CellPress

Current Biology
Magazine

Correspondence

Earliest Triassic ichthyosaur fossils push back oceanic reptile origins

Benjamin P. Kear[1,*], Victoria S. Engelschiøn[2], Øyvind Hammer[2], Aubrey J. Roberts[2] and Jørn H. Hurum[2,*]

Reptiles first radiated into oceanic environments after the cataclysmic end-Permian mass extinction (EPME)[1], 251.9 million years (Ma) ago. The geologically oldest fossils evincing this adaptive transition have been recovered from upper-Lower Triassic (lower Spathian) strata, ~248.8 Ma[2], and postdate a landmark turnover of amphibian-dominated to reptile-dominated marine ecosystems spanning the late Smithian crisis (LSC)[3], ~249.6 Ma[4] —less than ~2.3 Ma after the EPME. Here, we report ichthyopterygian (the group including ‘fish-shaped’ ichthyosaurians[1]) remains from the Arctic island of Spitsbergen that predate the LSC in later-middle to early-late Smithian[5] deposits up to ~250 Ma. Unexpectedly, however, their large size and spongy internal bone structure indicate a fully pelagic ichthyopterygian[1,6]. Given this unambiguous occurrence ~2 Ma after the EPME, these pioneering seagoing tetrapods can now be feasibly recast as mass extinction survivors instead of ecological successors[2,3] within the earliest Mesozoic marine predator communities.

The ichthyopterygian fossils (Natural History Museum, University of Oslo [PMO] 245.975) were found in the Lusitaniadalen Member (LM) of the Vikinghøgda Formation[7]. This unit crops out along Flowerdalen (‘Flower’s valley’) on the lowermost slopes of Marmierfjellet (‘Mt Marmier’) in western Spitsbergen (Figure S1). The LM exposures form steep banks that are capped by gently sloping consolidated scree and topsoil with no immediately overlying younger strata. Lithologically, they comprise dark grey laminated shaly mudstone with abundant green-grey calcitic concretions (commonly septarian with baryte)[7] preserving a distinctive marine vertebrate fossil assemblage of temnospondyl amphibians, coelacanths, actinopterygian fishes, and euselachian sharks[3]. Collectively, this faunal horizon is termed the ‘Fish Niveau’[8] and correlates with the middle Smithian *Euflemingites romunderi* zone, as well as the condensed lower-upper Smithian *Wasatchites tardus* zone[5,7]. The LSC immediately preceded the Smithian/Spathian boundary[4], which coincides with a regressive hiatus in sections from Marmierfjellet and in Ledalen on Botneheia, a mountain further to the west[5]. The sequentially overlying Vendomdalen Member (VM) records transgressive deeper water low-oxic conditions[7] and contains extremely fossiliferous faunal horizons. (1) The ‘*Grippia* Niveau’ Bonebed[5] with small and large-bodied ichthyopterygians, basal ichthyosauromorphs (the clade encompassing ichthyopterygians, antecedent ichthyosauriforms and their more distant relatives[9]), presumably aquatic archosaurian reptiles, actinopterygians, and euselachains[3,8,10] that demarcate the lower to middle Spathian *Bajarunia euomphala* and *Parasibirites grambergi* zones[5]. (2) The ‘Lower Saurian Niveau’ with numerous large and small-bodied ichthyopterygians[8], basal ichthyosauromorphs[8], coelacanths, ceratodont lungfish, actinopterygians and euselachains represents the upper Spathian *Keyserlingites subrobustus* zone[5]. Characteristically, the VM shales are interspersed with conspicuous yellow-weathering ferric dolomite beds and concretions, although dark grey (or black in fresh cross-section) calcitic concretions are concentrated near the top of the member and stratigraphically correspond to the ‘Lower Saurian Niveau’[5].

We used X-ray fluorescence (XRF) spectroscopy to geochemically compare the green-grey baryte infested calcitic matrix surrounding PMO 245.975 with both *in-situ* LM concretions collected elsewhere along Flowerdalen, and lithologically analogous VM concretions excavated up-sequence on Marmierfjellet (Figure 1A); thereby eliminating the possibility of down-scree transport. These analyses (Supplemental information) patently grouped PMO 245.975 with LM concretions sampled from the ‘Fish Niveau’, which integrate higher siliciclastic content (Si, Fe, Mn, K, Zr) denoting sandy sediment input[5]. By contrast, those from the ‘Lower Saurian Niveau’ have purer carbonate composition (Ca) and proportionately elevated vanadium (V) indicating decreased oxygenation[5]. This supports the interpretation of increasingly offshore conditions[5,7], as well as our field observation that PMO 245.975 had eroded directly from a restricted outcrop of LM mudstone before being broken up and dispersed by frost weathering.

PMO 245.975 consists of 11 articulated vertebral centra (Figure S2), together with 15 indeterminate bone fragments, perhaps from neural arches, limb and/or limb girdle elements. The centra are diagnostically amphicoelous with perforated notochordal canals and unfused neurocentral sutures[1]. Their articular surfaces are dorsoventrally elongate and hexagonal in outline unlike the cylindrical ‘spool-shaped’ centra of basal ichthyosauriforms[1]. Microtomographic (μCT) scans confirmed that the lateral centrum surfaces lack rib-bearing apophyses and that hemal arch facets are present on the ventral margins (Figure 1B), which is similar to early ichthyopterygian distal caudal vertebrae[10].

At ~60 mm high, ~30 mm long and ~40 mm in maximum width, the centra of PMO 245.975 are substantially larger than those of typical basal ichthyosauriforms[9,10], but are comparable with vertebrae from ‘middle-sized’ ichthyopterygian skeletons of ~3 m body length[1]. Their internal organization is also entirely cancellous incorporating a dense circumferentially oriented trabecular network (Figures 1C) that is compatible with ‘adult’ ichthyosaurian bone microstructure[6] (Figure S2) implying pelagic habits, accelerated growth, and elevated metabolism[1]. Such features are ubiquitous in advanced aquatic tetrapods and suggest that the earliest ichthyopterygian ancestors must have rapidly adapted as oceanic apex predators[1,2]. The new insight from PMO 245.975 is a closer stratigraphic proximity of specialized pelagic

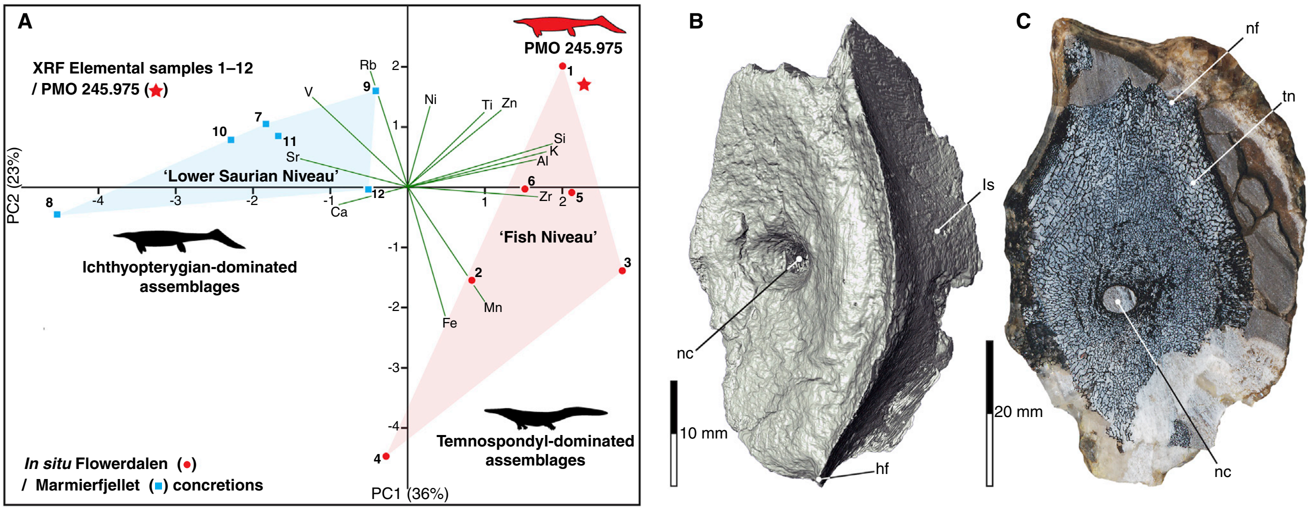

Figure 1. Stratigraphic context and morphology of the earliest ichthyopterygian fossils.
(A) XRF elemental geochemistry of calcitic matrix surrounding PMO 245.975 (red star) and *in situ* concretions from the 'Fish Niveau' along Flowerdalen (red circles) and 'Lower Saurian Niveau' on Marmierfjellet (blue squares). Elemental compositions and information for PMO 245.975 and samples 1–12 are listed on the open-access NIRD Research Data Archive (https://archive.sigma2.no/) under DOI:10.11582/2022.00058. (B) μCT image of a distal caudal centrum from PMO 245.975 in oblique view exposing the lateral surface. (C) Transverse section showing the densely cancellous internal bone structure. Abbreviations: hf, hemal arch facet; ls, lateral centrum surface; nc, notochordal canal; nf, neural arch facet; tn, trabecular network.

ichthyopterygians to the EPME. This recalibrates the traditionally assumed Mesozoic origin, land-to-water transition, and emergent radiation of not only ichthyosauromorphs, but also ichthyosauriforms and ichthyopterygians to both before the LSC[4] and within ~2 Ma of the Permian/Triassic boundary. Mean estimates for the initial ichthyosauromorph-ichthyosauriform divergence timescale range from ~1.7–17.7 Ma based on preferred phylogenetic and stratigraphic priors[2]. Consequently, we propose that these preludial marine reptiles most likely evolved before the EPME, but underwent opportunistic trophic niche diversification and ecological differentiation into shallower water amphibian-dominated versus deeper water ichthyopterygian-dominated habitats during the nascent dispersal of oceanic tetrapods in the earliest Triassic.

SUPPLEMENTAL INFORMATION

Supplemental information includes methods and two figures, which can be found with this article online at https://doi.org/10.1016/j.cub.2022.12.053.

DECLARATION OF INTERESTS

The authors declare no competing interests.

ACKNOWLEDGEMENTS

Financial support was provided by a Swedish Research Council grant (2020-3423) to B.P.K., A.J.R., and J.H.H. Hurtigruten Svalbard, Tullow Oil, National Geographic, and Bayern Gas contributed field exploration funding and logistics to J.H.H. Fossils were collected with a scientific permit (2013/01222-2) from the Governor of Svalbard.

AUTHOR CONTRIBUTIONS

B.P.K. and J.H.H. conceived and designed the study, analysed the data, interpreted the results, and wrote the manuscript. J.H.H., V.S.E., Ø.H., and A.J.R. collected the specimens. V.S.E. and Ø.H. conducted the XRF analysis and interpreted the results. Ø.H. and A.J.R. undertook the μCT scans, segmentation, and rendering. All authors were involved in discussing the results and revising the manuscript.

REFERENCES

1. Nakajima, Y., Shigeta, Y., Houssaye, A., Zakharov, Y.D., Popov, A.M., and Sander, P.M. (2022). Early Triassic ichthyopterygian fossils from the Russian Far East. Sci. Rep. *12*, 5546.
2. Motani, R., Jiang, D.J., Tintori, A., Ji, C., and Huang, J.D. (2017). Pre- versus post-mass extinction divergence of Mesozoic marine reptiles dictated by time-scale dependence of evolutionary rates. Proc. R. Soc. B *284*, 20170241.
3. Scheyer, T.M., Romano, C., Jenks, J., and Bucher, H. (2014). Early Triassic marine biotic recovery: the predators' perspective. PLoS One *9*, e88987.
4. Dai, X., Tuan, Z., Brayard, A., Mingtao, L., Liu, X., Jia, E., Du, Y., Song, H., and Song, H. (2022). Calibrating the late Smithian (Early Triassic) crisis: New insights from the Nanpanjiang Basin, South China. Glob. Planet Change *201*, 103492.
5. Hansen, B.B., Hammer, Ø., and Nakrem, H.A. (2018). Stratigraphy and age of the *Grippia* niveau bonebed, Lower Triassic Vikinghøgda Formation, Spitsbergen. Norw. J. Geol. *98*, 175–187.
6. Houssaye, A., Nakajima, Y., and Sander, P.M. (2018). Structural, functional, and physiological signals in ichthyosaur vertebral centrum microanatomy and histology. Geodiversitas *40*, 161–170.
7. Mørk, A., Elvebakk, G., Forsberg, A.W., Hounslow, M.W., Nakrem, H.A., Vigran, J.O., and Weitschat, W. (1999). The type section of the Vikinghøgda Formation: a new Lower Triassic unit in central and eastern Svalbard. Polar Res. *18*, 51–82.
8. Maxwell, E.E., and Kear, B.P. (2013). Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. GFF *135*, 85–94.
9. Qiao, Y., Liu, J., Wolniewicz, A.S., Iijima, M., Shen, Y., Wintrich, T., Li, Q., and Sander, P.M. (2022). A globally distributed durophagous marine reptile clade supports the rapid recovery of pelagic ecosystems after the Permo-Triassic mass extinction. Commun. Biol. *5*, 1242.
10. Ekeheien, C.P., Delsett, L.L., Roberts, A.J., and Hurum, J.H. (2018). Preliminary report on ichthyopterygian elements from the Early Triassic (Spathian) of Spitsbergen. Norw. J. Geol. *98*, 219–237.

[1]The Museum of Evolution, Uppsala University, Norbyvägen 16, SE-75236 Uppsala, Sweden.
[2]Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway.
*E-mail: benjamin.kear@em.uu.se (B.P.K.); j.h.hurum@nhm.uio.no (J.H.H.)

Supplemental Information:

Earliest Triassic ichthyosaur fossils push back oceanic reptile origins

Benjamin P. Kear, Victoria S. Engelschiøn, Øyvind Hammer, Aubrey J. Roberts, and Jørn H. Hurum

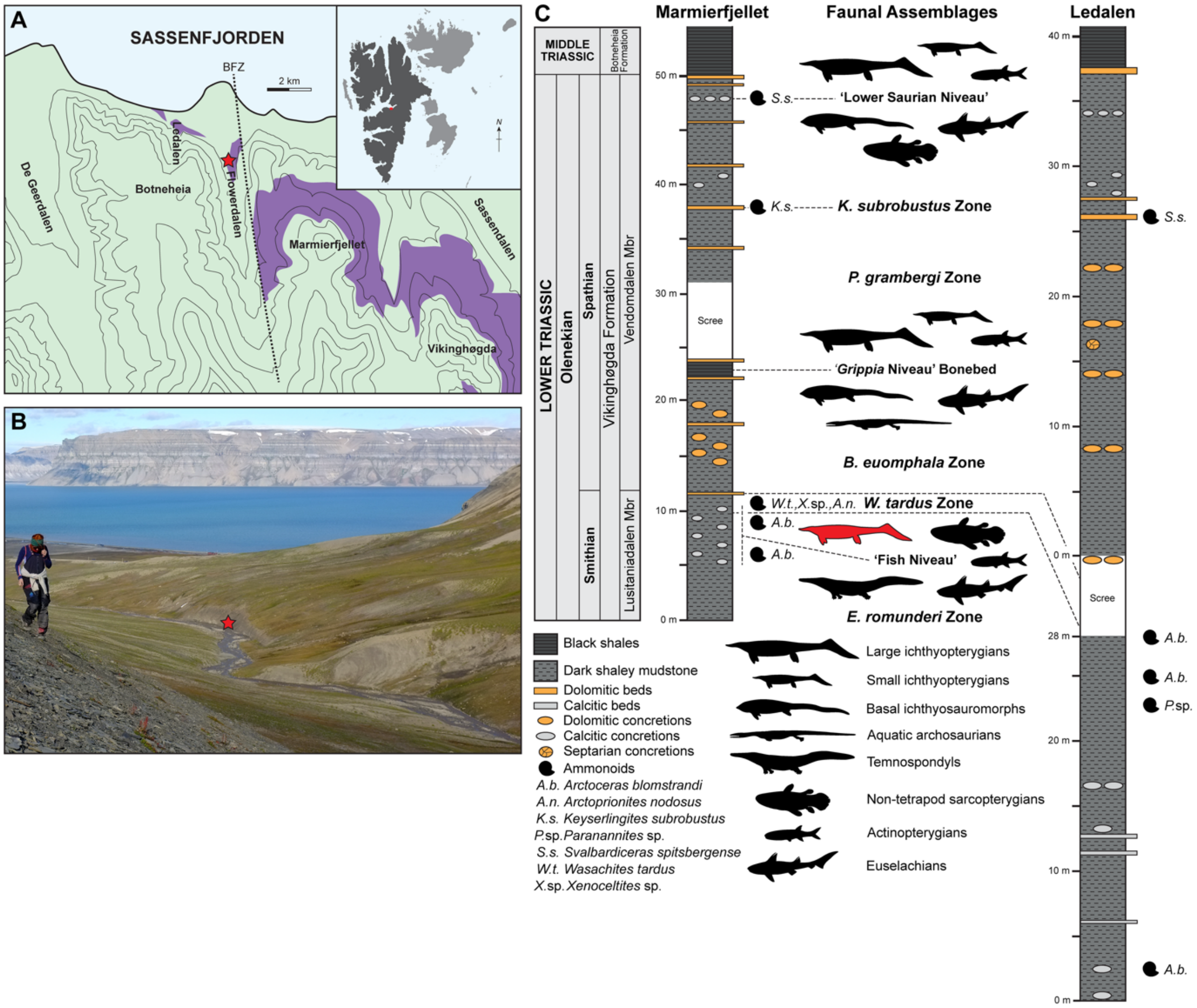

Figure S1. Locality and stratigraphic context of the earliest ichthyopterygian fossils. (A) Topographic diagram[S1,S2] of the Sassenfjorden area (red square) on Spitsbergen (dark grey) in the Svalbard archipelago (top right). Lower Triassic (Smithian–Spathian) Vikinghøgda Formation (VF) outcrops (purple fill) occur in Flowerdalen and Ledalen on Botneheia, as well as across adjacent sections on Marmierfjellet and Vikinghøgda ('Viking Hill') to the east. (B) On-site photograph of the source locality for PMO 245.975 (red star) in Flowerdalen. Northward directional view towards Sassenfjorden with V.S.E shown in the left foreground for perspective. Photograph taken by J.H.H. (C) Detailed stratigraphic logs[S3] of the Lower Triassic (Smithian–Spathian) strata on Marmierfjellet and Ledalen adjacent to the Flowerdalen fossil site. The faunal assemblage succession (black silhouettes) incorporates documented vertebrate groups[S4–S10] and age-diagnostic ammonoid taxa[S3]. PMO 245.975 (red silhouette) derives from the upper-middle to lower-upper Smithian 'Fish Niveau'. Abbreviations: BFZ, Billefjorden Fault Zone.

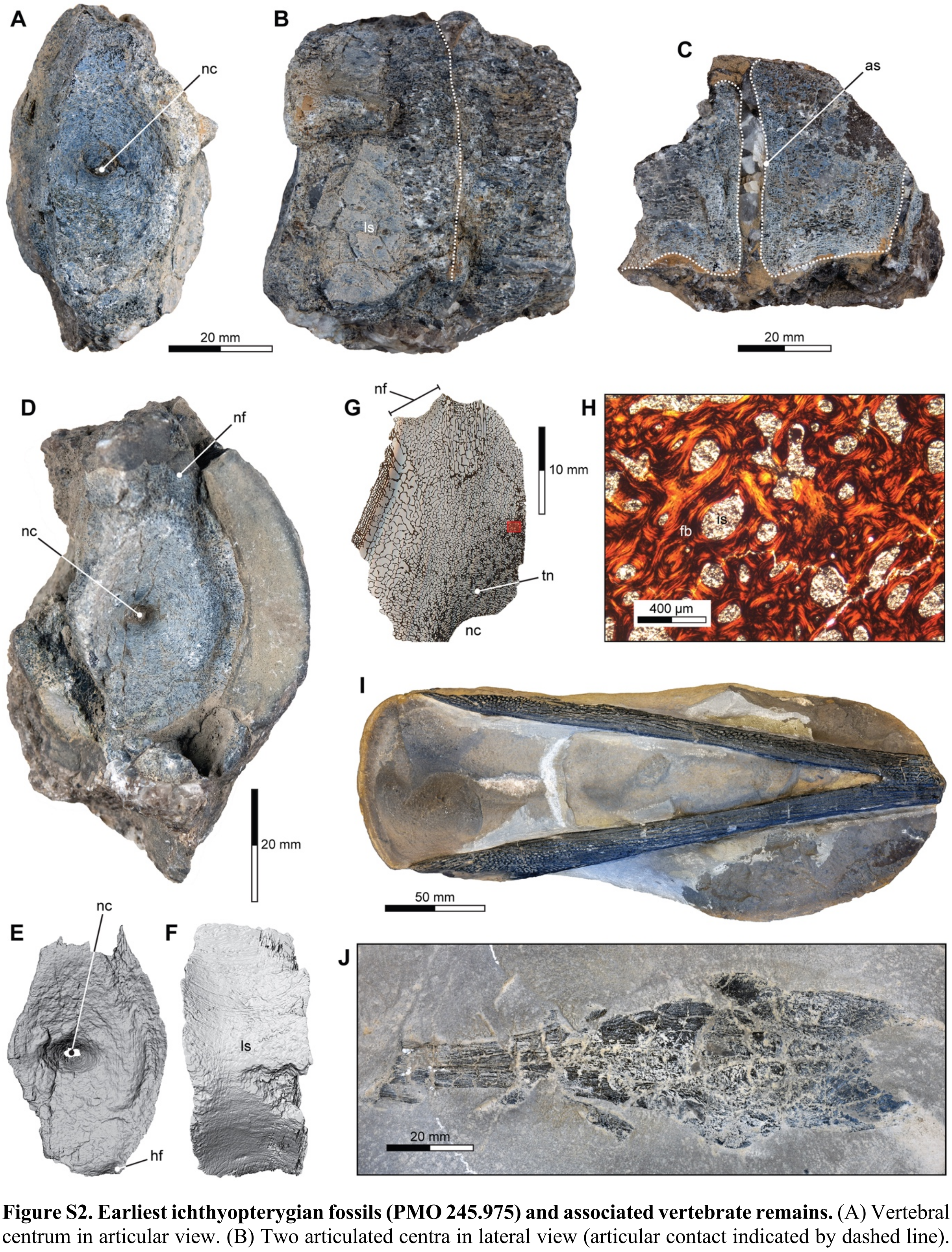

Figure S2. Earliest ichthyopterygian fossils (PMO 245.975) and associated vertebrate remains. (A) Vertebral centrum in articular view. (B) Two articulated centra in lateral view (articular contact indicated by dashed line). (C) Two articulated centra (dashed outlines) in transverse cross-section showing the articular surface contacts. (D) Isolated centrum in articular view with μCT renderings of the (E) articular and (F) lateral surfaces (see Figure 1C). (G) 50 μm transverse thin section (see Figure 1D) illustrating the dense trabecular network (tn) with an enlargement (red square) of (H) the small intertrabecular spaces (is) and diagnostic 'ichthyosaurian-like'[S11] fibrous trabecular bone (fb). (I) Isolated mandible (PMO 246.400) of the trematosaurid temnospondyl amphibian *Aphaneramma rostratum* in ventral view (rostrum to the right). (J) Articulated skull roof (PMO 246.401) of the saurichthyid actinopterygian *Saurichthys* sp. in dorsal view (rostrum to the left). Abbreviations: as, centrum articular surface; hf, hemal arch facet; ls, lateral centrum surface; nc, notochordal canal; nf, neural arch facet.

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Benjamin P. Kear (benjamin.kear@em.uu.se).

Materials availability

All fossil specimens (PMO 245.975, PMO 245.400, PMO 245.401) and carbonate concretion samples (PMO 245.977–PMO 245.981, PMO 234.335, PMO 245.983–PMO 245.987) used in this study are publicly accessible through the Palaeontological Collections at the Natural History Museum, University of Oslo (PMO), Norway (https://www.nhm.uio.no/).

Data and code availability

All data used for analysis is publicly available with this paper as of the date of publication. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Specimen information

PMO 245.975 was recovered during a field expedition undertaken from the 3rd–15th of August 2014. This surveyed Lower Triassic Sassendalen Group strata in Flowerdalen, together with adjacent sections on Marmierfjellet and Botneheia along the southern coast of Sassenfjorden (Figure S1). All requisite permissions including a scientific permit (2013/01222-2) were obtained from the *Governor of Svalbard* (https://www.sysselmesteren.no/). The discovery of PMO 245.975 occurred almost 150 years to the day after the 1864 expedition led by the eminent Swedish geologist Nils Adolf Erik Nordenskiöld, which is credited with finding the first Triassic marine vertebrate fossils documented from Spitsbergen[S1]. Comparisons of PMO 245.975 with documented VF faunal assemblages (Figure 1A) were based on first-hand inspection of specimens housed at PMO and the Palaeontological Collections at The Museum of Evolution, Uppsala University (PMU) in Sweden, as well as the published literature[S4–S10].

X-ray fluorescence spectroscopy (XRF)

Calcitic concretions were collected in-situ from the Lusitaniadalen Member (LM) outcrops in Flowerdalen (PMO 245.977–PMO 245.981, PMO 245.984), and from the Vendomdalen Member (VM) section on Marmierfjellet (PMO 234.335, PMO 245.983, PMO 245.985–PMO 245.987). These samples were washed and then flat pieces of rock selected for analysis using a hand-held *Thermo Scientific* Niton XL3t GOLDD+ XRF instrument with 8 mm aperture. The integration time was set at 120s in the 'Mining Cu/Zn' mode. Other calibrations followed methods detailed elsewhere[S12]. Element concentrations were converted to unit standard deviations and plotted using a Principal Components Analysis (PCA) in *PAST* v.4.11[S13]. All XRF elemental data has been deposited on the open-access NIRD Research Data Archive (https://archive.sigma2.no/) under DOI:10.11582/2022.00058.

Micro-CT (µCT) scanning

An isolated vertebral centrum from PMO 245.975 (Figure S2D) was selected for µCT scanning on a *Nikon* Metrology XT H 225 ST instrument at PMO. Scan parameters utilized 210 kV with 280 µA, and a 1s exposure time. This yielded four images/projection. Voxel size was set at 30 µm. The resulting volume was segmented and rendered using *Avizo* 2020.3 (*ThermoFisher Scientific*). All µCT scan data has been deposited on the NIRD Research Data Archive under DOI:10.11582/2022.00058.

Petrographic thin sectioning

Thin sections were prepared by the Thin Section Workshop & Laboratory at the University of Oslo (https://www.mn.uio.no/geo/english/research/about/infrastructure/facilities/workshops/). One of the more complete vertebral centra from PMO 245.975 (Figure 1D) was cut with a diamond microsaw before being impregnated with *EpoFix* (*Struers*) and attached to a glass sample plate using *CaldoFix* (*Struers*). Polishing was then undertaken on a *Logitech* PM6, a *Buehler Phoenix* 4000, and a *Thorlag* grinding and polishing automat applying increasingly finer grade paper for polishing up to 50 µm. Finally, the thin sections were imaged on a *Leica* DMPL microscope mounted with a *Leica* MC 170 HD camera attachment.

SUPPLEMENTAL REFERENCES

S1. Hurum, J.H., Engelschiøn, V.S., Økland, I., Bratvold, J., Ekeheien, C.P., Roberts, A.J., Delsett, L.L., Hansen, B.B., Mørk, A., Nakrem, H.A., Druckenmiller, P.S., and Hammer, Ø. (2018). The history of exploration and stratigraphy of the Early to Middle Triassic vertebrate-bearing strata of Svalbard (Sassendalen Group, Spitsbergen). Norw. J. Geol. *98*, 165–174.

S2. Dallmann, W.K. ed. (2015). *Geoscience Atlas of Svalbard*. Norwegian Polar Institute, Tromsø.

S3. Hansen, B.B., Hammer, Ø., and Nakrem, H.A. (2018). Stratigraphy and age of the *Grippia* niveau bonebed, Lower Triassic Vikinghøgda Formation, Spitsbergen. Norw. J. Geol. *98*, 175–187.

S4. Maxwell, E.E., and Kear, B.P. (2013). Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. GFF *135*, 85–94.

S5. Ekeheien, C.P., Delsett, L.L., Roberts, A.J., and Hurum, A.H. (2018). Preliminary report on ichthyopterygian elements from the Early Triassic (Spathian) of Spitsbergen. Norw. J. Geol. *98*, 219–237.

S6. Wiman, C. (1910). Ichthyosaurier aus der Trias Spitzbergens. Bull. Geol Instit. Univ. Upsala *10*, 128–148.

S7. Wiman, C. (1914). Über die Stegocephalen aus der Trias Spitzbergens. Bull. Geol Instit. Univ. Upsala *13*, 1–34.

S8. Wiman, C. (1918). Ein Archosaurier aus der Trias Spitzbergens. Bull. Geol Instit. Univ. Upsala *16*, 81–85.

S9. Stensiö, E.A. (1921). *Triassic Fishes from Spitzbergen. Part 1*. Adolf Holzhausen, Vienna.

S10. Nilsson, T. (1943). Über einige postkraniale Skelettreste der triassischen Stegocephalen Spitzbergens. Bull. Geol Instit. Univ. Upsala *30*, 227–272.

S11. Houssaye, A., Nakajima, Y., and Sander, P.M. (2018). Structural, functional, and physiological signals in ichthyosaur vertebral centrum microanatomy and histology. Geodiversitas *40*, 161–170.

S12. Hammer, Ø., Jones, M.T., Schneebeli-Hermann, E., Hansen, B.B., and Bucher, H. (2019). Are Early Triassic extinction events associated with mercury anomalies? A reassessment of the Smithian/Spathian boundary extinction. Earth-Sci. Rev. *195*, 179–190.

S13. Hammer, Ø., Harper, D.A.T., and Ryan, P.D. (2001). PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. *4*(1), 9.