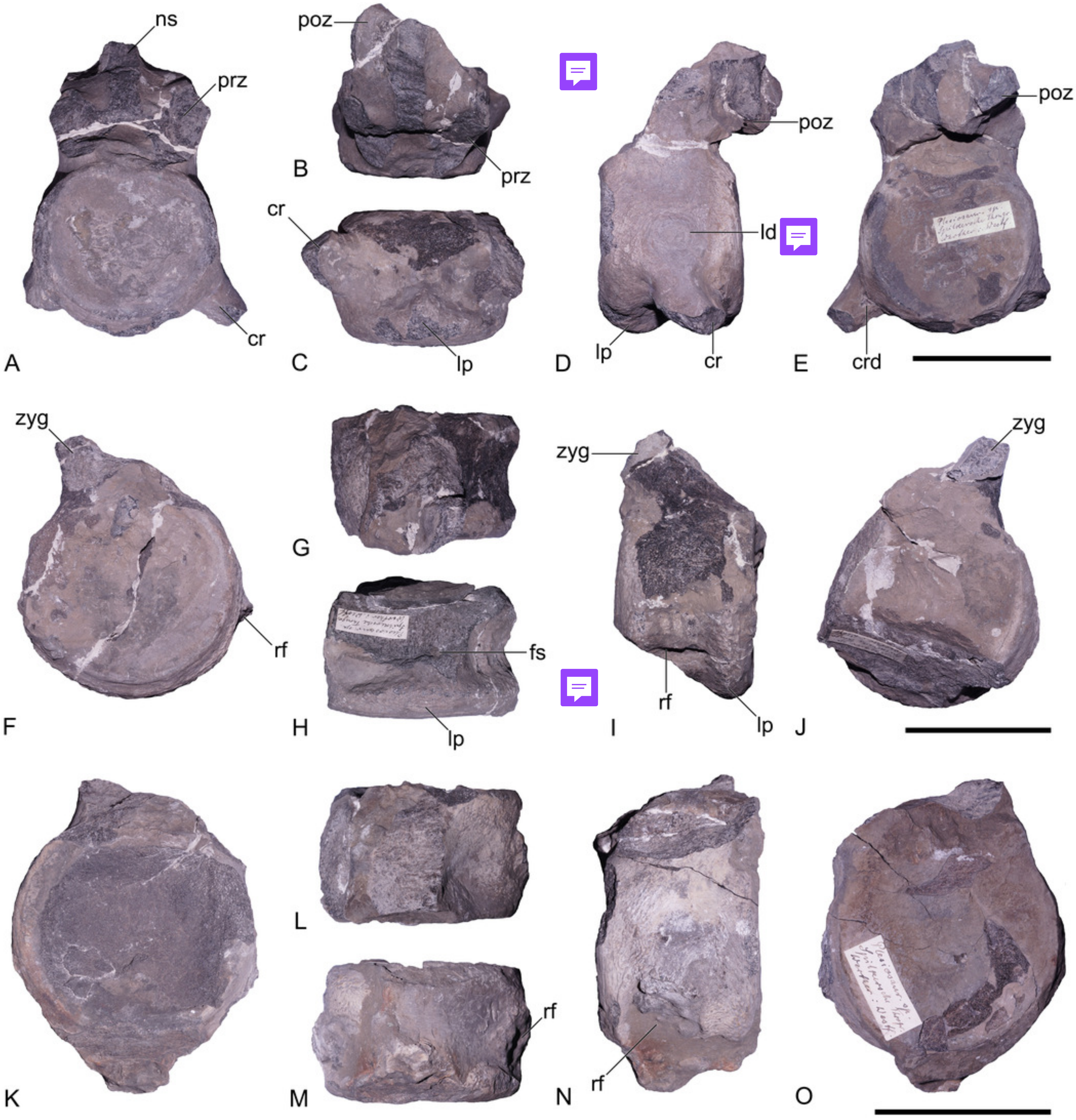
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Figure 5

GZG (unnumbered), indeterminate vertebrae

(A) A damaged vertebra, (B–C) a centrum in (B) articular and (C) damaged lateral view, (D–E) a damaged centrum in (D) articular and (E) lateral view. Scale equals 5 cm. Abbreviation: nc, neural canal.

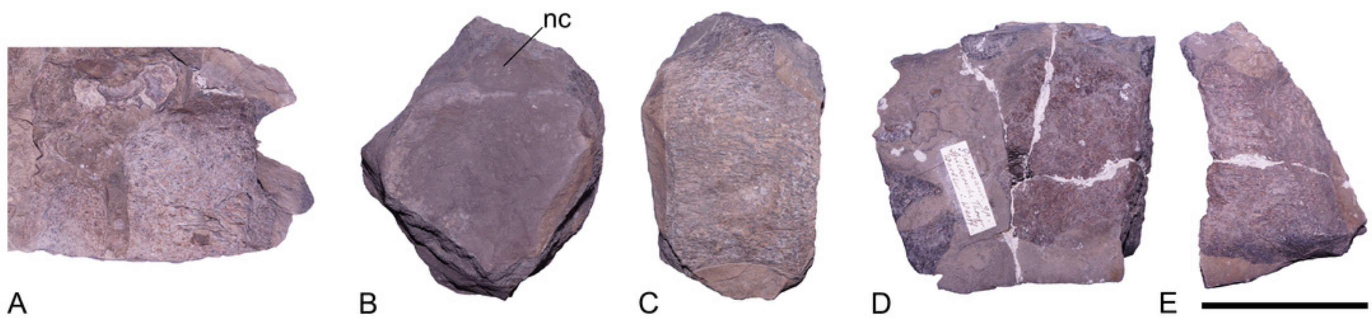


Figure 6

Namu ES/jL-3868, pectoral or anterior dorsal vertebrae

(A) Anterior, (B) right lateral, (C) dorsal, (D) posterior, (E) left lateral, and (F) ventral view. Scale bar equals 5 cm. Abbreviations: bt, broken rib facet or transverse process; nc, neural canal; poz, postzygapophysis; prz, prezygapophysis; sdf, subdiapophyseal fossa.

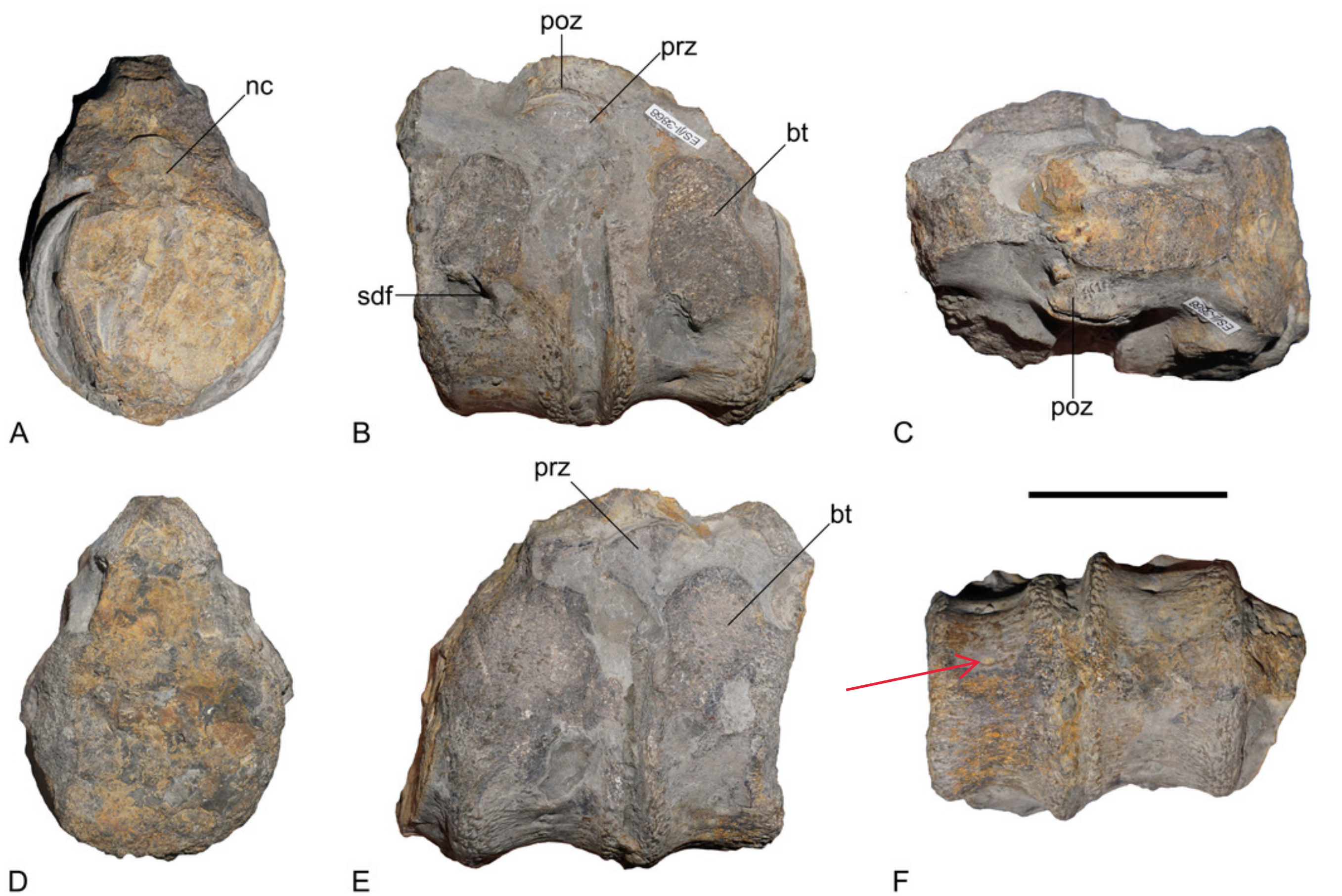
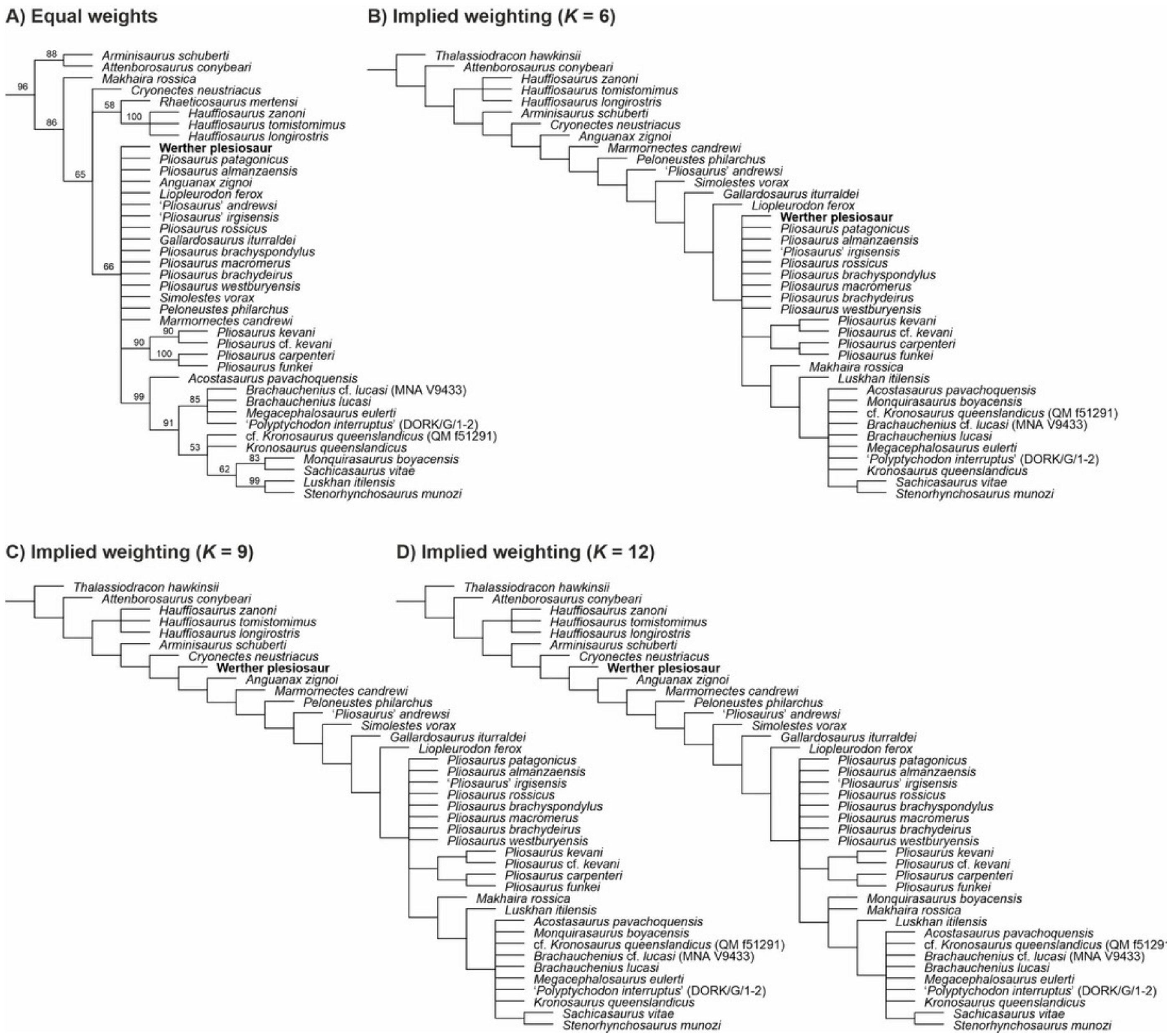


Figure 7

The phylogenetic placement of the Werther plesiosaur (GZG [unnumbered]) showed on the pliosaurid segment of Plesiosauria

(A) Reduced majority rule consensus tree reconstructed through parsimony analysis using equal weights (numbers at nodes indicate the percentage of the most parsimonious trees that found the nodes) and reduced strict consensus trees reconstructed through weighted parsimony analyses with *K* set to (B) 6, (C) 9, and (D) 12. The full topologies resulting from particular parsimony analyses, the Bremer support values for particular nodes inferred through the analysis using equal weights, and the results of Symmetric Resampling are provided in Supplementary Information 2.


A) Equal weights
B) Implied weighting (K = 6)
C) Implied weighting (K = 9)
D) Implied weighting (K = 12)
Arminisaurus schuberti
Attenborosaurus conybeari
Makhaira rossica
Cryonectes neustriacus
Rhaeticosaurus mertensi
Hauffiosaurus zanoni
Hauffiosaurus tomistomimus
Hauffiosaurus longirostris
Werther plesiosaur
Pliosaurus patagonicus
Pliosaurus almanzaensis
Anguanax zignoi
Liopleurodon ferox
'Pliosaurus' andrewsi
'Pliosaurus' irgisensis
Pliosaurus rossicus
Gallardosaurus iturraldei
Pliosaurus brachyspondylus
Pliosaurus macromerus
Pliosaurus brachydeirus
Pliosaurus westburyensis
Simolestes vorax
Peloneustes philarchus
Marmornectes candrewi
Pliosaurus kevani
Pliosaurus cf. kevani
Pliosaurus carpenteri
Pliosaurus funkei
Acostasaurus pavachoquensis
Brachauchenius cf. lucasi (MNA V9433)
Brachauchenius lucasi
Megacephalosaurus eulerti
'Polyptychodon interruptus' (DORK/G/1-2)
cf. Kronosaurus queenslandicus (QM f51291)
Kronosaurus queenslandicus
Monquirasaurus boyacensis
Sachicasaurus vitae
Luskhan itilensis
Stenorhynchosaurus munozi
Thalassiodracon hawkinsii