

Vertebral size ratios and the ichthyosaurian vertebral column – a case study based on Late Jurassic fossils from North-East Greenland

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Vertebral centra are some of the most common fossils from ichthyosaurs and thus valuable for understanding these marine reptiles. This study sets out to provide further information on the dimensional ratios of centra and how these might be used to obtain more information about an assemblage of Late Jurassic disarticulated centra found at Kingofjeldet on Kuhn Ø in North-East Greenland in 2017. The centra are used to test whether vertebral ratios (H:W and H:L) can be used to assign disarticulated and possibly weathered centra to a region in the vertebral column. In order to evaluate this, the ratios of the centra from Greenland were compared with those of five articulated and well-known ophthalmosaurid specimens, as well as classical traits based on morphology. Assigning the correct position in the vertebral column from ratios is, however, not straightforward. Firstly, comparing different ichthyosaur taxa gives different possible positions for the disarticulated centra. Secondly, centra from different vertebral regions commonly display similar ratios. Thirdly, ratios are sensitive to alteration by taphonomic processes. The ratios of the centra hints towards an ichthyosaur with a more regionalised vertebral column being present in the Late Jurassic sea of North-East Greenland. Further studies are needed to improve our understanding of the significance of the degree of regionalisation of the vertebral column among ichthyosaurs.

Keywords: Ichthyosaur, vertebrae, ratios, morphology, vertebral regionalisation, Ugpik Ravine Member, Kuhn Ø, Greenland.

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Ichthyosaurs first appeared during the Early Triassic (Olenekian) and existed until the early Late Cretaceous (Cenomanian), becoming one of the most successful groups of Mesozoic marine reptiles (Bardet 1992; Motani 2009; Motani *et al.* 2015; Jiang *et al.* 2016). Derived taxa were the first air-breathing vertebrates to adapt to a fully pelagic lifestyle, by developing fish-shaped bodies with a stiff trunk, a flexible tail with a vertical half-moon-shaped caudal fin and flipper-like front- and hind-limbs (Sander 2000; Buchholtz 2001; Motani 2005; Massare *et al.* 2006). Ichthyosaurs had a global distribution (Fernández & Maxwell 2012; Zammit

2012; Druckenmiller & Maxwell 2013; Delsett *et al.* 2017; Prasad *et al.* 2017). However, material from the world's largest island, Greenland, is scarce, hampering the understanding of palaeobiogeography and taxonomic relationships in northern latitudes (Marzola *et al.* 2018; Delsett & Alsen 2020). Newly described vertebrae from Late Jurassic ichthyosaurs from Kingofjeldet of North-East Greenland might answer these questions, but it has so far not been possible, as the assemblage only comprise vertebral centra (Delsett & Alsen 2020).

The robust vertebral centra are among the most

common fossil remains of ichthyosaurs, as they have a high preservation potential (McGowan & Motani 2003). Therefore, developing an understanding of vertebral centra and their usage in the studies of ichthyosaurs is of great interest and will allow more to be deduced about this group. Previous studies have used vertebral centra and the pattern of their changing dimensions along the vertebral column to describe ichthyosaurs and infer swimming style as well as possible taxonomic, intraspecific and/or ontogenetic variability (Buchholtz 2001; Massare *et al.* 2006; Fischer *et al.* 2012; Zammit *et al.* 2014; Delsett *et al.* 2017; Vakil *et al.* 2020). Many of the studies used relatively complete and articulated specimens, which are quite rare. It is far more common to find vertebrae isolated and/or disarticulated, such as the assemblage from Kingofjeldet, which is the focus in this study. Due to the high occurrence of isolated and/or disarticulated vertebrae, studies on these are also relevant and broadly applicable.

To effectively study the vertebral column of ichthyosaurs, the centra must be appropriately aligned along the vertebral column in their original positions. Normally, disarticulated vertebral centra from ichthyosaurs are assigned a position in the vertebral column (henceforth referred to as PVC) based on their morphology, which varies from region to region (McGowan & Motani 2003). Especially the position and appearance of the rib-facets on the lateral surfaces of the centra are used (Buchholtz 2001; McGowan & Motani 2003; Massare *et al.* 2006). Among many ichthyosaur taxa, the ratios of vertebral centra (dorsoventral height:mediolateral width and height:anteroposterior length) also vary considerably through the vertebral column (Buchholtz 2001). This provides the possibility of using the ratios of disarticulated centra to help assign them PVCs. A method based on vertebral ratios will provide a quantitative method for assigning PVCs and it will help narrowing down the possible PVCs of a disarticulated vertebra. This will especially be of great use when having to assign PVCs to weathered or broken centra, missing their rib facets and other morphological features, or to centra with anomalously positioned rib-facets (e.g., Vakil *et al.* 2020). Correct positioning of such centra will allow for a larger number of centra being used to reconstruct the ichthyosaurian vertebral column and provide further knowledge of anatomy, locomotion and possibly taxonomic, intraspecific and/or ontogenetic variability.

This study uses the disarticulated Kingofjeldet centra as a case study to test and discuss the efficiency of the method of using ratios of ichthyosaur centra to assign PVCs to isolated, disarticulated vertebrae. Furthermore, the ratio method will be compared with

the classical method of using morphological features such as rib-facets. Therefore, this study serves to fill some of the gaps still present in our knowledge of how vertebrae can be used to study ichthyosaurs. The results will also be used to discuss vertebral anatomy and the possible taxonomy of the Kingofjeldet centra, thereby improving our poor understanding of ichthyosaurs from this region.

Geological setting and location

The assemblage of fossil vertebrae studied herein was collected from a stratigraphic level close to the base of the Ugpik Ravine Member (Bernbjerg Formation) on Kingofjeldet, Kuhn Ø, North-East Greenland (Figs 1–2). Kuhn Ø is situated in the northern part of the Wollaston Forland area and the associated Wollaston Forland Basin in North-East Greenland (Fig. 1a; Maync 1947; Surlyk 1977; Alsgaard *et al.* 2003). The Wollaston Forland Basin stretches from Hochstetter Forland in the north to Clavering Ø in the south.

The Wollaston Forland Basin is part of the late Palaeozoic to Mesozoic, East Greenlandic rift-basin complex, which was formed prior to and during the opening of the Atlantic, where Greenland and Norway ended up drifting apart (Surlyk 2003). During the Mesozoic, the area was situated at 45–50°N, at the western margin of a 500 km wide and 2000 km long epicontinental sea between Greenland and Norway (Surlyk 2003). The Wollaston Forland Basin was formed in the Middle Jurassic. Subsidence of the area resulted in marine transgression of the basement rocks (Surlyk 2003). Faulting during the Middle Jurassic to the earliest Cretaceous rifting resulted in the fragmentation of the Wollaston Forland – Kuhn Ø block that was divided into several smaller blocks (Surlyk 2003). Individual blocks rotated with a general dip in a W–SW-direction, forming several half grabens in the area (Alsgaard *et al.* 2003; Surlyk 2003). The whole Wollaston Forland area was covered by the sea from the Middle to Late Jurassic due to repeated transgressions (Surlyk 1977).

On Kuhn Ø, the Middle Jurassic Pelion Formation is resting directly on crystalline basement. The Pelion Formation is overlain by the Payerdal Formation, which is overlain by the Upper Jurassic Bernbjerg Formation. Only the lower sandy and grey mudstone-dominated Ugpik Ravine Member of the latter formation is preserved at the studied locality at Kingofjeldet, where the sedimentary succession is unconformably overlain by plateau basalts (Fig. 1b; Maync 1947). The Ugpik Ravine Member is sand-dominated at the base and becomes upwards progressively more fine-

grained and is dominated by laminated mudstones at the top (Maync 1947; Surlyk 1977). Therefore, the Ugpik Ravine Member represents a transition from the shoreface/shelf sandstone of the underlying Payer Dal Formation to the black, offshore mudstones of the Bernbjerg Formation. The Ugpik Ravine Member is approximately 43 m thick at Kingofjeldet (Maync 1947). At Kingofjeldet, the Ugpik Ravine Member con-

sists of seven sandy, heterolithic coarsening-upward cycles, which are 5–14 m thick, each representing a shallowing upward cycle from an offshore environment to a shoreface environment (Fig. 2; Alsgaard *et al.* 2003). The cycles are separated from each other by transgressive erosion surfaces and sometimes layers of belemnite-breccia (Maync 1947; Alsgaard *et al.* 2003).

The ichthyosaur vertebrae are assumed to be

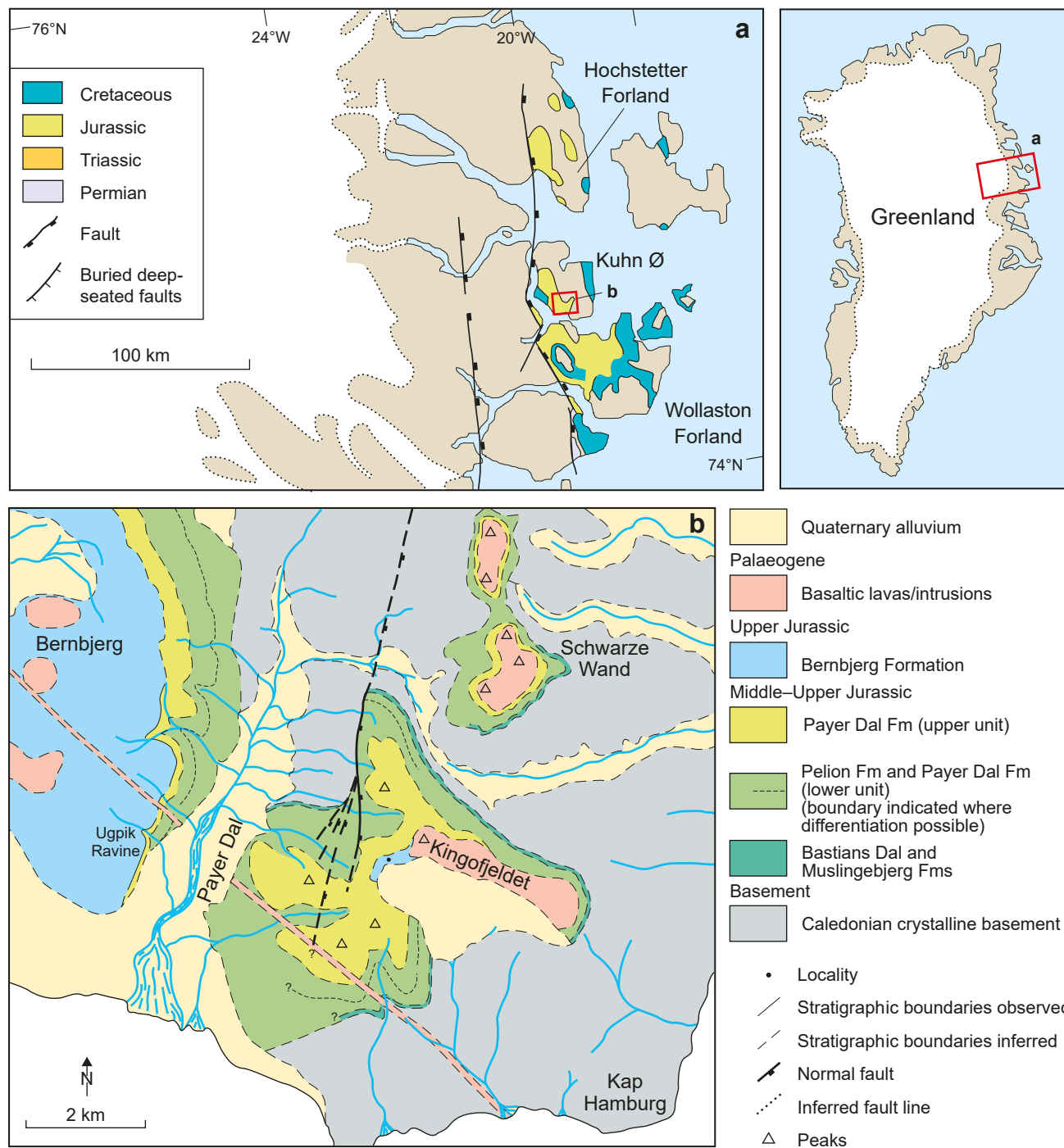


Fig. 1. **a:** Simplified geological map of the Kuhn Ø region in North-East Greenland. **b:** A more detailed geological map of the study area around Kingofjeldet. Modified from Alsgaard *et al.* (2003).

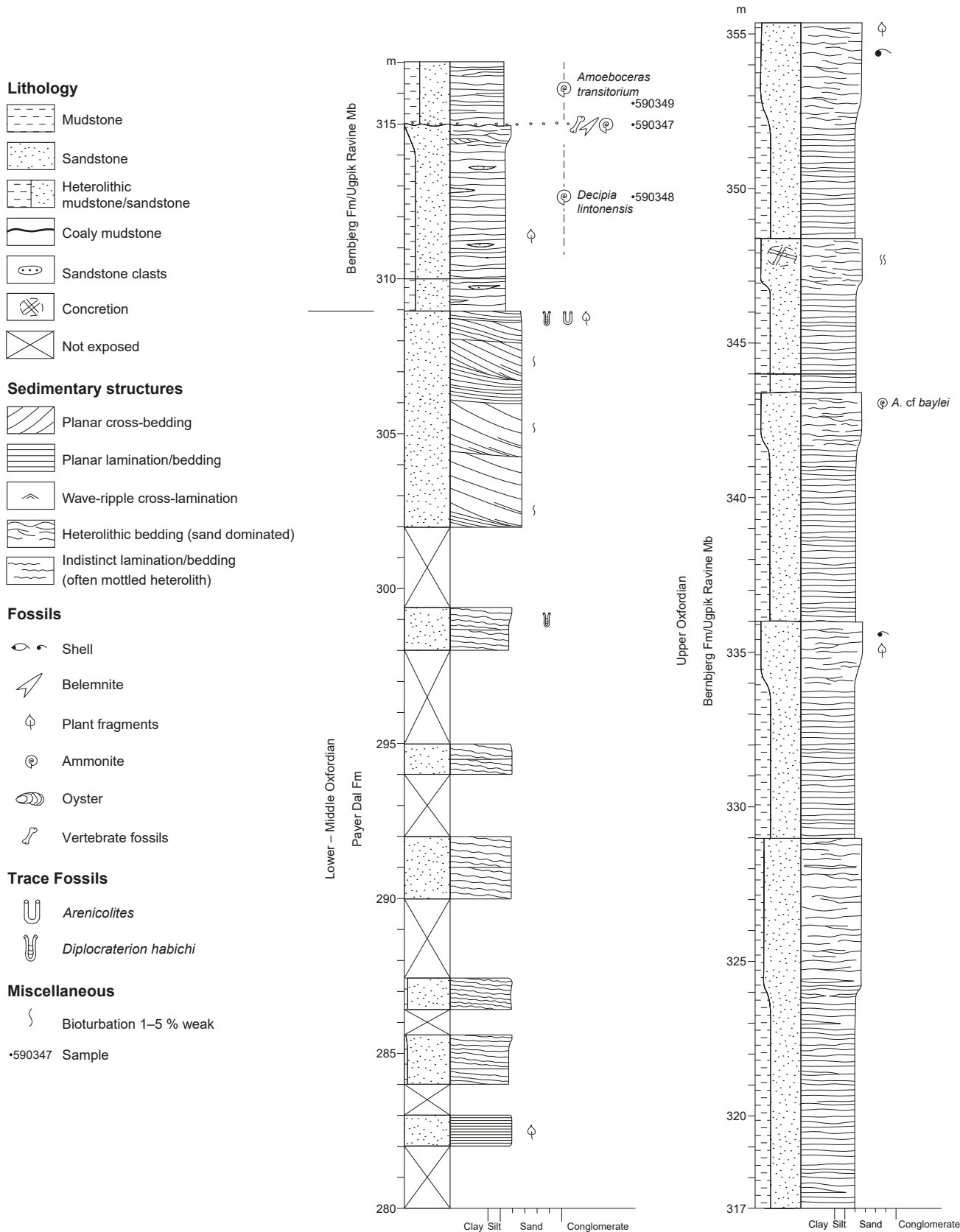


Fig. 2. Sedimentological log of the Payer Dal Formation and Bernbjerg Formation/Uggpik Ravine Member at Kingofjeldet on Kuhn Ø. The stratigraphic level yielding the fossil assemblage (GEUS 590347) is marked. The log was measured by Henrik Vosgerau in 1994.

from one of these shallow-marine, reworked layers (belemnite-breccia), as they were found together with an abundance of belemnites. The age of the fossil assemblage has been estimated to late Oxfordian based on the presence of the ammonites *Decipia lintonensis* (found as an imprint a few metres above the base of the unit) and *Amoeboceras transitorium* (found together with the fossil vertebrae; Delsett & Alsen 2020). These species are indicative of the Ilovaiskii subzone of the Glosense Zone (Callomon & Birkelund 1980).

Materials and methods

The vertebrae described by Delsett & Alsen (2020) were found on a weathered surface at Kingofjeldet on Kuhn Ø, North-East Greenland. They are all assumed to be from the same level in the succession and therefore of the same age (late Oxfordian; Delsett & Alsen 2020). A few of the centra were found embedded in the deposits, whereas most have been exposed to weathering. Several of the centra only consist of smaller frag-

ments, in seven cases successfully pieced together to complete centra. The assemblage was given the sample number GEUS 590347 and the individual centra were given sub-numbers 1–72. However, illustrated fossils will have their repository at the type collections of the Natural History Museum of Denmark (NHMD) and are therefore assigned NHMD numbers as well (Table 1). The centra are referred to as the Kingofjeldet centra.

The aim of this study is to assign a PVC to each of the centra based on their ratios, in order to evaluate whether this is a reliable method. As the Kingofjeldet centra are all disarticulated, their ratios will be compared with those of centra belonging to articulated ichthyosaur specimens, whose ratios and PVCs are known from the literature. Each Kingofjeldet centrum will be tentatively assigned to a PVC, based on their similarity to ratios of the articulated ichthyosaurs. These PVCs will be compared with the PVCs indicated by the morphological features of the Kingofjeldet centra, based on criteria outlined below. Thus, PVCs obtained from morphology are used to evaluate the PVCs obtained from dimensional ratios. Based on previous studies (Buchholtz 2001; McGowan & Motani

Table 1. Measurements, ratios and positions of the Kingofjeldet centra

GEUS no	NHMD no	Height	Width	Dorsal length	Ventral length	Mean length	H:W	H:L	PVC morphology
590347-01	657919	58.45	65.23	29.02	28.56	28.79	0.90	2.03	Cervical
590347-02	608564	46.82	46.40	17.46	18.19	17.83	1.01	2.63	Cervical
590347-03		33.78	34.58	13.46	11.38	12.42	0.98	2.72	Cervical
590347-05		68.03	61.85	28.18	28.33	28.26	1.10	2.41	Cervical
590347-06	608565	46.39	48.28	22.40	19.02	20.71	0.96	2.24	Cervical
590347-07	657920	44.72	46.89	17.16	18.68	17.92	0.95	2.50	Posterior dorsal
590347-08		30.12	32.36	11.85	13.32	12.59	0.93	2.39	Cervical
590347-09		38.56	41.53	13.97	17.26	15.62	0.93	2.47	Cervical
590347-10	657921	50.59	52.00	11.68	13.42	12.55	0.97	4.03	Preflexural caudal
590347-11		46.11	43.20	18.05	17.99	18.02	1.07	2.56	Posterior dorsal/ preflexural caudal
590347-12	657922	44.54	47.04	14.55	15.11	14.83	0.95	3.00	Preflexural caudal
590347-13		29.19	32.98	11.50	12.02	11.76	0.89	2.48	Cervical
590347-14	657923	32.51	38.11	10.19	10.11	10.15	0.85	3.20	Preflexural caudal
590347-15		48.92	47.96	15.31	16.02	15.67	1.02	3.12	Preflexural caudal
590347-16	657924	23.10	35.66	13.92	12.96	13.44	0.65	1.72	Preflexural caudal
590347-17	608566	71.28	75.73	29.50	28.13	28.82	0.94	2.47	Preflexural caudal
590347-18		49.32	52.27	14.60	16.11	15.36	0.94	3.21	Preflexural caudal
590347-19		32.79	32.63	10.47	11.26	10.87	1.00	3.02	Preflexural caudal
590347-20		38.27	44.13	15.50	16.17	15.84	0.87	2.42	Preflexural caudal
590347-21	657925	46.66	52.14	16.73	17.72	17.23	0.89	2.71	Preflexural caudal
590347-22	657926	38.06	39.83	12.91	13.92	13.42	0.96	2.84	Posterior dorsal/ preflexural caudal
590347-23	608567	35.72	42.42	13.23	13.31	13.27	0.84	2.69	Preflexural caudal
590347-24	657927	20.71	18.31		11.72	11.72	1.13	1.77	Postflexural caudal
590347-25		23.63	22.01	12.62	12.25	12.44	1.07	1.90	Postflexural caudal

Measurements are in mm, and the positions in the vertebral column (PVC) are based on morphology.

2003), the morphology of the Kingofjeldet centra are assumed to give a good indication of where in the vertebral column the centra were actually placed, which is referred to as the correct PVC. If the two methods yield the same PVC, it could indicate that ratios are a good indicator of the PVCs of the centra.

Different terminologies have been used to subdivide the ichthyosaurian vertebral column into different regions (Fig. 3; Kirton 1983; Buchholtz 2001; McGowan & Motani 2003). In this study, the vertebral column of ichthyosaurs will be divided into five different regions: cervical, anterior dorsal, posterior dorsal, preflexural caudal (tail stock) and postflexural caudal (fluke; Fig. 3). The two latter regions are often combined into the caudal region. It is not possible to define sharp boundaries between the

different regions, as the transition from one region to another and the change in centrum morphology happen gradually (McGowan & Motani 2003). A method of using the morphology of vertebral centra to assign disarticulated vertebrae to one of the vertebral regions have been well-known for a long time and thoroughly described by for example Buchholtz (2001) and McGowan & Motani (2003). The following criteria for morphology are commonly used:

- Cervical centra: two rib facets (diapophysis and parapophysis) sit dorsally high on each lateral surface with the diapophyses being confluent with the neural arch facets and the parapophyses positioned further ventrally. Some of these centra have a ventral keel, giving them a pentagonal/heart shape in ante-

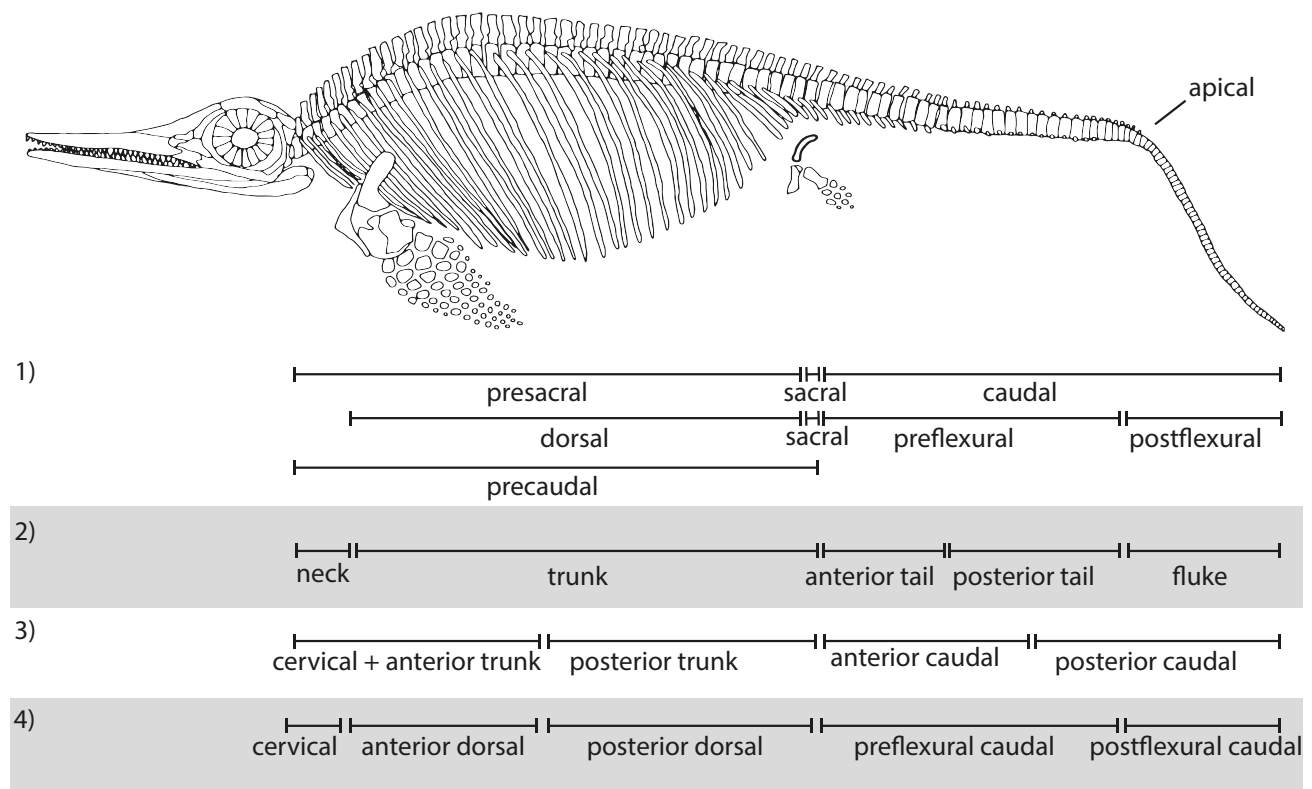


Fig. 3. Summary of the different terminologies used for subdivision of the ichthyosaurian vertebral column. Several of these definitions are sometimes used in other combinations. 1) McGowan & Motani 2003. Presacral vertebrae = from the atlas to the centrum at the distal end of the ilium. Dorsal = presacral vertebrae posterior to the level of the anterior margin of the pectoral girdle. Preflexural = caudal vertebrae anterior to apex of tailbend. Postflexural = posterior to apex of tailbend. Precaudal is used for the combination of presacral and sacral vertebrae. 2) Buchholtz 2001. Trunk = starts at the rapid increase in centrum width and height and includes the sacral vertebrae at the approximate location of the pelvis or where the ribs are rapidly decreasing in length. Anterior tail = the highest and widest centra, nearly round in cross section. Posterior tail = height decreases abruptly into dorsoventrally compressed centra with greater relative length. Fluke = starts at the change into laterally compressed centra. 3) Kirton 1983. No clear separation between cervical and anterior trunk vertebrae. Division between anterior and posterior trunk vertebrae is where the neural arch facet loses contact with the diapophysis. The anteriormost caudal vertebra is the one where the diapophysis and parapophysis merge to form a single rib facet and is associated with a sudden increase in centrum height. Posterior caudal vertebrae are small, slightly laterally compressed. 4) The subdivision of the ichthyosaurian vertebral column used in this study. See main text for explanations of the different regions.

rior and posterior view (Buchholtz 2001; McGowan & Motani 2003).

- Anterior dorsal centra: the rib facets are placed in an increasingly ventral position on the lateral surfaces in more posteriorly placed vertebrae, resulting in the diapophyses losing contact with the neural arch facets and the centra are generally round in anterior and posterior view (Buchholtz 2001; McGowan & Motani 2003).
- Posterior dorsal centra: the rib facets are positioned on the ventral half of the lateral surfaces and the centra are round in anterior and posterior view (Buchholtz 2001; McGowan & Motani 2003).
- Preflexural caudal centra: only one rib facet (apophysis) found on the ventral half of each lateral surface and the centra are very disc-shaped and increasingly dorsoventrally compressed in the posterior part of this region (Buchholtz 2001; McGowan & Motani 2003).
- Postflexural caudal centra: these are positioned posterior to the tail bend and are typically laterally compressed with no rib facets (Buchholtz 2001; McGowan & Motani 2003).

The dimensions of the Kingofjeldet centra were measured with a digital caliper. Width, height as well as dorsal and ventral length were measured for each centrum, if allowed by their preservational state. Centrum width (W) was measured as the maximum mediolateral width without rib facets. Centrum height (H) was measured as the maximum dorsoventral height without diapophyses and neural arch facets. The dorsal length (DL) was measured as the maximum dorsal anteroposterior length and always within the mediolateral extent of the pit of the neural canal. The ventral length (VL) was measured as the maximum ventral anteroposterior length. Mean lengths (L) of the centra were calculated from the dorsal length and ventral length measurements. From the measurements, H:W and H:L ratios were calculated.

In order to assign PVCs, the ratios of the Kingofjeldet centra were compared with the ratios of centra from five well-known Late Jurassic/Cretaceous ichthyosaur specimens, which have larger parts of their vertebral column preserved. As these specimens are more or less articulated, the correct PVCs of their centra are known. *Keilhauia nui* (PMO 222.655) consists of an articulated, partial skeleton with dorsal and preflexural caudal vertebrae preserved (Delsett *et al.* 2017). Zverkov & Prilepskaya (2019) considered *Keilhauia nui* a *nomen dubium*, referring it to *Arthropterygius* instead. The necessary H:W and H:L ratios were provided for five dorsal vertebrae and 20 preflexural caudal vertebrae (Delsett *et al.* 2017). H:W and H:L ratios were read from a plot (Delsett *et al.* 2017, fig.

6) with a margin of error of ± 0.05 . *Ophthalmosaurus icenicus* (PMAG R340) consists of a nearly complete skeleton with 101 vertebrae running continuously from the atlas to the mid of the postflexural caudal region (Buchholtz 2001). The necessary H:W and H:L ratios were provided for nine cervical, 27 dorsal, 36 preflexural caudal and 25 postflexural caudal vertebrae (Buchholtz 2001). H:W and H:L ratios were read from a plot (Buchholtz 2001, fig. 4A) with a margin of error of ± 0.01 . *Ophthalmosaurus natans* (UW 24205 and UW 34786) consists of a composite vertebral column going from the cervical region to the postflexural caudal region (Massare *et al.* 2006). The necessary H, W and L measurements needed for H:W and H:L ratios were provided for \approx nine cervical, \approx 25 dorsal and 34 preflexural caudal vertebrae (Massare *et al.* 2006). H, W and L measurements were read from a plot (Massare *et al.* 2006, fig. 3A) with a margin of error of ± 1 mm. *Platypterygius americanus* (UW 5547) consists of a partially complete skeleton with 65 centra, the anterior dorsal region being partially disarticulated and with some of the mid-dorsal region missing (Maxwell & Kear 2010). The necessary H, W and L measurements needed for H:W and H:L ratios were provided for 16 cervical, 14 dorsal and 35 preflexural caudal vertebrae (Maxwell & Kear 2010). H, W and L measurements were read from a plot (Maxwell & Kear 2010, fig. 3A) with a margin of error of ± 0.5 mm. *Sveltonectes insolitus* (IRSNB R269) consists of a nearly complete skeleton with a discontinuous series of 76 vertebrae (Fischer *et al.* 2011). The necessary H:W and H:L ratios were provided for 23 cervical, 16 dorsal, 22 preflexural caudal and 11 postflexural caudal vertebrae (Fischer *et al.* 2011). H:W and H:L ratios were read from a plot (Fischer *et al.* 2011, fig. 3A) with a margin of error of ± 0.05 . The measurements shown on plots were more precisely read with the described margins of errors by adding additional gridlines to the plots.

Comparisons of ratios with the Kingofjeldet centra were carried out by making bivariate plots of ratios in the statistical software PAST (version 4.03; Hammer *et al.* (2001)). The bivariate plots show the distribution of the centra from the different regions of the vertebral column of the known ichthyosaur specimens based on their ratios (H:W and H:L), together with the ratios of the Kingofjeldet material. Convex hulls in the bivariate plots each represent a vertebral region of the known ichthyosaur specimen and contains all H:W/H:L ratio pairs for the centra of that particular region. For each bivariate plot, a PVC for each Kingofjeldet centrum was assigned based on a qualitative assessment of which region-field its ratios most closely resembled. Close resemblance was considered to be the case if the ratios of a Kingofjeldet centrum were within the convex hull of a certain region. If the ratios of a

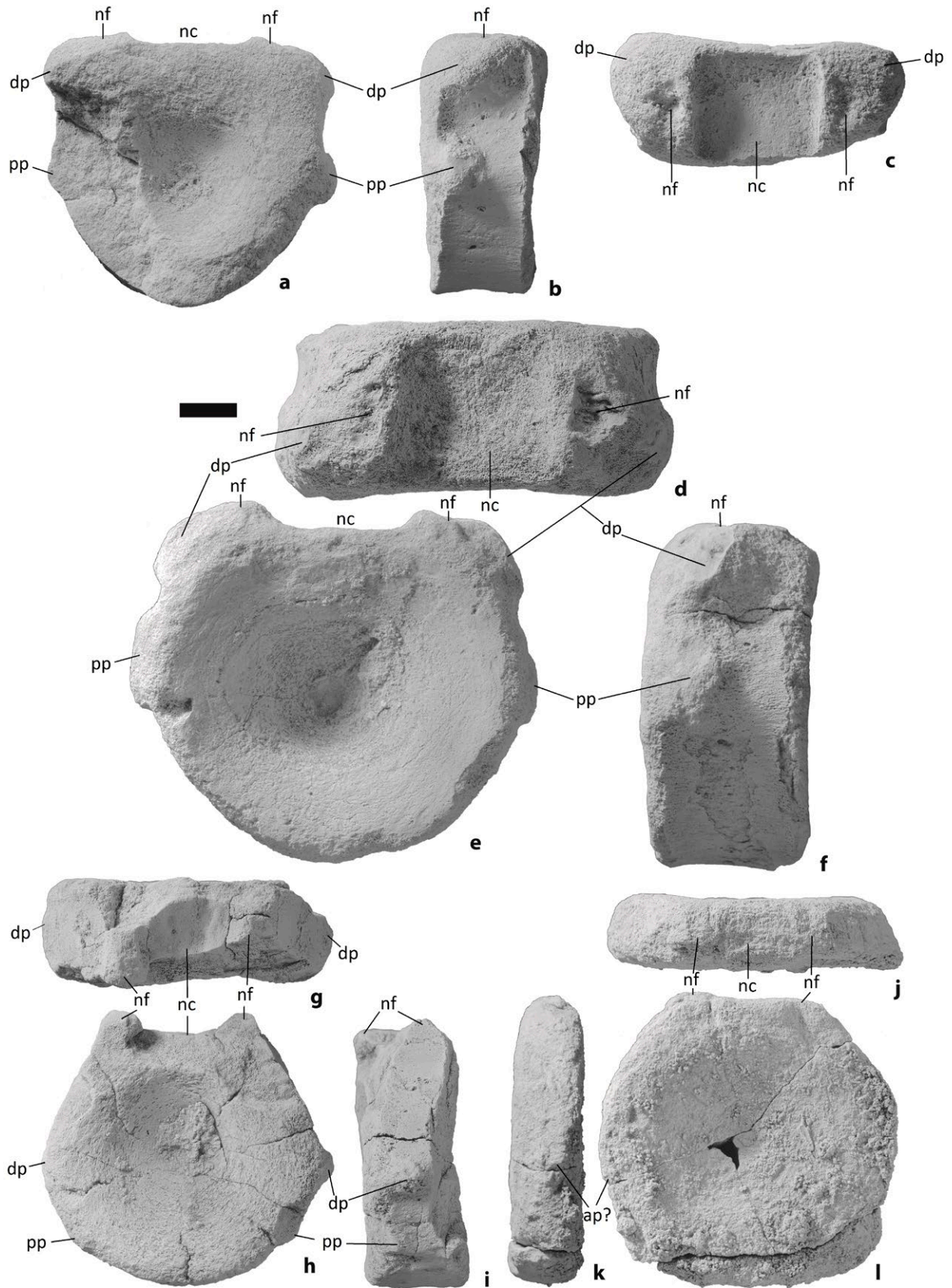


Fig. 4. Selected vertebral centra of GEUS 590347, coated with ammonium chloride. NHMD 608565 (cervical) in anterior (a), left lateral (b) and dorsal (c) view. NHMD 657919 (cervical) in dorsal (d), anterior (e) and left lateral (f) view. NHMD 657920 (posterior dorsal) in dorsal (g), anterior/posterior? (h) and lateral (i) view. NHMD 657921 (preflexural caudal) in dorsal (j), lateral (k) and anterior/posterior? (l) view. Scale bar is 1 cm. ap: apophysis, dp: diapophysis, nf: neural arch facet, nc: neural canal, pp: parapophysis.

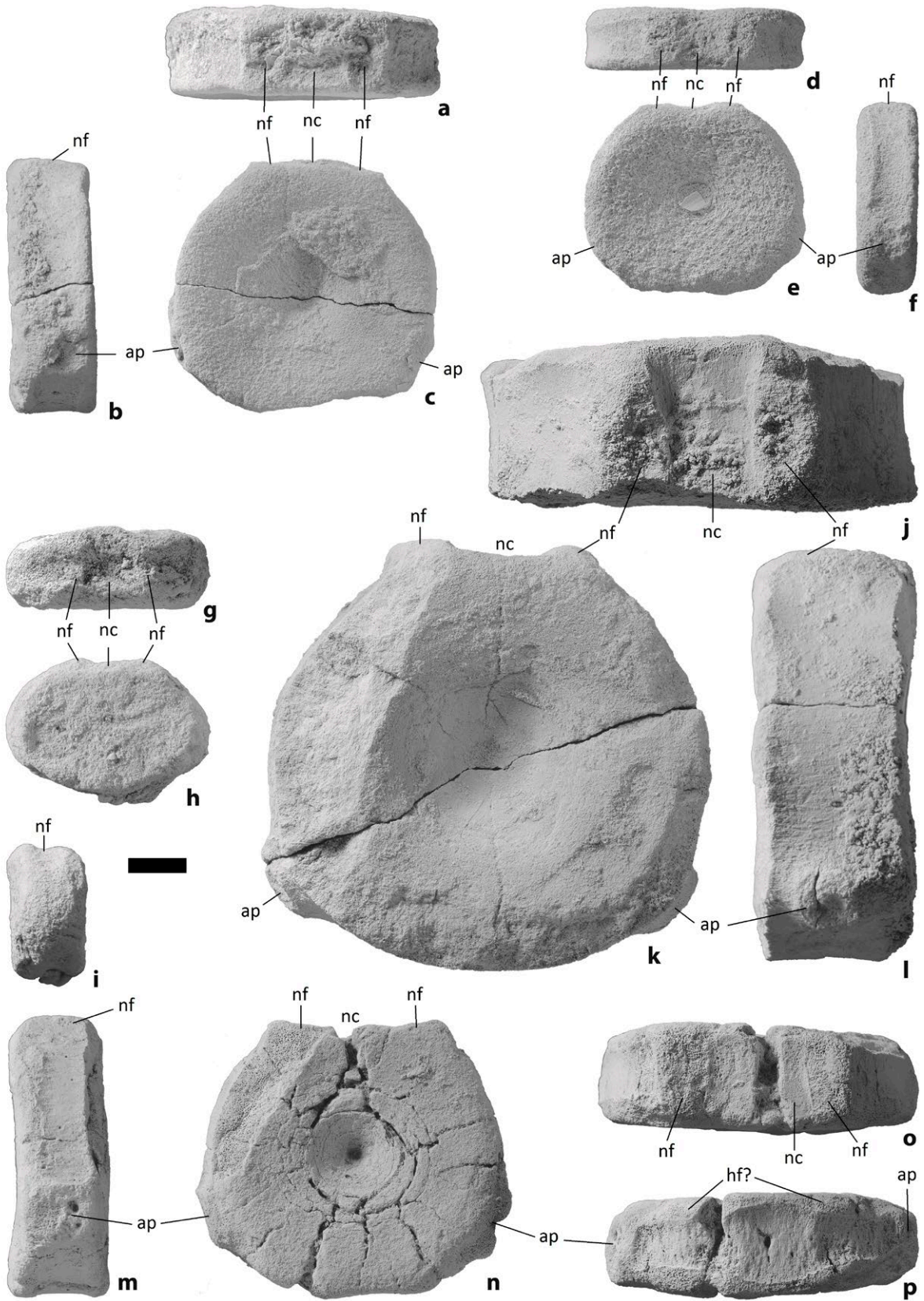


Fig. 5. Selected vertebral centra of GEUS 590347, coated with ammonium chloride. NHMD 657922 (preflexural caudal) in dorsal (a), lateral (b) and anterior/posterior? (c) view. NHMD 657923 (preflexural caudal) in dorsal (d), anterior/posterior? (e) and lateral (f) view. NHMD 657924 (preflexural caudal) in dorsal (g), anterior/posterior? (h) and lateral (i) view. NHMD 608566 (preflexural caudal) in dorsal (j), anterior/posterior? (k) and lateral (l) view. NHMD 657925 (preflexural caudal) in lateral (m), anterior/posterior? (n), dorsal (o) and ventral (p) view. Scale bar: 1 cm. ap: apophysis, hf: haemal arch facet, nf: neural arch facet, nc: neural canal.

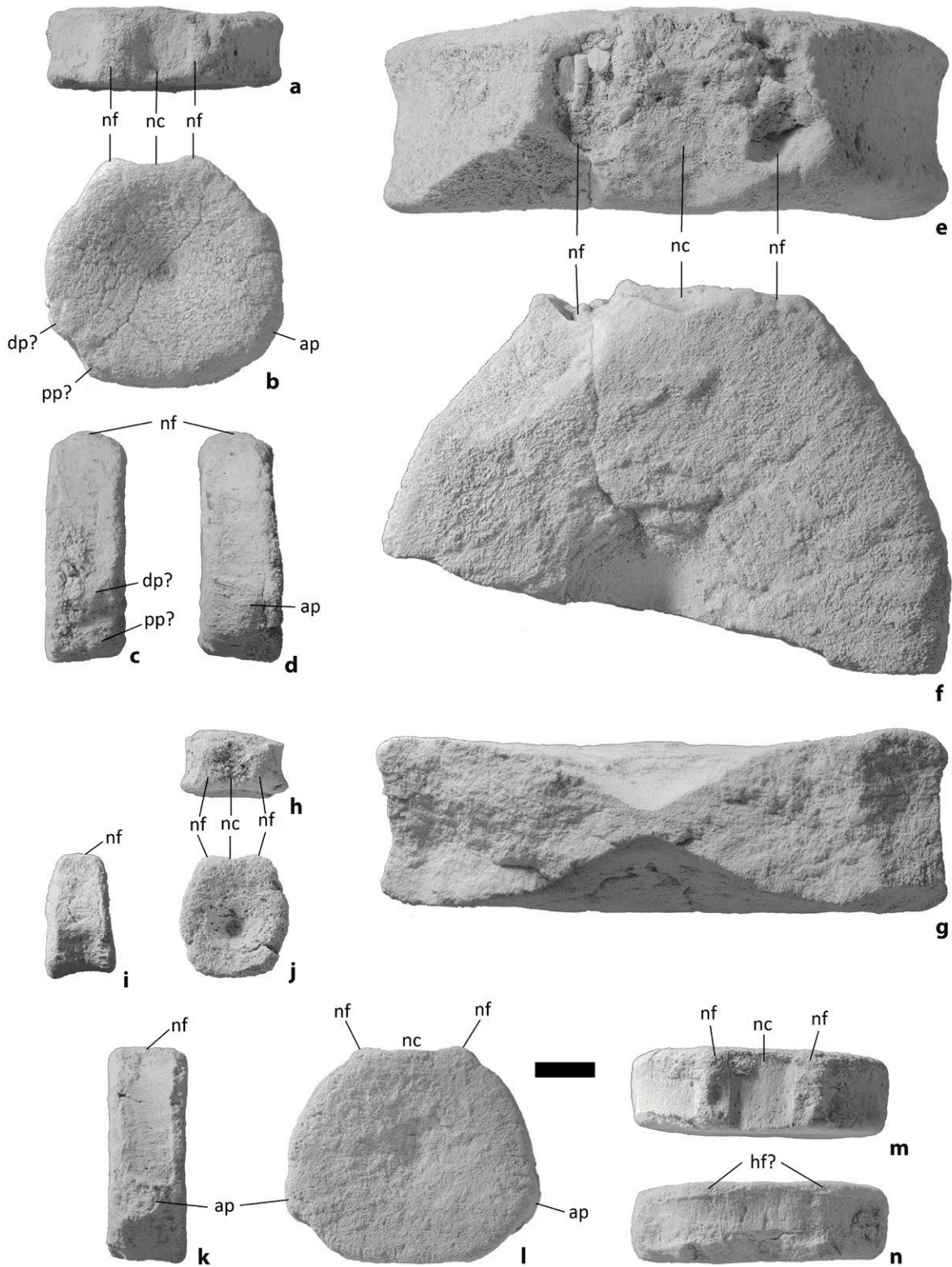


Fig. 6. Selected vertebral centra of GEUS 590347, coated with ammonium chloride. NHMD 657926 (posterior dorsal/preflexural caudal) in dorsal (a), anterior/posterior? (b) and lateral (c–d) view. NHMD 657928 (preflexural caudal) in dorsal (e), anterior/posterior? (f) and ventral (g) view. NHMD 657927 (postflexural caudal) in dorsal (h), lateral (i) and anterior/posterior? (j) view. NHMD 608567 (preflexural caudal) in lateral (k), anterior/posterior? (l), dorsal (m) and ventral (n) view. Scale bar: 1 cm. ap: apophysis, dp: diapophysis, hf: haemal arch facet, nf: neural arch facet, nc: neural canal, pp: parapophysis.

Kingofjeldet centrum were outside the convex hulls of the different regions, comparison of ratios was not possible and no PVC was given based on ratios. When comparing PVCs based on ratios with the PVCs based on morphology, the two PVCs were considered to be in agreement, if they indicated the same vertebral region. The ratios of some of the Kingofjeldet centra were within the convex hull of multiple vertebral regions in the bivariate plots, indicating multiple possible PVCs for these centra. In these cases, the PVC based on ratios was considered inconclusive and could not be matched with the PVC based on morphology.

Results

Description of the fossils

Ichthyosauria indet. (Reptilia: Ichthyopterygia)

Referred specimens. Twenty-five complete and 44 incomplete vertebral centra (GEUS 590347-01–590347-25 and GEUS 590347-31–590347-72). Some of the better-preserved centra are illustrated in Figs 4–6. The referred specimens have previously been described by Delsett & Alsen (2020) who suggested that they represent several ichthyosaur specimens. The vertebrae likely belong to the family Ophthalmosauridae, although the material cannot be referred to this family with certainty because of the lack of skull, flipper and girdle material (Delsett & Alsen 2020). Based on this assumption the Kingofjeldet centra have been compared with centra from other ophthalmosaurids.

Taphonomy. The vertebral centra vary in preservation: some are well preserved, whereas others are weathered, broken into several pieces; and some are incomplete, missing half or more of the centrum. For some vertebrae, one or both neural arch facets have been heavily eroded. This is also the case for some rib facets on the lateral surfaces of some of the centra. Only the complete and nearly complete, three-dimensional centra (GEUS 590347-01 to 590347-25, except 590347-04) are used in the analysis and are in a suitable condition for having their height, width and length measured.

Vertebral region based on morphology. Based on the morphological features of the centra, it was possible with some certainty to assign the 24 most well-preserved specimens to regions of the vertebral column (Table 1; Buchholtz 2001; McGowan & Motani 2003). The vertebrae assigned to the cervical region possess a diapophysis positioned in the dorsal portion on the lateral surface, close to the dorsal surface of the centra. The parapophysis is situated below the diapophysis

in the dorsal half (Buchholtz 2001; McGowan & Motani 2003). In some of the vertebrae, the diapophysis is clearly confluent with the neural arch facet (GEUS 590347-01, -02, -03 and -06, Fig. 4a–f), whereas this is less apparent on others due to weathering and erosion (GEUS 590347-05, -08, -09 and -13). The cervical vertebrae are approximately oval (GEUS 590347-01, -08 and -13, Fig. 4d–f) or almost heart-shaped (GEUS 590347-02, -03, -06 and -09, Fig. 4a–c) in anterior/posterior view, the heart-shape resulting from a ventral keel. The rib facets of these vertebrae tend to lie at/be confluent with the anterior margin of the lateral surface of the centrum. The posterior surface of GEUS 590347-09 is eroded to such a degree that it is no longer concave.

Only one vertebra (GEUS 590347-07, Fig. 4g–i) was confidently assigned to the posterior dorsal region based on the presence of a diapophysis in the middle of the lateral surface and the parapophysis positioned even further ventrally. It is approximately circular in anterior and posterior view (Buchholtz 2001; McGowan & Motani 2003). Due to its circular appearance in anterior and posterior view and the apparent lack of rib facets on the dorsal half of the lateral surfaces, GEUS 590347-11 might also be a posterior dorsal vertebra. Because it is heavily eroded and misses part of one lateral surface, a preflexural caudal position cannot be excluded.

The majority of the Kingofjeldet centra were assigned to the preflexural caudal region, based on the presence of only one apophysis on the ventral half of each lateral surface and the generally circular and disc-shaped appearance in anterior and posterior view, for example GEUS 590347-10, -12 and -17 (Figs 4j–l, 5a–c, 5j–l; Buchholtz 2001; McGowan & Motani 2003). Some of the centra are dorsoventrally compressed, which give them a characteristic ellipse-shaped appearance in anterior and posterior view, for example GEUS 590347-14, -16, -21 and -23 (Figs 5d–i, 5m–p, 6k–n). Some of the preflexural caudal centra (GEUS 590347-12, -16, -19, -21 and -23) have a thick anterior and posterior margin laterally on the ventral surface, which narrows anteroposteriorly in a medial direction, thereby outlining a spindle-shaped depression on the mid-ventral surface (Figs 5p, 6n). This might be haemal arch facets, as also proposed by Prasad *et al.* (2017). GEUS 590347-15 was assigned to the preflexural caudal region, in contrast to its dorsal position suggested by Delsett & Alsen (2020). In contrast to the other centra, GEUS 590347-16 is not biconcave and has a flat anterior and posterior surface, without preserved rib facets, which might be due to erosion (Fig. 5g–i). A larger, but broken preflexural caudal centrum (GEUS 590347-31, Fig. 6e–g), is also identified, without rib facets on the dorsal half. GEUS 590347-22 is identified as a preflexural caudal vertebra. However, it

might also belong to the posterior dorsal region, as one lateral surface seems to have two separate rib facets on the ventral half, whereas the other lateral surface has one elongate rib facet on the ventral half (Fig. 6a–d). The latter is possibly the result from the fusion of the diapophysis and parapophysis.

Two vertebrae (GEUS 590347-24 and -25) were assigned to the postflexural caudal region, based on their mediolaterally compressed shape in anterior

and posterior view and lack of rib facets (Fig. 6h–j; Buchholtz 2001; McGowan & Motani 2003). GEUS 590347-24 is only concave on one side (Fig. 6j), the other is flattened.

Measurements, plots of ratios and positioning of centra

The height, width and length measurements of GEUS 590347-01–590347-25 are shown in Table 1 together

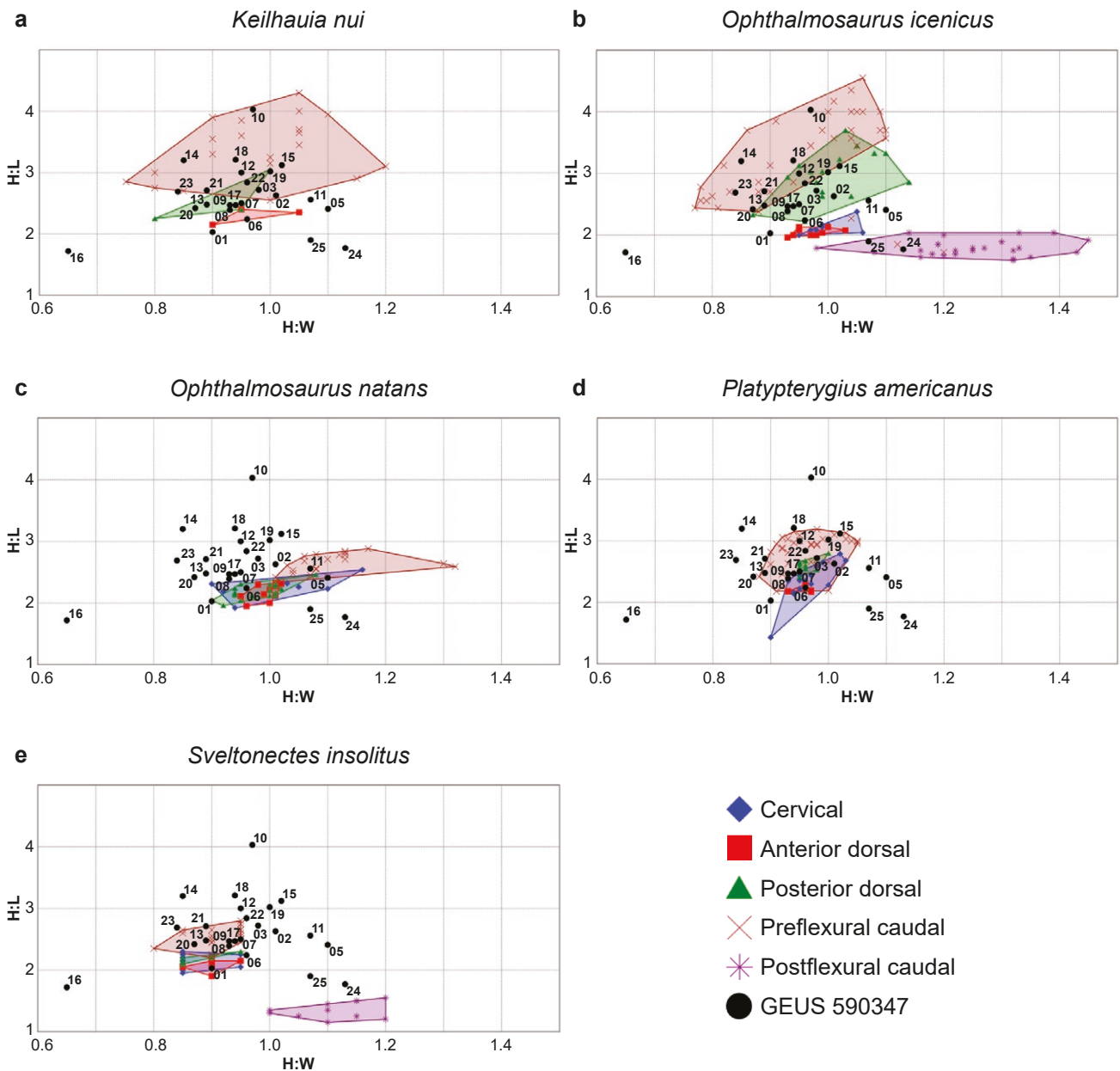


Fig. 7. Bivariate plots for comparison of ratios of vertebral centra from *Keilhauia nui* (a), *Ophthalmosaurus icenicus* (b), *Ophthalmosaurus natans* (c), *Platypterygius americanus* (d) and *Sveltonectes insolitus* (e) with GEUS 590347. The bounded region-areas are based on ratios of vertebral centra from the known ophthalmosaurids. GEUS 590347-01–590347-25 are plotted according to their H:W and H:L ratios and have been assigned positions based on which region-field they lie within on the plots. The plots are based on data from Delsett *et al.* (2017; a), Buchholtz (2001; b), Massare *et al.* (2006; c), Maxwell & Kear (2010; d) and Fischer *et al.* (2011; e).

with the ratios (H:W and H:L). The ratios of the Kingofjeldet centra were compared with those of *K. nui*, *O. icenicus*, *O. natans*, *P. americanus* and *S. insolitus* (Fig. 7). For *O. icenicus*, a few centra plotted far away from the rest of the centra from the same region and were considered anomalous for the respective regions and therefore not included in the bounding of the different vertebral region-fields (Fig. 7b). This included a cervical vertebra, which plotted outside of the displayed ratio-intervals of Fig. 7 and three preflexural caudal vertebrae. For *O. natans*, cervical centra were included in the trunk region in Massare *et al.* (2006). It was therefore uncertain how many centra were in fact cervical centra. By comparison with the vertebral column of *O. icenicus*, which has approximately the same number of vertebrae, it was estimated that the first eight to ten centra in the vertebral column of *O. natans* are cervical centra (Fig. 7c).

The different ophthalmosaurid taxa show different ratios in the different vertebral regions, even though the ratios of the same vertebral regions in the differ-

ent ophthalmosaurids to some extent overlap each other (Fig. 7). The five taxa show different degrees of overlap between the vertebral regions of its own vertebral column (Fig. 7). The vertebral regions of *O. natans*, *P. americanus* and *S. insolitus* exhibit considerable overlap, whereas the vertebral columns of *K. nui* and *O. icenicus* exhibit lesser overlap between regions. The H:L ratios of the vertebral centra of *K. nui* and *O. icenicus* become progressively higher and more extreme compared with the H:L ratios of *O. natans*, *P. americanus* and *S. insolitus* when moving posteriorly from the cervical to the preflexural caudal region (Fig. 7). The plotting of the Kingofjeldet centra show that these centra have dispersed ratios, with values and a distribution more similar to the ratios of *K. nui* and *O. icenicus* than to the ratios of *O. natans*, *P. americanus* and *S. insolitus* (Fig. 7).

The assigned PVC for each Kingofjeldet centrum based on ratios and how it compares to the PVC based on morphology can be seen in Table 2. Comparison of Kingofjeldet centrum ratios with those of *K. nui* and

Table 2. Assigned position in the vertebral column (PVC) for each vertebral centrum of GEUS 590347

GEUS no	NHMD no	<i>Keilhauia nui</i>	<i>Ophthalmosaurus icenicus</i>	<i>Ophthalmosaurus natans</i>	<i>Platypterygius americanus</i>	<i>Sveltonectes insolitus</i>	PVC (morphology)
590347-01	657919	NA	NA	PD	NA	C/AD	C
590347-02	608564	PrC	PD	NA	C/PrC	NA	C
590347-03		PrC	PD	NA	PD/PrC	NA	C
590347-05		NA	NA	C/PrC	NA	NA	C
590347-06	608565	AD	PD	C/PD	C/AD/PrC	NA	C
590347-07	657920	PD	PD	NA	C/PD/PrC	PrC	PD
590347-08		PD	PD	NA	PrC	PrC	C
590347-09		PD	PD	NA	PrC	PrC	C
590347-10	657921	PrC	PrC	NA	NA	NA	PrC
590347-11		NA	NA	PrC	NA	NA	PD/PrC
590347-12	657922	PrC	PD/PrC	NA	PrC	NA	PrC
590347-13		PD	PD/PrC	NA	PrC	PrC	C
590347-14	657923	PrC	PrC	NA	NA	NA	PrC
590347-15		PrC	PD	NA	PrC	NA	PrC
590347-16	657924	NA	NA	NA	NA	NA	PrC
590347-17	608566	PD	PD	NA	PrC	PrC	PrC
590347-18		PrC	PrC	NA	NA	NA	PrC
590347-19		PrC	PD	NA	PrC	NA	PrC
590347-20		PD	PrC	NA	NA	PrC	PrC
590347-21	657925	PrC	PrC	NA	NA	PrC	PrC
590347-22	657926	PD/PrC	PD/PrC	NA	PrC	NA	PD/PrC
590347-23	608567	NA	PrC	NA	NA	NA	PrC
590347-24	657927	NA	PoC	NA	NA	NA	PoC
590347-25		NA	PoC	NA	NA	NA	PoC

Column three to seven show the ratio-based PVCs of each centrum depending on which ophthalmosaurid they were compared with. NA marks cases where the ratios of the centrum in question did not plot within the ratios of the different vertebral regions of the ophthalmosaurid, which it was compared with. The last column shows the PVC of the centra based on their morphology.

Colours: green: PVC based on ratios matches with the PVC based on morphology, blue: PVC based on ratios does not match with the PVC based on morphology. AD: anterior dorsal, C: cervical, PD: posterior dorsal, PoC: postflexural caudal, PrC: preflexural caudal.

O. icenicus gave the highest number of PVCs agreeing with the PVCs based on morphology, which is nine and ten correctly positioned centra respectively. Some of the Kingofjeldet centra were assigned more than one possible PVC for each ophthalmosaurid they were compared with (Table 2). The analysis and bivariate plots show that when multiple PVCs are possible, it is not necessarily two adjacent regions within the vertebral column, but it might also be two non-adjacent regions (Fig. 7; Table 2). For example, four Kingofjeldet centra were assigned to a cervical position and a posterior dorsal or a preflexural caudal position when compared with either *O. natans* or *P. americanus* (Table 2). Cervical, posterior dorsal and preflexural caudal to some degree overlap with each other at lower H:L values (e.g., Fig. 7c–e). The ratio-based PVCs of each Kingofjeldet centrum also show that cervical centra (based on morphology) are often assigned a posterior dorsal or preflexural caudal position based on ratios (Table 2).

Discussion

Ratio-based positioning of the vertebral centra

Comparison with *O. icenicus* gave the highest amount of correctly positioned centra based on vertebral ratios (ten correct PVCs). That the highest amount of correctly positioned centra based on ratios represents just under half of the Kingofjeldet centra suggest that ratios cannot always be used on their own to assign centra to a vertebral region with certainty. Several factors seem to complicate the process of using vertebral centrum ratios to position disarticulated centra within the different regions of the vertebral column.

Firstly, the ratios for a certain vertebral region vary between the different ophthalmosaurid taxa to which the Kingofjeldet centra were compared. This will result in different possible PVCs for a disarticulated centrum, depending on which ophthalmosaurid it is compared with, which influences the analysis of the Kingofjeldet centra. This problem can be solved if comparisons of the ratios of disarticulated centra are restricted to centra from taxa known to have approximately the same degree of regionalisation of the vertebral column. Obviously, comparing with the same species is optimal, but when only looking at a few disarticulated centra, it is close to impossible to know the species and the degree of regionalisation. In addition, even among individuals of the same species, variation in ratios occurs within the same vertebral region, for example observed for *Acamptonectes densus* and *Platypterygius australis* (Fischer *et al.* 2012; Vakil *et al.* 2020). Such variation might represent ontogenetic

stages, sexual dimorphism, intraspecific variation, or differential weathering and/or deformation of the centra.

Secondly, a gradual transition between the different vertebral regions and the lack of a unidirectional change in ratios along the vertebral column means that centra of adjacent and non-adjacent regions may have similar, overlapping ratios. This is clearly seen in Fig. 7 and is also apparent from previous studies of ichthyosaurian vertebral columns (e.g., Buchholtz 2001; McGowan & Motani 2003; Massare *et al.* 2006; Vakil *et al.* 2020). Therefore, a disarticulated centrum may be assigned to multiple regions based on its ratios, as was the case in this study. Some centra were here assigned both to the posterior dorsal and preflexural caudal regions or the cervical, posterior dorsal and/or preflexural caudal regions (Table 2). The postflexural caudal region seems to be the only clearly distinguishable region based on both ratios and morphology of the centra, for example in *O. icenicus* and *S. insolitus* (Fig. 7b, e). GEUS 590347-22 serves as an example on how difficult it can be to mark a sharp boundary between different regions based on ratios but also morphology. GEUS 590347-22 could be part of the transitional area from the posterior dorsal region to the preflexural caudal region, indicated by its ratios when compared with *K. nui* and *O. icenicus* and by its morphology. The distinction between the different regions of the vertebral column based on ratios becomes even less apparent in less regionalised ichthyosaurs. Thus, it may be even more difficult to assign a disarticulated centrum to one specific region based on its ratios when comparing it with less regionalised taxa.

Thirdly, several of the Kingofjeldet centra plotted outside of the defined regions based on the ratios of the five known ophthalmosaurids, which meant that assigning a PVC based on ratios was inconclusive (Fig. 7; Table 2). This might be a result of inadequate data for comparison caused by a relatively sparse set of measured centra from more or less articulated specimens. Inconclusive ratios can also be a result of weathering and/or deformation/compression. Such processes can alter the dimensions and ratios of the centra, causing them to plot differently than they would without being affected by these processes. The Kingofjeldet centra were found in the muddy sandstone deposits of the Ugpik Ravine Member, which might have been subject to some compression. It is common for disarticulated vertebrae to be compressed in an anteroposterior direction (e.g., Delsett *et al.* 2016), causing them to attain higher H:L ratios. Besides causing the centra to plot differently, this might also explain why so many cervical centra were identified as posterior dorsal and preflexural caudal vertebrae based on their ratios. The posterior dorsal region and

especially the preflexural caudal region tend to have higher H:L ratios than the cervical region (Fig. 7). Possible dorsoventral compression could also explain the very low H:W and H:L ratio of GEUS 590347-16, which plots far from all the other Kingofjeldet centra and the centra of the five known ophthalmosaurids.

Biological implications of the vertebral centra

Previous studies have used centrum ratios, their gradual change through the vertebral column and regionalisation as a way to distinguish between different ophthalmosaurid taxa (Massare *et al.* 2006; Maxwell & Kear 2010; Vakil *et al.* 2020). Based on the bivariate plots in this study, it is fairly easy to distinguish the more regionalised ophthalmosaurids from the less regionalised ophthalmosaurids (Fig. 7). *Keilhauia nui* and *O. icenicus* have more strongly regionalised vertebral columns (Buchholtz 2001, fig. 4A; Delsett *et al.* 2017, fig. 5) with more dispersed and less overlapping regions (Fig. 7a–b). A more complete vertebral column of *K. nui* is required to give a more precise estimate of the regionalisation of the vertebral column and the dispersal of regions within a bivariate plot. *Ophthalmosaurus natans*, *P. americanus* and *S. insolitus* show a weaker degree of regionalisation of the vertebral column (Massare *et al.* 2006, fig. 3A; Maxwell & Kear 2010, fig. 3; Fischer *et al.* 2011, fig. 3B) with less dispersed and more overlapping regions (Fig. 7c–e). Changes in H:L ratios and not H:W ratios, seem to cause the greatest variation between the different regions of the vertebral column and between the more regionalised and less regionalised ophthalmosaurids. Vakil *et al.* (2020) showed a similar importance of centrum length and used it to distinguish between different specimens of *P. australis*. H:W ratios only seem to be important in the postflexural region related to the extreme mediolateral compression of vertebrae in this region.

In this study, comparisons with less regionalised ophthalmosaurids (*O. natans*, *P. americanus* and *S. insolitus*) result in more inconclusive PVCs of the Kingofjeldet centra than comparison with the stronger regionalised ophthalmosaurids (*K. nui* and *O. icenicus*; Table 2). This is because the Kingofjeldet centra have ratios that are less similar to those of less regionalised ophthalmosaurids than to those of more regionalised ophthalmosaurids. The ratios of the Kingofjeldet centra show values and a distribution similar to the ratios of *K. nui* and *O. icenicus*. Comparison with these two taxa also resulted in the highest amounts of Kingofjeldet centra being assigned a PVC based on ratios that matched the PVC suggested by morphology (Fig. 7, Table 2). This could indicate that the Kingofjeldet centra are from an ophthalmosaurid with a more regionalised vertebral column, bearing in mind that the Kingofjeldet centra might have been subjected to

taphonomic processes. As mentioned earlier, this could have slightly altered their ratios through weathering and deformation, causing some centra (e.g., GEUS 590347-10) to appear more like those from more regionalised ichthyosaurs than is the case.

Despite the clear difference between more regionalised and less regionalised ophthalmosaurids in the bivariate plots, regionalisation does not seem to bear any taxonomic signal, at least not above species level. This is indicated by the similarities between the plots of *K. nui* and *O. icenicus* (Fig. 7a–b) and the similarities between the plots of *O. natans*, *P. americanus* and *S. insolitus* (Fig. 7c–e), the only exception being the preflexural caudal region of *O. natans*. These similarities are probably a consequence of regionalisation being an adaptive trait associated with locomotion and preferred swimming style (Buchholtz 2001) and is therefore a character affected by homoplasy (Paparella *et al.* 2017).

Generally, the taxonomic value of isolated centra have been questioned (McGowan & Motani 2003; Zammit 2010). However, it is worth noting that the ratios of the Kingofjeldet centra resemble those of *O. icenicus*. Only four centra are outside the range of the ratios of *O. icenicus* (Fig. 7b) and ten out of 24 centra were correctly positioned when compared with *O. icenicus* (Table 2). The morphology of the Kingofjeldet centra also have a certain resemblance to the vertebral centra of *O. icenicus* (Moon & Kirton 2016). This is especially the case for GEUS 590347-02, -06, -12, -14, -17, -21 and -23.

Conclusion

The ratios of 24 disarticulated vertebral centra from Uggvik Ravine Member, Greenland, were compared with those of five different ophthalmosaurids and based on this the centra were assigned positions in the vertebral column (PVCs). Multiple factors complicated the assigning of the correct PVCs to the centra when only ratios were considered. Firstly, it is uncertain which ophthalmosaurid is most suitable for the comparison. Comparison with arbitrary ophthalmosaurids in this study often resulted in inconclusive PVCs. Secondly, it is possible to obtain multiple different PVCs for a centrum due to weak regionalisation of the vertebral column and/or due to gradual transitions and a lack of a unidirectional change in ratios from one vertebral region to another. Thirdly, the method is sensitive to taphonomic alterations of the ratios through weathering and/or compaction, potentially causing centra to attain anomalous ratios or ratios resembling that of centra from other vertebral regions. Postflexural caudal centra were the only centra with

ratios clearly separating them from the other regions. A prerequisite for assigning PVCs to disarticulated centra based on their ratios, is that they belong to an ichthyosaur with a relatively regionalised vertebral column, which seems to be the case for the Kingofjeldet centra, bearing in mind potential diagenetic alterations of ratios. If the vertebral column is only weakly regionalised, it becomes difficult to place the centra and it will be more precise to use morphology. In conclusion, effective positioning of centra based on their ratios requires strongly regionalised vertebral columns where the ratios of the different regions can be clearly distinguished from each other. However, the studied ophthalmosaurids show that this is rarely the case. Yet, the pattern and difference in overlap of vertebral regions in the bivariate plots for more regionalised columns and less regionalised columns is interesting to note. More studies into these differences might help to better distinguish between more regionalised ichthyosaurs and less regionalised ones and improve our understanding of their different adaptive traits and the related locomotory importance.

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