RESEARCH PAPER

Cymbospondylus (Ichthyopterygia) from the Early Triassic of Svalbard and the early evolution of large body size in ichthyosaurs

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Abstract

Ichthyosaurs were a highly successful group of marine reptiles in the Mesozoic. The ichthyosaur radiation is part of the recovery from the Permian-Triassic mass extinction. In the Early Triassic, this group underwent extensive global radiation, filling ecological niches for the first time that were later occupied by various other lineages of marine amniotes. However, the evolution of body size in ichthyosaurs is not fully understood, as most large-bodied taxa originate from the Middle Triassic and later, and are mostly known from only a few specimens. In this study, we describe three articulated posterior dorsal vertebrae (IGPB R660) of the ichthyosaur *Cymbospondylus* sp. from the latest Olenekian *Keyserlingites subrobustus* zone of the Vikinghøgda Formation of the Agardhdalen area, eastern Spitsbergen, Svalbard. We numerically estimated the total body length of IGPB R660 from dorsal vertebral centrum length using a comparative dataset of other species of the genus and two different allometric analyses. This approach yields total length estimates of 7.5 m and 9.5 m for the individual, respectively, the highest for any unambiguous Early Triassic ichthyosaur find. Earlier, higher estimates of 11 m were based on taxonomically and stratigraphically inconclusive material but do not appear unreasonable based on evidence provided in this paper. Our study underscores both the rapid ecosystem recovery after a major mass extinction and extremely rapid increases in body size in ichthyosaurs after their adaptation to a secondarily aquatic lifestyle.

Keywords *Cymbospondylus* · Early Triassic · Svalbard · Ichthyosaur · Body size · Vertebra

Introduction

The largest mass extinction of all time occurred at the Permian–Triassic boundary, about 252 mya. It is considered as the most impactful extinction event of the Phanerozoic with an estimated loss of marine biodiversity of 80 to 96% of all species (Penn et al. 2018; Qiao et al. 2019; Shen et al. 2019). In the aftermath of the extinction, opportunities for ecological diversification into the marine realm became available for several groups of amniotes, including ichthyosaurs (Motani et al. 2015). These marine reptiles were among the first tetrapods that adapted to a secondary aquatic lifestyle. Ichthyosaurs appeared in different localities around the Northern Hemisphere in the late Early Triassic (Olenekian) and left an extensive global fossil record until their extinction in the late Cenomanian (Sander 2000; Fischer et al. 2016; Kelley et al. 2016). Early ichthyosaur evolution is generally seen as part of the rapid recovery of marine ecosystems in the Early Triassic (Scheyer et al. 2014; Motani et al. 2017; Moon and Stubbs 2020; Sander et al. 2021; Qiao et al. 2022). However, a recent find from Svalbard pushing back ichthyosaur origins to no more than two million years after the beginning of the Triassic is suggestive of a pre-Triassic history of the clade and its secondary marine adaptation (Kear et al. 2023).

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The objective of the present paper is to describe the remains of an ichthyosaur (*Cymbospondylus* sp., IGPB R660) of large size from the Early Triassic of eastern Spitsbergen (Svalbard archipelago, Norway; Figs. 1, 2), estimate its body length, and examine implications for the evolution of ichthyosaur body size. Although specimen IGPB R660 consists only of three articulated vertebrae (Fig. 3), it is sufficient for an estimate of body size due to its good preservation and because recently published datasets for ichthyosaur body size (Scheyer et al. 2014; Moon and Stubbs 2020; Sander et al. 2021) provide the foundation for regression analyses based on vertebral length.

Stratigraphy of Early Triassic vertebrate finds from Svalbard

The archipelago of Svalbard preserves one of the best studied sections of marine Early Triassic rocks, the stratigraphy of which as it concerns vertebrate fossils is highly relevant to the current study. Vigran et al. (2014) provided an overview of the Early Triassic litho- and biostratigraphy of Svalbard, which ranges from the Permian–Triassic boundary to the Olenekian–Anisian boundary (Fig. 2). The entire Lower Triassic is assigned to the Vikinghøgda Formation in eastern Svalbard (Fig. 2). The Vikinghøgda Formation is divided into the Deltadalen, Lusitaniadalen, and Vendomdalen members (Mørk et al. 1999; Maxwell and Kear 2013; Hurum

et al. 2018; Kear et al. 2023). The formation consists of gray silty shales and yellow siltstone and sandstone beds (Hurum et al. 2018). Hurum et al. (2018) also indicated that there is some abundance of carbonate concretions, relevant to this study because the specimen it is based on was encased in such a concretion.

Stratigraphic division of the Vikinghøgda Formation is also aided by vertebrate macrofossils and their abundance (Maxwell and Kear 2013; Kear et al. 2023). Wiman (1910) established the 'Fish Niveau' and the 'Lower Saurian Niveau' as vertebrate-bearing horizons, whereas the 'Grippia Niveau' was established as a vertebrate-bearing horizon by Stensiö (1921) (see also Hansen et al. 2018). The early Olenekian (Smithian) Lusitaniadalen Member contains the 'Fish Niveau' whereas the late Olenekian (Spathian) Vendomdalen Member hosts the 'Grippia Niveau' and the 'Lower Saurian Niveau' (Maxwell and Kear 2013; Hurum et al. 2018). The Vikinghøgda Formation is also rich in fossils of invertebrates such as bivalves and ammonoids (Fig. 2) with a total of six taxa serving as zonal fossils (Mørk et al. 1999; Vigran et al. 2014; Hansen et al. 2018; Hurum et al. 2018).

Large-bodied Early Triassic ichthyosaur finds

Evidence for the existence of large-bodied ichthyosaurs in the Early Triassic has come from localities around the
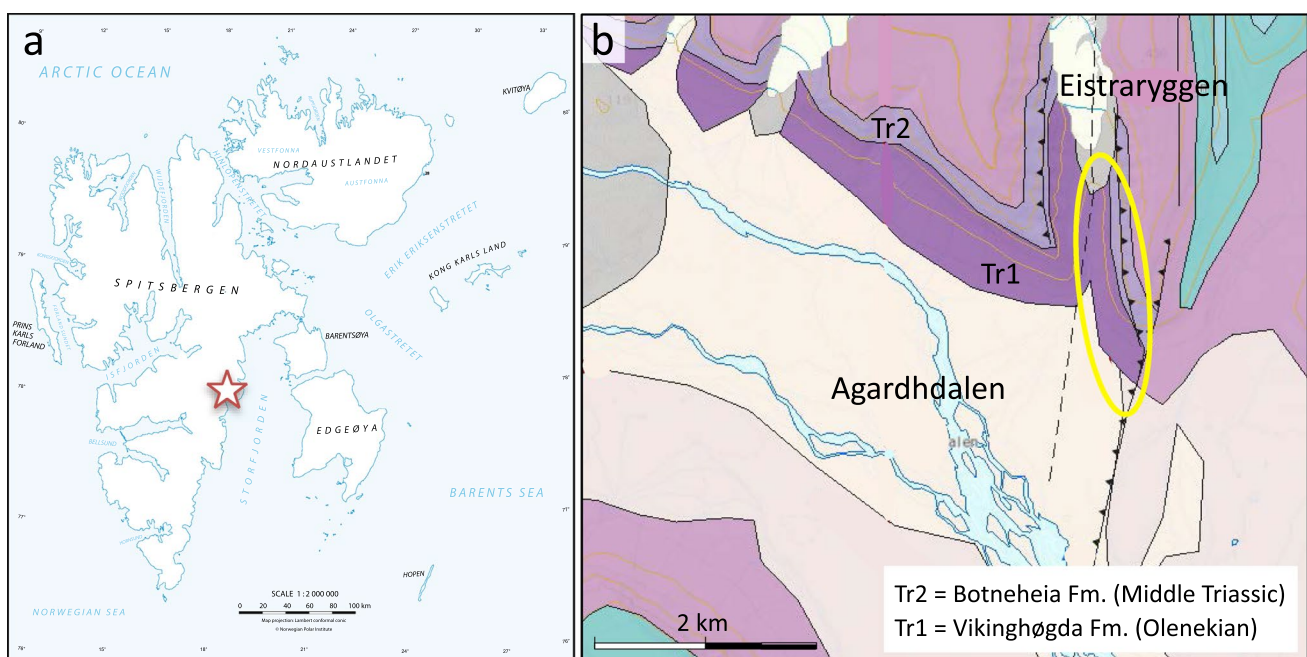

Fig. 1 a Location of Agardhdalen on Spitsbergen, Svalbard Archipelago, modified from Hurum et al. (2018) and based on Dallmann (2015). **b** Geologic map of Agardhdalen, based on the Geological Map of Svalbard, Norsk Polar Institute. Specimen IGPB R660 came from the outcrops of the Vikinghøgda Formation marked by the yellow ellipse. The geological map is provided by the Norwegian Polar Institute under the usage of the CC BY 4.0 Copyright license and is modified from Dallmann (2015).

Fig. 2 **a** Stratigraphic column of the Lower Triassic of Svalbard modified from Vigran et al. (2014). The ammonoid zones (Dagys and Weitschat 1993; Zatoń et al. 2016) are related to the palynological record and the regional lithostratigraphy (Vigran et al. 2014) which changes from west to east across the island. IGPB R660 comes from the Vikinghøgda Formation of eastern Svalbard. The exact stratigraphic horizon is the *Keyserlingites subrobustus* Zone (light blue). **b** The specimen of the ammonoid *Svalbardiceras spitzbergensis*, typical of the *Keyserlingites subrobustus* Zone. The ammonoid specimen was preserved in the same concretion as the vertebrae and is inventoried with the ichthyosaur bones
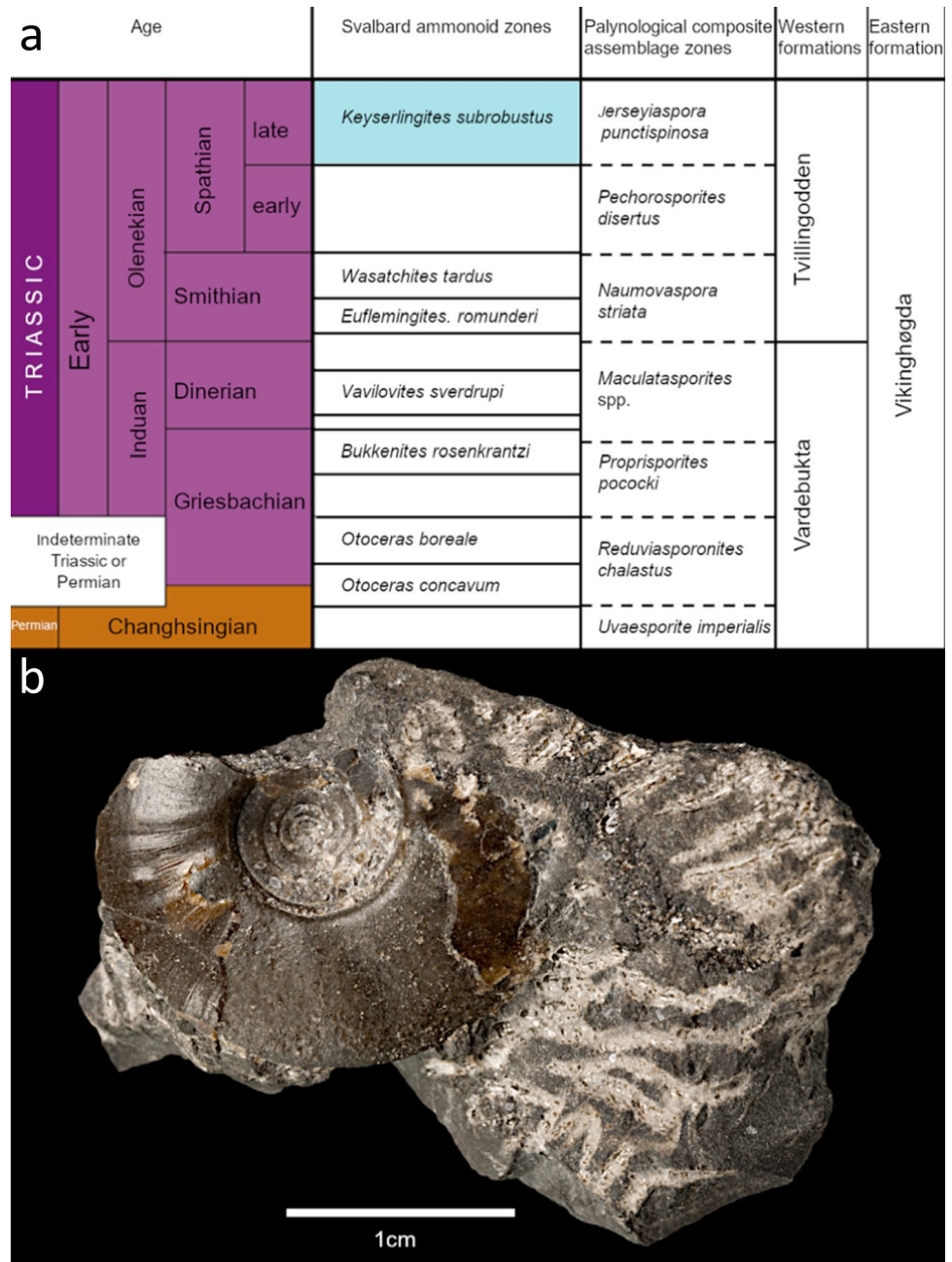

globe. Most notably, Scheyer et al. (2014) suggested that some Early Triassic ichthyosaurs reached large body size (11 m long). Their evidence consists of a putative humerus surface collected on Lower Triassic (Olenekian) rocks in Idaho, United States (Scheyer et al. 2014). However, the study of Scheyer et al. was met with skepticism as to the ichthyosaurian affinities and stratigraphic age of the specimen (Jiang et al. 2016, p. 7). Most recently, Nakajima et al. (2022) again argued in favor of the Idaho specimen representing an ichthyosaurian humerus, based on its similarity to another humerus from the Early Triassic. This 131 mm-long bone comes from the lower Spathian of Primorye (far-eastern Russia) and, in turn, closely resembles the humerus of the giant *C. youngorum* from the middle Anisian of Nevada (Sander et al. 2021). The body length of the Primorye find was estimated at approximately 5 m. Nevertheless, returning to the Idaho humerus, its ichthyosaurian affinities remain uncertain until further evidence, including histological evidence, is obtained. Similarly, whereas the stratigraphic origin from Spathian rocks appears likely, only a similar in-situ find would be able to corroborate this.

The archipelago of Svalbard with its main island of Spitsbergen is one of the most important localities for

Fig. 3 IGPB R660, three articulated posterior dorsal vertebrae of *Cymbospondylus* sp. from the Lower Triassic of Svalbard. **a** Anterior view. **b** Posterior view; the sagittal cut originates from sampling for histology. **c** Left lateral view. **d** Right lateral view. **e** Ventral view. The sagittal cut and plaster reconstruction (white dashed line) originates from sampling for histology. **f** Dorsal view. Anterior is towards the left in images (**c-f**). Note the labelling of the anatomical features. Anterior is towards the left in images (**d-f**) and to the right in image (**c**). *d* diapophysis, *na* neural arch, *ns* neurocentral suture, *pz* prezygapophysis, *r* rib head
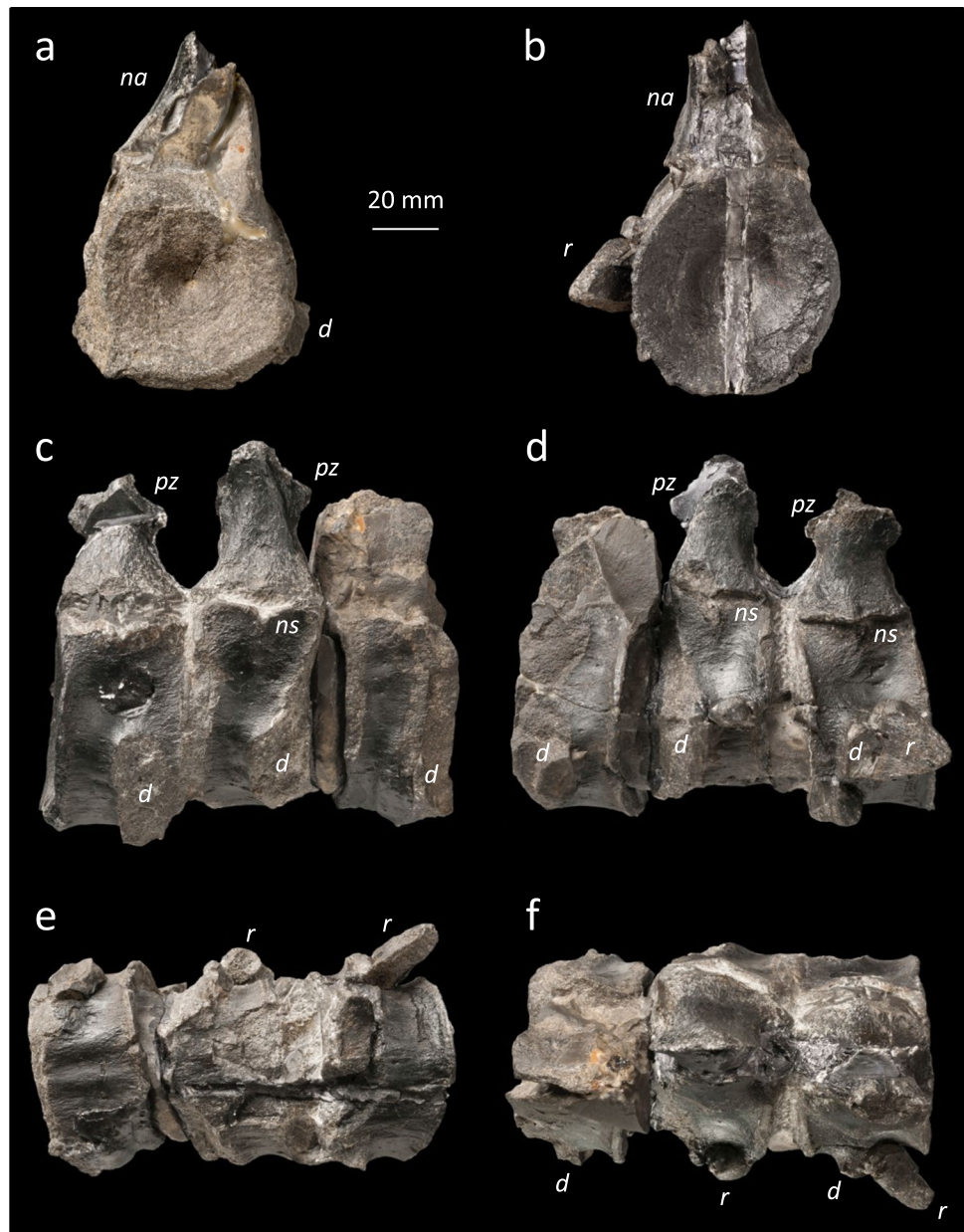
Triassic ichthyosaur fossils in general (Mazin and Sander 1993; Sander 2000; Maxwell and Kear 2013; Hurum et al. 2018; Kear et al. 2023). Before the publication by Kear et al. (2023) and the current study, all of the larger-bodied Lower Triassic (Olenekian) ichthyosaur material reported from Spitsbergen was disarticulated and rather fragmentary (Wiman 1910; Maisch and Matzke 2003; Maxwell and Kear 2013; Hurum et al. 2018), being derived from near-surface collections and from concentration deposits, i.e., bonebeds (Hurum et al. 2018). Only the small-bodied *Grippia* is represented by articulated partial skeletons (Wiman 1933; Motani 1998, 2000).

The first hints at the existence of large-bodied ichthyosaurs in the Lower Triassic of Spitsbergen are found in Wiman (1933, p. 5) who reported a large "*Pessopteryx*-like bone" in the lower Spathian 'Grippia Niveau' (listed as PMU 26962 on p. 87 of Maxwell and Kear 2013). However, the size of this animal is difficult to constrain, given that the bone is anatomically unidentified, and a clarification of what Wiman meant by "large" would be needed as well. A better-constrained estimate can be made from the material described by Wiman in his classical 1910 paper. This material includes a humerus of about 160 mm in length (Wiman 1910, plate VIII, fig. 1). Applying the allometric analysis published by Sander et al. (2021, fig. S8A) to this humerus, it represents an animal of about 5.6 m in length.

Recently, isolated vertebrae of large-bodied late Early Triassic ichthyosaurs collected from the upper Spathian of

Svalbard have been assigned to the genus *Cymbospondylus* (Engelschiøn et al. 2018). These isolated vertebrae resemble our find in morphology and stratigraphic age, coming from the 'Lower Saurian Niveau' of Marmierfjellet in the Isfjorden area, about 45 km northwest of the discovery locality of IGPB R660. Specifically, Engelschiøn et al. (2018) described and figured three dorsal centra, one anterior dorsal and two middle dorsals. The middle dorsals, especially PMO 230.177, are very similar in morphology, presumably pertaining to the same species as IGPB R660. However, the largest of the vertebral centra (PMO 230.177) is over 20% smaller in linear dimensions than IGPB R660 (Table 2) and may be from a younger individual, considering that the neurocentral suture was unfused as indicated by the missing neural arch (see also below).

Based on the Marmierfjellet specimens, Engelschiøn et al. (2018) noted that "the evolution of large-bodied ichthyosaurians occurred earlier than previously thought; before the *late* Middle and Late Triassic." (Engelschiøn et al. 2018, p. 263, italics added for emphasis) but did not pursue this issue further. In fact, the extensive skeletal material described by Merriam from the *early* Middle Triassic (middle to late Anisian) of Nevada had already revealed ichthyosaur body lengths in excess of 9 m (Merriam 1908), augmented by more recent finds from the same beds in excess of 17 m (Sander et al. 2021).

The most recent and important contribution to the topic of early evolution of large body size in ichthyosaurs is by Kear et al. (2023). From the Early Triassic of Spitsbergen, they described an articulated series of caudal vertebrae of a relatively large ichthyosaur. The find is from the 'Fish Niveau' of Flowerdalen in the Isfjorden area of central Spitsbergen. The origin from the 'Fish Niveau' has major implications because of the Smithian age of this horizon, which predates the late Smithian crisis (Kear et al. 2023). This crisis is dated at about 249.6 Ma, compared to the beginning of the Triassic at about 251.9 Ma. The ichthyosaur from the 'Fish Niveau' thus lived about 2 Ma after the beginning of the Triassic and is the oldest clearly dated ichthyosaur occurrence in the fossil record (Kear et al. 2023). The total body length of the animal was conservatively estimated at 3 m by Kear et al. (2023) based on a comparison with the material described by Nakajima et al. (2022), but we suggest that the Flowerdalen ichthyosaur actually was considerably larger (see Discussion). The large body size, fully pelagic lifestyle, and early occurrence of this ichthyosaur led Kear et al. (2023) to suggest a pre-Triassic origin of the clade.

The genus *Cymbospondylus*

Cymbospondylus is one of the first large-bodied representatives of the Ichthyosauria in the Triassic and occurs mainly in the Middle Triassic. Named species are exclusively from the Middle Triassic (Sander et al. 2021). A presumably cosmopolitan distribution of the genus had already been suggested by Massare and Callaway (1990) and confirmed by Sander (1992). The best-known and most abundant *Cymbospondylus* remains are from western North America, particularly from the Middle Triassic of Nevada, USA (Merriam 1908; Fröbisch et al. 2006; Klein et al. 2020; Sander et al. 2021). Fragmentary finds from the region are from the Lower Triassic of Idaho (Massare and Callaway 1994). A partial skeleton of *Cymbospondylus* was described from the Middle Triassic "Upper Saurian Niveau" of Svalbard (Sander 1992), and the isolated *Cymbospondylus* bones from the Lower Triassic have already been discussed (Engelschiøn et al. 2018). Apart from these records from Svalbard, the genus is known in Europe from the Germanic Basin and the Southern Alps (Sander 1989a; Ballini and Renesto 2012).

In the middle and late Anisian Fossil Hill Member (Middle Triassic) of Nevada, there is a record of a radiation of medium-sized to colossal species of *Cymbospondylus*, the Fossil Hill Fauna (Sander et al. 2021). Four of the five valid named *Cymbospondylus* species are from this fauna, also making the genus the most speciose of any Triassic ichthyosaur genus. In addition, the Fossil Hill Fauna is the most diverse Triassic ichthyosaur fauna known, with currently eight valid species (Sander et al. 2021).

The osteology of the presacral vertebrae of *Cymbospondylus*

Cymbospondylus is characterized by high vertebral counts, in excess of 60 in the presacral column (Sander 2000; Moon 2019), a feature that is also found in some shastasaurids. The vertebral column of Triassic ichthyosaurs exhibits marked morphological variation between taxa and along the vertebral column, from the cervical vertebrae to the posterior caudal vertebrae, as described in detail by Merriam (1908) and, most recently, by Zverkov et al. (2022). These variations also occur in the genus *Cymbospondylus* and allow the assignment of a series of articulated vertebrae or even isolated vertebrae to specific locations in the vertebral column. For the presacral centra of *Cymbospondylus petrinus*, Merriam (1908) reported that the anterior centra have a round shape in anterior view, whereas the posterior ones have a more rectangular or even triangular shape. As in many other ichthyosaurs, the rib facets of the posterior centra are displaced toward the ventral margin of the centrum in *Cymbospondylus*, whereas these facets are more dorsal in the anterior vertebrae (Merriam 1908; Zverkov et al. 2022). In addition, the centra of *Cymbospondylus* markedly increase in dorsoventral height along the column, with the

highest centra occupying the posteriormost part of the dorsal column, the sacral region, and the anterior caudal region.

However, the most important, and autapomorphic, feature of the vertebral anatomy of *Cymbospondylus* is found throughout the dorsal column (Merriam 1908; Sander 1989a, 1992; Zverkov et al. 2022), and this is the single elongate rib articular facet that extends in anteroventral direction to meet the anterior articular surface of the centrum. In the side view, the rib facet appears truncated by the anterior margin of the centrum. In the anterior and middle dorsals, the rib articular facet dorsally contacts the middle of the base of the neural arch. This contact is gradually lost, but a connection between the base of the arch and the facet is maintained via a sharp ridge until far back along the dorsal column. Only in the posteriormost dorsals, the ridge is lost, and the facet is moved down to the lower third of the side of the centrum (Merriam 1908, plate 8; Zverkov et al. 2022, fig. 12). Only the Late Triassic *Callawayia neoscapularis* shows a somewhat similar but not identical morphology, including the triangular posterior dorsals (Zverkov et al. 2022, fig. 12). More detailed osteological descriptions of the axial skeleton of *Cymbospondylus* can be found in the literature (e.g., Merriam 1908; Sander 1989a, 1992; Massare and Callaway 1994; McGowan and Motani 2003; Fröbisch et al. 2006; Ballini and Renesto 2012; Engelschiøn et al. 2018; Zverkov et al. 2022). Other morphological features that allow the assignment of isolated centra to the genus include the morphology of the articular surface, both in terms of outline and nature of the amphicoely, and the shape of the neural spine. These differences in morphology are also useful as characters in phylogenetic analyses (e.g., Sander 2000; Moon 2019; Zverkov et al. 2022).

Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IGPB, Section Paleontology, Institute of Geosciences, University of Bonn, Bonn, Germany; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; PIMUZ, Paleontological Institute and Museum of the University of Zurich, Zurich, Switzerland; PMO, Natural History Museum, University of Oslo, Oslo, Norway; PMU, Museum of Evolution, Uppsala University, Uppsala, Sweden; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

Materials and methods

Cymbospondylus sp. IGPB R660

The specimen consists of three posterior dorsal vertebrae in articulation and is accessioned in the collections of the

IGPB as IGPB R660 (Fig. 3). The individual vertebrae are numbered in anteroposterior sequence as IGPB R660.1 to IGPB R660.3. The specimen was found in a carbonate concretion in the Agardhdalen region of eastern Spitsbergen by the late ammonoid specialist Dr. Wolfgang Weitschat (e.g., Weitschat and Lehmann 1978; Weitschat and Bandel 1991) of the University of Hamburg in 1986. The concretion also contained a specimen of the ammonoid *Svalbardiceras spitzbergensis* (Fig. 2) which is inventoried with the ichthyosaur bones as IGPB R660.

The specimen was donated to the former Institute of Paleontology (now Section Paleontology) of the University of Bonn in the early 1990s in the course of the description by PMS of similar material from the Middle Triassic of Spitsbergen (Sander 1992; Lindemann 2015). Specimen IGPB R660 consists of three articulated posterior dorsal vertebrae and fragments of ribs. A sagittal thin section of vertebrae IGPB R660.2 and IGPB R660.3 was made for histological examination. These sections are published in Wintrich et al. (2020, fig. S10) as part of a larger study on intervertebral disk evolution. After sectioning, the two vertebrae were reconstructed with plaster and reattached to vertebra IGPB R660.1 (see Fig. 3).

In addition to stratigraphic information provided by the *Svalbardiceras spitzbergensis* (Fig. 2) associated with the specimen, the exact stratigraphic horizon of the discovery was also communicated by W. Weitschat. The tight articulation of the vertebrae in IGPB R660 suggests that they may represent the remains of a complete or partial articulated skeleton, most of which was either not collected or destroyed by weathering. The state of preservation of IGPB R660 had suggested to us that articulated skeletons of large-bodied ichthyosaurs are to be found in the Vendomdalen Member of the Early Triassic Vikinghøgda Formation. This notion is corroborated by the finds of Kear et al. (2023) and by recent fieldwork of the first author. Previous reports of articulated ichthyosaur remains from the Vendomdalen Member had been restricted to small-bodied, *Grippia*-like ichthyosaurs (Wiman 1910, 1929, 1933; Motani 1998, 2000; Maxwell and Kear 2013).

Geologic setting

The specific locality W. Weitschat reported in a letter to the first author is Eistraryggen, a north–south trending mountain ridge on the northeastern side of the valley of Agardhdalen in eastern Spitsbergen (Fig. 2). Eistraryggen is separated by an unnamed valley from Roslagenfjellet to the west. Extensive outcrops of the Vikinghøgda Formation are found on either slope of this valley, but only the eastern slopes would fit the locality designation 'Eistraryggen' of Weitschat. The stratigraphic horizon of the find was determined by Weitschat as the Early Triassic late Spathian

Keyserlingites subrobustus zone (Dagys and Weitschat 1993; Zatoń et al. 2016), named after the ammonoid *Keyserlingites subrobustus* and located in the uppermost Vikinghøgda Formation (Vigran et al. 2014, p. 91). The ammonoid *Svalbardiceras spitzbergensis* is typical for the *Keyserlingites subrobustus* zone (Hansen et al. 2018). This ammonoid is characteristically very abundant in the upper Vendomdalen Member (Weitschat 2008; pers. observation PMS; pers. communication B. Kear 2022), near the top of which is the 'Lower Saurian Niveau' (Hansen et al. 2018), the reported horizon of origin of IGPB R660.

Approach to size estimation

Although body mass has been used as a size proxy (Gutarra et al. 2019), ichthyosaur size is most commonly expressed as total body length. Estimating total body length from the skull or postcranial bones of the skeleton generally comes with a large margin of error, however. The morphology and proportions of different skeletal parts vary widely between taxa, making it difficult to find a reliable proxy with constant proportions to the rest of the skeleton (Moon and Stubbs 2020).

Previously, two different body length proxies have been used, the anteroposterior length of the skull (e.g., Fröbisch et al. 2006; Moon and Stubbs 2020; Klein et al. 2020) and the humerus length (e.g., Scheyer et al. 2014; Sander et al. 2021). Both proxies can be related to body length in complete skeletons, and then body length can be computed from an allometric regression equation (e.g., for humerus length: Scheyer et al. 2014; Sander et al. 2021). In a more simple approach, known proportions between a corresponding anatomical structure and body length have been used (e.g., Sander 1989a; Fröbisch et al. 2006; see below).

In this study, we employ a total length proxy novel to ichthyosaurs, the anteroposterior length of the dorsal centra (Tables 1, 2 and 3), in a comparative data set of species of the genus *Cymbospondylus* (Table 3). The regression approach can be used for the Spitsbergen specimen IGPB R660 because the size range of *Cymbospondylus* species is large (Sander et al. 2021), but their vertebral morphology and count is similar across species.

Centrum length has been used successfully as a size proxy in other fossil reptiles before (e.g., Romer and Price 1940; Currie 1978, 1981; Sander 1988, 1989b) because it is closely linked with the length of the entire animal. However, this proxy obviously is sensitive to the number of segments (i.e., vertebrae) in the vertebral column which may vary widely between different ichthyosaur clades (Sander 2000; Moon 2019). We alleviate the problem of varying vertebral counts in ichthyosaurs in general by restricting our analysis to *Cymbospondylus*, the clade of interest.

In *Cymbospondylus*, the length of the centra remains remarkably constant in the presacral column (Merriam 1908; Fröbisch et al. 2006; Klein et al. 2020), allowing length estimates from vertebrae of different positions. On the other hand, the width and especially height of the vertebral centra vary greatly from anterior to posterior (Merriam 1908; Sander 2000; Zverkov et al. 2022), and thus are not useful for estimating body size in this genus.

Published size estimates of *Cymbospondylus* species

We obtained length data for dorsal vertebrae and total length estimates of the five named species of *Cymbospondylus* from publications and verified these by personal observations (Table 3). A major caveat here is that none of the named *Cymbospondylus* species is known from a complete skeleton, and the total lengths in Table 3 are numerical estimates. In the following, we present a detailed review of how these length estimates were obtained.

The pivotal specimen is UCMP 9950 in combination with UCMP 9947. These two specimens had been combined into a graphic composite (Merriam 1908, fig. 128), the scale of which was indicated as 1/41 of the original size. In addition, Merriam (1908, p. 105) noted that the individual represented by the fossil UCMP 9950 was "over 30 feet in length", equaling over 9.14 m. After decades of being inaccessible, UCMP 9950 recently could be measured by author PMS (Fig. S2). The preserved length of the specimen is 6.66 m, consisting of 1.14 m for the skull, 0.3 m for six articulated cervicals, and 5.22 m for the remainder of the postcranial (Fig. S2). This includes the first 12 caudals. Merriam (1908) then added to this UCMP 9947, which is a tail lacking the base and the tip, associated with a pelvic

Table 1 Dimensions of posterior dorsal vertebrae of *Cymbospondylus* sp. IGPB R660

Vertebra	Height total[a]	Height centrum	Height neural arch[a]	Width centrum[b]	Length centrum
R660.1	108.1	70.3	32.8	66.5	39.1
R660.2	114.6	69.2	54.3	65.1	42.0
R660.3	108.9	71.0	41.2	66.4	42.1

[a]As preserved

[b]Measured across articular surface

Table 2 Measurements of dorsal vertebral centra of nine *Cymbospondylus* specimens including IGPB R660 for comparison, organized by centrum length

Specimen	Taxon	Centrum position	Length	Height	Width	Ratio H/L	References
IGPB R660.1	*C.* sp.	PD	39.1	70.3	66.5	1.80	This study
IGPB R660.2		PD	42.0	69.2	65.1	1.65	
IGPB R660.3		PD	42.1	71.0	66.4	1.69	
LACM DI 158109	*C. duelferi*	AD	25.0	–	–	–	This study[a]
LACM DI 158109		–	21.5	35.8	–	1.67	Klein et al. (2020)
LACM DI 158109		–	22.5	44.4	–	1.97	
LACM DI 158109		–	22.5	41.1	–	1.83	
LACM DI 158109		–	20.1	45.6	–	2.27	
LACM DI 158109		–	25.2	47.1	–	1.86	
LACM DI 158109		–	22.0	44.0	–	2.00	
PMO 162.003	*C.* sp.	26	30.8	61.5	55.8	1.99	Sander (1992)
PMO 162.003		32	29.7	–	66.5	–	
PMO 162.003		42	31.7	69.1	51.3	2.18	
PIMUZ T 4351	*C. buchseri*	8	31.1	48.0	–	1.54	Sander (1989a, b)
PIMUZ T 4351		42	29.2	56.7	–	1.94	
PMO 230.177	*C.* sp.	MD	33.0	70.0	64.5	2.12	Engelschiøn et al. (2018)[b]
FMNH PR2251	*C. nichollsi*	3	37.0	63.0	–	1.70	Fröbisch et al. (2006)
FMNH PR2251		17	41.0	–	–	–	
FMNH PR2251		28	37.0	87.0	–	2.35	
UCMP 9950	*C. petrinus*	AD	47.3	68.6	–	1.45	Merriam (1908)[b]
UCMP 9950		PD	54.0	115.8	–	2.14	
LACM DI 157871	*C. youngorum*	PC	60.0	–	–	–	Sander et al. (2021)

AD anterior dorsal, *H/L* height/length, *MD* middle dorsal, *PC* posterior cervical, *PD* posterior dorsal

[a] Average of four consecutive anterior dorsals in block 6 of the holotype of *C. duelferi* (Klein et al. 2020, fig. 1)

[b] Values obtained from illustrations in the respective papers cited

Table 3 Total length allometric analyses of specimen IGPB R660, regressing total body length estimates on vertebral centrum length. Three different analyses were performed. Analysis 1 is based on estimates in the pre-2021 literature, whereas analyses 2 and 3 are based on the latest regression analysis (Sander et al. 2021). Analysis 3 differs from analysis 2 in that a hypothetical higher value for centrum length (70 mm vs. 60 mm) was used for the largest species, *C. youngorum*, to test for sensitivity to underestimating centrum length in this species. See text and Table 2 for further explanations about the analyses and values in this table

Analysis 1 (pre-2021)	*C. duelferi*	*C. buchseri*	*C. nichollsi*	*C. petrinus*	*C.* sp. IGPB R660
Centrum length (mm)	25.0	30.2	40.7	50.6	41.0
Body length (mm)	4300	5500	7600	9300	**7525**
Analysis 2 (hu/length)	*C. duelferi*	*C. buchseri*	*C. petrinus*	*C. youngorum*	*C.* sp. IGPB R660
Centrum length (mm)	25.0	30.2	50.6	60.0	41.0
Body length (mm)	4996	5314	12,563	17,648	**9473**
Analysis 3 (sensitivity)	*C. duelferi*	*C. buchseri*	*C. petrinus*	*C. youngorum*	*C.* sp. IGPB R660
Centrum length (mm)	25.0	30.2	50.6	70.0[a]	41.0
Body length (mm)	4996	5314	12,563	17,648	**8920**

[a] Hypothetical value

girdle and hindlimb. Based on the illustration and the proportions in Merriam (1908, fig. 128), UCMP 9947 is nearly exactly 50% the length of UCMP 9950. Thus, adding 3.33 m to 6.66 m, the composite specimen lacking the tip of the tail is almost exactly 10 m long. However, since much of the posterior caudals are missing in UCMP 9947, a total length of 11—12 m is not unreasonable. This revised estimate obtained directly from the specimens lends credibility to the length estimate of 12.56 m (Table 3) obtained from the Sander et al. (2021) regression based on humerus length. Since we wanted to use published data in the initial analysis, we did not correct those data based on the new measurements of UCMP 9950 provided above.

The total published length estimate of *C. buchseri* is 5.5 m. According to Sander (1989a), this estimate is based on a proportional calculation with UCMP 9950/9947. The total preserved length of the holotype of *C. buchseri* is 2.3 m. The anatomically corresponding part of UCMP 9950 is 4.4 m. This results in a minimum length of 5 m for the holotype of *C. buchseri*, but Sander (1989a) suggested a length of 5.5 m based on Merriam's (1908) estimate of "over 30 feet" (9.1 m).

The total published length of the *C. nicholsi* holotype was also estimated by proportional calculation based on UCMP 9950/9947. Fröbisch et al. (2006, p. 531) estimated a total length of 7.6 m for the *C. nicholsi* holotype based on skull length posterior to the external nares. This measurement is 84% of UCMP 9950.

Instead of the proportional approach, the regression approach based on humerus length (Scheyer et al. 2014; Sander et al. 2021) was applied to estimate the total length of *C. duelferi* in the original publication of Klein et al. (2020). Using the Scheyer et al. (2014) regression, a body length of 4.3 m was estimated by Klein et al. (2020) for the holotype of *C. duelferi*.

The most recent published length estimate for a *Cymbospondylus* species is that for the largest of them all, *C. youngorum*, published in 2021 (Sander et al. 2021) and represents the latest research. Our estimate was obtained via an improved regression analysis based on Scheyer et al. (2014).

Vertebral centrum measurements

We measured the centrum length of IGPB 660 to the nearest 10th of an mm with a calliper (Tables 1, 3). Centrum length is defined as the distance between the anterior and posterior articular surfaces of the centrum in lateral view. For the body length estimate, we averaged the length of the three centra of IGBP R660, obtaining a length of 40.1 mm. IGPB R 660 shows little morphological distortions, corroborated by the sagittal thin sections (Fig. S1), presumably because the bone was protected from compaction by early diagenetic concretion growth.

Vertebral centrum measurements of eight *Cymbospondylus* individuals are provided in Table 2. These individuals belong to five different named and two indeterminate species and are all but one geologically younger (Middle Triassic) than IGPB R660. Starting with the smallest species, *C. duelferi*, we re-measured the length of four consecutive anterior dorsals in block 6 of LACM DI 158109, the holotype (Klein et al. 2020, fig. 1) and averaged their length (Tables 2, 3). The original study erroneously gave dorsal length as varying widely (Klein et al. 2020, table 1), and that study also did not specify the position of the measured vertebrae.

Next in size are the vertebrae of *C. buchseri* (PIMUZ T 4351) and the specimen from the Middle Triassic Botneheia Formation of Spitsbergen (PMO 162.003), respectively, for which Sander (1989a) and Sander (1992) have provided some measurements. Since no measurements were given by Engelschiøn et al. (2018) for three isolated *C.* sp. dorsal vertebral centra from the Early Triassic Vikinghøgda Formation of Spitsbergen, we obtained the values for the largest (PMO 230.177) from the illustrations of this specimen in Engelschiøn et al. (2018, fig. 3).

Height and length of some vertebrae of the holotype of *C. nicholsi* (FMNH PR2251) are provided in Fröbisch et al. (2006). The average centrum length in *C. nicholsi* and IGPB R660 is rather similar (40.7 mm vs. 40.1 mm), suggesting similar-sized animals. Their sizes are intermediate between the relatively small *C. duelferi*, *C. buchseri*, and *C.* spp. from Spitsbergen and the much larger to giant *C. petrinus* and *C. youngorum.*

Although Merriam (1908) did not provide measurements of the presacral vertebrae of *C. petrinus*, as previously mentioned in Fröbisch et al. (2006), dimensions of the vertebrae can be obtained from his illustrations. Specifically, the dimensions of the dorsal vertebrae in fig. 10 of plate 8 and fig. 1 of plate 9 in Merriam (1908) can be computed based on the magnification factor given in the plate captions ("four-ninths of natural size"). In the most recently described and by far largest species of the genus, *C. youngorum*, the holotype includes anterior to middle dorsal vertebrae, but these are not yet prepared. Instead, only the length of the posterior cervicals is available (Sander et al. 2021) which provides a minimum estimate of dorsal vertebral length given that in other species the cervicals are about the same anteroposterior length than the dorsals (Merriam 1908; Sander 1989a; Fröbisch et al. 2006).

A caveat might be that primary centrum length measurements were affected by diagenetic deformation through sediment compaction. Although we cannot prove the lack of deformation in the other specimens as well as for IGPB R660 (see above), close personal inspection (if not personal excavation) of all specimens in the dataset (Tables 2, 3) by the first author revealed that none of the

Early and Middle Triassic *Cymbospondylus* specimens are compacted to any extent, unlike the specimens from the Toarcian black shales of Europe. This lack of compaction even applies to the *C. buchseri* holotype which comes from a dolomite bed of the Besano Formation and not from its highly compacted bituminous shales (Sander 1992). Even if there were slight compaction in the fossils studied, this would have affected centrum length the least because length is measured in the direction of any compaction vector and not oblique to it.

Regression analysis of body length on centrum length

To estimate the total body length of IGPB R660, we performed three different allometric regression analyses, each

with four *Cymbospondylus* species, in which we used centrum length as a predictor of total body length (Table 3). In analysis 1 (Fig. 4a), we applied estimates on both parameters from the pre-2021 literature. Thus, *C. youngorum* was not part of this dataset. In analysis 2 (Fig. 4b), we used total lengths (Table 3) from a recent regression of total length on humerus length (Sander et al. 2021) which was used to estimate the body length of the giant *C. youngorum*.

Analysis 1 was conducted with body length estimates published pre-2021 (as reviewed above) for *C. duelferi* (4300 mm; Klein et al. 2020), *C. buchseri* (5500 mm; Sander 1989a), *C. nichollsi* (7600 mm; Fröbisch et al. 2006), and *C. petrinus* (9300 mm; Merriam 1908).

In analysis 2, we used the revised body length estimates for *C. duelferi* (4996 mm), *C. petrinus* (12,563 mm), and the new one for *C. youngorum* (17,648 mm) as
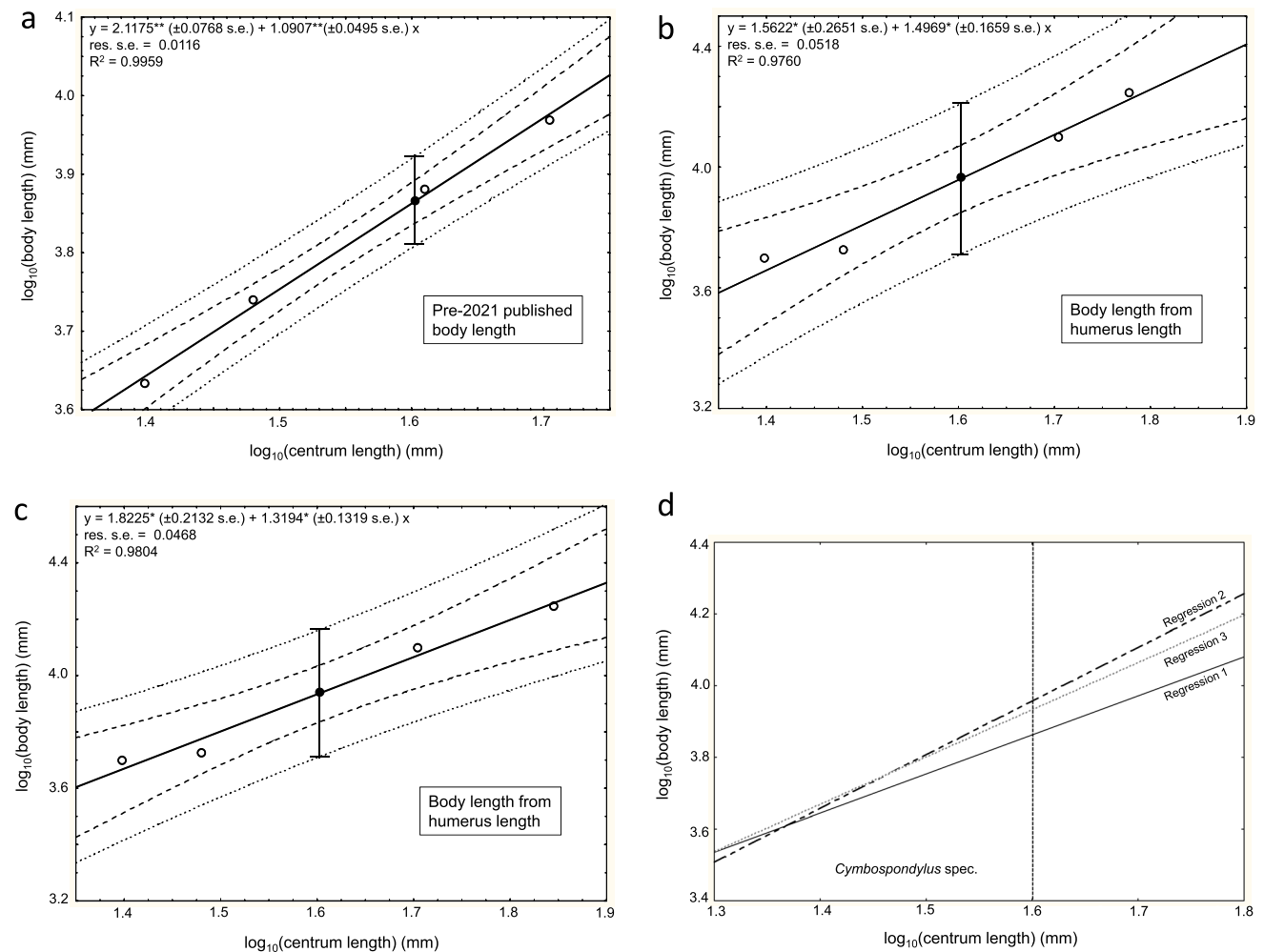

Fig. 4 Allometric analyses of body length based on centrum length of *Cymbospondylus* species and resulting regression equations and statistical support. **a** Analysis 1, based on pre-2021 published body length estimates, see Table 3 for data. **b** Analysis 2, based on body length estimates obtained from humerus length (Sander et al. 2021). **c** Analysis 3, sensitivity analysis of analysis 2, assuming a centrum length of 70 mm for the largest individual in the analysis. **d** Comparison of the three analyses. See text for details and Table 3 for data

calculated by Sander et al. (2021, table 2), and we added a new size estimate of 5314 mm for the holotype of *C. buchseri* (Sander 1989a) using the regression of total length on humerus length of Sander et al. (2021). Note that this new size estimate for the holotype of *C. buchseri* had not been included in Sander et al. (2021) because this species is not from the Fossil Hill Fauna of Nevada but from the southern Alps (Sander 1989a). Also note that *C. nichollsi* is not part of analysis 2 because no humerus is preserved for this species.

In analysis 3, we repeated analysis 2 with a hypothetical higher value for dorsal centrum length for *C. youngorum* (70 mm instead of the 60 mm length of the cervicals, Table 3) to explore the sensitivity of the regression equation to an underestimate of this species' dorsal vertebral length (Fig. 4c). Our reasoning was that dorsal vertebral length is not well constrained in *C. youngorum* (we only know that it is greater than the known length of the cervicals, but not by how much; Sander et al. 2021).

Prior to all regression analyses, we log$_{10}$-transformed both centrum length and total estimated body length of all species. We then carried out an ordinary least squares linear regression analysis for each *Cymbospondylus* dataset (analysis 1, 2, and 3) in the software R, version 4.2.1, applying the built-in function *lm* (R Core Project 2021). We assessed the goodness-of-fit of the regression from the residual standard error, the coefficient of determination (R^2), the significance of slopes and intercepts, F-statistic, and 95% confidence interval belts. To estimate the total body length and its margins of error for IGPB R660, we evaluated each of the three regression equations and their 95% prediction interval belts (Fig. 4), again using the software R.

Systematic paleontology

Diapsida Osborn, 1903
Ichthyopterygia Owen, 1860
Huenosauria Maisch and Matzke, 2000 (sensu Moon 2019).

Genus *Cymbospondylus* Leidy, 1868

Cymbospondylus **sp.**

Referred material. IPBG R660, a series of three articulated posterior dorsal vertebrae with incomplete neural spines and two holocephalous rib heads.

Locality and horizon. West slope of Eistraryggen ridge on the northeastern side of Agardhdalen valley, eastern Spitsbergen, Norway (Fig. 1). 'Lower Saurian Niveau',

Keyserlingites subrobustus Zone, Vendomdalen Member, Vikinghøgda Formation (late Olenekian, Early Triassic).

Description

The series of three articulated vertebrae IGPB R660 shown in Fig. 3 includes the centra together with their dorsally incomplete neural arches and two left rib fragments associated with the second and third centra (Fig. 3). Preparation damage is evident in some areas such as the lateral surface of the centra. Table 1 shows the dimensions of the vertebrae. The centra of IGPB R660 have lower height/length ratios (the average is 1.71) and are thus relatively longer than the other posterior dorsals in the comparative *Cymbospondylus* data set (Table 2).

All centra are nearly round in anterior view, with a deeply amphicoelous, non-notochordal articular surface that evenly slopes to its center, as best seen in the thin sections figured in Wintrich et al. (2020, fig. S10). This morphology differs from some Middle Triassic *Cymbospondylus* species, such as *C. petrinus*, in which the posterior dorsals are triangular in anterior view and only the central area of the articular surface of the presacrals is distinctly funnel-shaped (Merriam 1908). The diapophyses are best preserved in the left lateral view of vertebra 2 and 3 (Fig. 3). The diapophysis was dorsoventrally elongated, anteroventrally slanted, and located on the ventral portion of the centra. The diapophysis is truncated anteriorly by the anterior articular surface of the centrum. The morphology of the diapophysis is consistent with the preserved single but broad and flared rib heads. The neurocentral suture is ventrally concave with a sharp ventral tip, but there is no distinct ridge or crest connecting this tip with the diapophysis (Fig. 3). All neural arches are in articulation with the centra. The paired prezygapophysis and postzygapophysis are visible in vertebrae 2 and 3 (Fig. 3).

The distinct anteroposterior morphological change of the vertebrae in the column of *Cymbospondylus* (Merriam 1908; Sander 1989a, 1992; Engelschiøn et al. 2018; Zverkov et al. 2022) and the pattern of the diapophysis decreasing in size and moving away from the neurocentral suture (Sander 1992) are helpful for determining the position of the three vertebrae of IGPB R660 in the vertebral column. Specifically, the ventral position of the diapophysis on the lateral side of the centra, the lack of the crest connecting the diapophysis with the neural arch (Fig. 3), and the ratio of dorsoventral height to length (Table 1) are all indicators of a posterior dorsal position of the vertebrae of IGPB R660.

Ontogenetic stage

For size comparisons with other ichthyosaurs, determining the ontogenetic stage of IGPB R660 is obviously relevant. The tight articulation of the neural arch with the centrum

suggests that IGPB R660 represents an adult, if not old, specimen. This is suggested by the patterns of disarticulation in the other species of *Cymbospondylus*, organized by size (Table 3): most arches are disarticulated from the centra in the medium-sized species *C. buchseri* (Sander 1989a; length estimate 5.5 m), all arches in *C.* sp. (Sander 1992; same length estimate as for *C. buchseri*), and seemingly in *C. petrinus* (UCMP 9950, Merriam 1908; length estimate 9.3 m). *C. nichollsi* has tightly articulating arches (Fröbisch et al. 2006; length estimate 7.6 m), as in IGPB R660, and the condition in the smallest species (4.3 m), *C. duelferi* (Klein et al. 2020) cannot be determined with certainty. The late ontogenetic stage of IGPB R660 is corroborated by vertebral centrum histology. Sagittal histological sections of the centra (Fig. S1; see also Wintrich et al. 2020, fig. S10) show abundant secondary trabeculae, typical of skeletally mature ichthyosaurs (see Houssaye et al. 2018; Klein et al. 2020).

Body length estimate of IGPB R660

Although only data for four *Cymbospondylus* species each could be used to establish the three regression equations, their residual standard errors were small (res. s.e., 0.012–0.052), their coefficients of determination were very high (R^2, 0.976–0.996), their slopes and intercepts significantly differed from zero, and the *F*-statistic was always significant (range of *p* values, 0.002–0.012). All of these statistics indicate strong support for an allometric relationship between centrum length and total body length in *Cymbospondylus*. As expected for small sample sizes, the 95% confidence and prediction belts of all regressions were broad, and belt width increased with increasing residual standard errors and decreasing coefficients of determination (Fig. 4).

Analysis 1 (Fig. 4a), based on total length estimates published before 2021 (Table 3), resulted in a total body length estimate for IGPB R660 of 7525 mm, rounded to 7.5 m. The lower limit of the 95% prediction interval of its length is 6590 mm and the upper limit is 8593 mm. The residual standard error and the *p* value of the *F*-statistic are the lowest among the three regressions, and the coefficient of determination is the highest ($R^2 = 0.996$). Analysis 2 (Fig. 4b), which was based on total length estimates using humerus length as the predictor variable, resulted in a higher length estimate of 9.5 m (9473 mm). The lower limit of the 95% prediction interval is 5331 mm for IGPB R660, and the upper limit is 16,831 mm. The residual standard error and the *p* value of the *F*-statistics are the largest, and the coefficient of correlation is the lowest ($R^2 = 0.976$) among the three regressions.

In the sensitivity analysis (analysis 3, Fig. 4c), which assumed that the dorsals of *C. youngorum* were 70 mm in length, an estimate similar to analysis 2 of 8920 mm is still obtained. For this regression, the residual standard error (0.047) and the *p* value of the *F*-statistic (0.010) were somewhat smaller, and the coefficient of determination ($R^2 = 0.980$) was somewhat higher than in analysis 2. This supports the assumption that the cervical centra are indeed shorter than the dorsal centra in *C. youngorum*. In analysis 3, the lower limit of the 95% prediction interval of the length of IGPB R660 is 5311 mm, and the upper limit is 14,980 mm.

Discussion and conclusions

Challenges of size estimation

Even though IGPB R660 is not diagnostic at the species level, the specimen can safely be assigned to the genus *Cymbospondylus*, making it one of the oldest records of this clade together with the isolated centra described by Engelschiøn et al. (2018) and the scanty material from Idaho (Massare and Callaway 1994). Unlike most other Middle Triassic ichthyosaur clades, *Cymbospondylus* has a documented Early Triassic (Olenekian, possibly Smithian, see below) lineage beginning but continued to diversify and thrive in the Middle Triassic (Sander et al. 2021). Identification of IGPB R660 as *Cymbospondylus* sp. is relevant because it allows our taxonomically well-constrained size estimate through comparative quantitative analysis within a single clade.

As discussed earlier, size estimation is challenging in Triassic ichthyosaurs, and total length estimation for a specific individual can vary depending on the method used. In addition, the proportions of the skull and humerus can vary within a single clade of ichthyosaurs, the former primarily through variation in rostral length. Interestingly, as seen in Fig. 4, the coefficient of determination is higher and the residual standard error is smaller in analysis 1 based on the published (and seemingly less stringent) total length estimates than those of analysis 2 (seemingly more stringent). The length estimates in analysis 2 would appear more stringent because it was based on a larger ichthyosaur data set that was analyzed by Sander et al. (2021) and not only on four species. Possible reasons for the greater length estimate for IGPB R660 from analysis 2 are the greater input length of *C. petrinus* and the addition of the giant *C. youngorum*, lacking in analysis 1. The original length estimate, used in analysis 1, for *C. petrinus* is 30 feet (Merriam 1908), or about 9.3 m, which was based on the graphic overlay of two partial skeletons (UCMP 9950 and UCMP 9947, Merriam 1908, fig. 128). However, Sander et al. (2021) calculated a different and much greater length of 12.53 m for *C. petrinus* based on humerus length, which is more consistent with the revised measurements provided above. The giant *C. youngorum* could not be included in

analysis 1 because this would have resulted in circular reasoning.

The strong statistical support for an allometric relationship between centrum length and total body length in *Cymbospondylus* suggests that our regression equations provide sufficient size estimates for other *Cymbospondylus* species. Whereas for centrum lengths shorter than about 25 mm (*C. duelferi*), all three regressions provide rather similar estimates of body length, predictions differ more for longer ones (Fig. 4d). Specifically, beyond the 25 mm threshold, the regression equation from analysis 1 always reveals the shortest length, that of analysis 2 yields the longest, and analysis 3 an intermediate value (Fig. 4d). We anticipate that the currently large 95% prediction belts around the regressions (Fig. 4) will decrease when more information on centrum length and body length in *Cymbospondylus* becomes available. Ideally, our proxy of dorsal vertebral length will be rigorously tested in the rich samples of different species of well-preserved Jurassic ichthyosaurs, in particular from the Early Jurassic of Germany and the UK.

At between 7.5 m and 9.5 m, IGPB R660 would likely have been one of the largest marine tetrapods in its ecosystem (see data and discussion in Scheyer et al. 2014), together with other large ichthyosaurs. Other Early Triassic marine reptiles were clearly smaller, at most 4 m (Scheyer et al. 2014, 2019), as were the marine temnospondyl amphibians (1.5 m; Scheyer et al. 2014), bony fish (1.5 m; Scheyer et al. 2014) and hybodont sharks (1.5 m; Scheyer et al. 2014). For comparison with living aquatic tetrapods, the size estimate for IGPB R660 is similar to some body length measurements noted for very large individuals of modern saltwater crocodiles (Britton et al. 2012) and orcas (Ford 2017). Although the isolated centrum PMO 229.177 described in Engelschiøn et al. (2018) reaches less than 80% of the anteroposterior length of those of IGPB R660 (33 mm vs. 42 mm), it and the associated material described by Engelschiøn et al. (2018) suggest a certain abundance of large-bodied ichthyosaur individuals in the Early Triassic sea covering what now is Svalbard.

Size of Smithian PMO 245.975

These considerations raise the question of the size of the Smithian ichthyosaur described by Kear et al. (2023). This specimen, PMO 245.975, preserves the tail segment, consisting of 11 centra plus 15 indeterminate bone fragments. As noted above, the total length estimate of 3 m by Kear et al. appears overly conservative.

The series of vertebral centra PMO 245.975 pertains to the middle or posterior region of the tail. This is indicated by the lack of rib articular facet. Comparison with *Cymbospondylus petrinus* would indicate a position posterior to the caudal peak based on morphology,

specifically the lack of articular facets, which are lost at the caudal peak in UCMP 9947 (Merriam 1908, fig. 132, plate 9). The maximum transverse width of the centra in PMO 245.975 is clearly greater than the width at the base of the neural and hemal arches, giving the centra a somewhat elongate hexagonal shape (Kear et al. 2023), also seen in the middle caudals of *Cymbospondylus petrinus* (UCMP 9947; Merriam 1908).

We review similarities and differences of PMO 245.975 from the caudals of other Early and Middle Triassic ichthyosaurs. As noted by Kear et al. (2023), basal ichthyosaurs such as Omphalosauridae (i.e., *Sclerocormus*, see Qiao et al. 2022), *Chaohusaurus*, *Grippia*, and *Utatsusaurus* have much longer, spool-shaped caudals than PMO 245.975. Such caudals are at least as long as high (e.g., McGowan and Motani 2003; Motani 2005; Maxwell and Kear 2013), excluding basal ichthyosaurs from consideration. Phylogenetic analyses picking up on the elongated shape are, e.g., Motani (1999, character 99) and Moon 2019 (characters 171 and 172). *Xinminosaurus*, which in some ways resembles *Cymbyspondylus* (including the high presacral count of ca. 60; Jiang et al. 2008), appears to have tall, laterally flattened midcaudal centra like PMO 245.975. Mixosauridae have autapomorphically very high middle caudals without lateral widening. In addition, no mixosaurs are known that would even come close in size to PMO 245.975. Moving up the tree, *Besanosaurus* caudals are isometric in anteroposterior view except for the posterior caudals (Dal Sasso and Pinna 1996, fig. 13G), leaving the caudals of *Cymbospondylus* as the best match with PMO 245.975.

One might argue that we cannot know the proportions of the animal from which PMO 245.975 derives, but an elongate body with a long tail is the most reasonable assumption. This is because, with a few exceptions (all small-bodied; Mixosauridae, Toretocnemidae, *Qianichthyosaurus*), all Triassic ichthyosaurs outside of Parvipelvia have the elongated body and long, straight tails of anguiliform (eel-like) swimmers, also seen in early cetaceans and scyliorhinid sharks (Motani et al. 1996).

The first centrum after the caudal peak is the forty-first caudal in *C. petrinus* specimen UCMP 9947 (Merriam 1908, fig. 132). UCMP 9947, in a composite with UCMP 9950, is the source of the often-cited length estimate of 9.3 m for *C. petrinus* (Merriam 1908, fig. 128) which we now revise to between > 10 m and 12.5 m (see above; Table 3; Fig. S2). Merriam (1908, table on p. 117) provides the measurements for the forty-first caudal centrum of UCMP 9947 as being 119 mm high and 46 mm long. This compares with a height of ca. 60 mm and a length of ca. 30 mm in the centra of PMO 245.975 (fide Kear et al. 2023). Simple proportional calculations thus would indicate a minimum length of the Svalbard Smithian specimen of 5.04 m based on centrum

height and 6.52 m based on the centrum length, using the 10 m value for *C. petrinus* UCMP 9950/9947 obtained by direct measurements (see above). However, if PMO 245.975 was not located right after the caudal peak but further posterior, the animal would have been larger.

Similarly high estimates of well over 5 m would be obtained if we were to assume the length of the caudal centra in PMO 245.975 was the same as that of the dorsals of the animal and apply our regression equations of dorsal vertebral centrum length vs. total length to PMO 245.975. Since the caudals of PMO 245.975 certainly were shorter and not longer than the dorsals (as in all other ichthyosaurs with tall caudals), this > 5 m-estimate also is an absolute minimum. Based on these considerations regarding the minimum length of PMO 245.975, the Smithian specimen may have been the same size as the Spathian IGPB 660.

Evolutionary implications of early occurrence of large ichthyosaurs

Given the short time span represented by the global record of Olenekian ichthyosaur localities and the difficulty of exact correlation between these localities (Nakajima et al. 2022), our respective size estimates for IGPB R660 and PMO 245.975 suggest that some of the first ichthyosaurs preserved in the fossil record already had reached the size of small whales. This is consistent with the appearance of giant forms such as *C. youngorum* in the middle Anisian, about four to five million years later (Sander et al. 2021). Based on a detailed quantitative analysis using skull length as a proxy, Moon and Stubbs (2020) and Sander et al. (2021) showed that an Early Burst model of size evolution describes this pattern best. Future work should include IGPB R660 in the quantitative analyses of these two studies, but this requires establishing a quantitative relationship between the different ichthyosaur size proxies (skull length, humerus length, and presacral vertebral length) first.

Sander et al. (2021) suggested that the rapid size evolution in ichthyosaurs may be related to the great abundance of small-bodied marine life forms such as ammonoids following the mass extinction at the Permian–Triassic boundary, even though the ecosystem lacked modern primary producers (Sander et al. 2021). A case in point is the recognition that the Omphalosauridae, a clade of putative ammonite specialists, must have been globally distributed based on their presence in all major Northern Hemisphere Early and Middle Triassic marine reptile faunas (Qiao et al. 2022).

Our results would seem to support the notion of an undiscovered pre-Triassic history of ichthyosaurs by Kear et al. (2023) and would appear inconsistent with earlier analysis by Motani et al. (2017) that a Permian divergence

of ichthyosaurs is unlikely. Clearly, the ichthyosaurs of the Early Triassic need further study to understand not only their origin and their rapid body size increase but also the regeneration of ecosystems after major mass extinctions.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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