

A highly articulated Early Jurassic ichthyosaur, *Stenopterygius*, from the historical collection of the Jagiellonian University, Poland

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The Posidonia Shale Formation is one of the best-known examples of fossil Konservat-Lagerstätten in the world. One of the most characteristic taxa from this formation is the genus *Stenopterygius*, a medium-sized thunnosaurian ichthyosaur represented by numerous specimens which are very often articulated, featuring specimens exhibiting life activities such as live-birth or with preserved soft tissues. Herein, we describe an extremely well-preserved skeleton of *Stenopterygius quadriscissus* CEP-DG-7264-N, housed at the Nature Education Centre of the Jagiellonian University (NEC Kraków, Poland) and its remarkable story, which ultimately led this fossil to become the centrepiece of the NEC collection. The specimen, based on analysis of observed taphonomic distortions, is inferred to have landed post-mortem rostrum first onto the seafloor, causing a snout fracture and spine distortion. Associated belemnites (preserved as rostra) have been interpreted as possible gastrointestinal content, which has probably been displaced around the individual due to the expanding volume of gas buildup.

Key words: Ichthyosauria, *Stenopterygius*, Posidonia Shale, Early Jurassic, taphonomy, 3D scanning.

INTRODUCTION

Ichthyosaurs (Ichthyosauria) were Mesozoic marine reptiles that displayed an extreme degree of adaptation to a secondarily marine lifestyle (De Buffrenil and Mazin, 1990; Motani, 2005; Bernard et al., 2010; Maxwell, 2012; Houssaye et al., 2014). The Ichthyopterygia clade, which includes the Ichthyosauria, occupied predatory niches throughout most of the Mesozoic (Anderson et al., 2019). One of the best preserved and most

common ichthyosaur taxa in the fossil record is *Stenopterygius*, a medium-sized thunnosaurian represented by numerous specimens (e.g., Urlichs et al., 1979; Dick, 2015; Maxwell et al., 2022), which are very commonly complete and articulated, often featuring individuals captured during their life activities such as live birth or feeding (van Loon, 2013), or preserving soft tissues (Lindgren et al., 2018), which are exceptional phenomena when it comes to fossils of large vertebrates.

The genus *Stenopterygius* is exceptionally well studied (e.g., Quenstedt, 1856; Jaekel, 1904; von Huene, 1922, 1931, 1939, 1949; McGowan, 1979; Godefroit, 1994; Maisch, 1998, 2008; McGowan and Motani, 2003; Maxwell, 2012; Maxwell et al., 2012, 2022; Dick, 2015; Dick and Maxwell, 2015a, b; Maxwell and Vincent, 2015; Anderson et al., 2019; Miedema and Maxwell, 2022) due to the availability of several thousand excellently preserved specimens (Sander, 2000; Maxwell, 2012). The first modern attempts at understanding the alpha taxonomy of the representatives of the genus were conducted

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by von Huene (1922, 1931, 1939, 1949) followed by McGowan (1979) and McGowan and Motani (2003), Godefroit (1994) and Maisch (1998, 2008). The most recent classification scheme by Maxwell (2012) recognized three species of *Stenopterygius*: *S. quadriscissus* Quenstedt, 1856, *S. triscissus* Quenstedt, 1856, and *S. uniter* von Huene, 1931, which commonly occur in the Toarcian of western Europe. Later that year, another species was recognized (Maxwell et al., 2012) – *S. aalensis* – which, however, comes from the Aalenian of the Opalinuston Formation. As such, we base our classification mainly on the anatomical characteristics pointed by Maxwell (2012).

In this article, we explore the remarkable story of preservation of the CEP-DG-7264-N specimen of *Stenopterygius quadriscissus* in the Nature Education Centre of the Jagiellonian University (NEC Kraków, Poland) through the meanders of history, and provide a description of the anatomical details and taphonomy of this articulated skeleton.

GEOLOGICAL SETTING

CEP-DG-7264-N was excavated from the Toarcian Posidonia Shale of Bad Boll (Fig. 1, 48°38'22"N 9°36'56"E), Baden-Württemberg (south-west Germany). Its date of discovery is unknown, but it had to precede 1850/1851 (the date of acquisition of the specimen by the Jagiellonian University). The Posidonia Shale is developed as an black oil shale, on average 5–15 m thick (Ulrichs, 1977; Riegraf et al., 1984; Röhl et al., 2001), intercalated with limestone horizons, that crops out in the region of the Swabian Jura (Röhl et al., 2001; Muscente et al., 2023). The Swabian Jura has been famously subdivided into 3 lithostratigraphic units by Buch (1839) – the 'Schwarzer Jura' (which covers the Posidonia Shale), the 'Brauner Jura', and the 'Weißer Jura' ('Black Jurassic' Lower; 'Brown Jurassic' Middle; and 'White Jurassic' Upper, respectively; Muscente et al., 2023). The stratigraphy of the Posidonia Shale, also termed Lias Epsilon, has been extensively studied (Maxwell, 2012). The formation is subdivided into three divisions, corresponding to ammonite zones: ϵ I – *Dactyloceras tenuicostatum* zone, ϵ II –

D. tenuicostatum and *Harpoceras falciferum*, and ϵ III – *Hildoceras bifrons* (Riegraf et al., 1984; Röhl et al., 2001; Maxwell, 2012). Vertebrate fossils are common throughout, but the ϵ II zone is the most prolific level (Maxwell, 2012).

The Posidonia Shale is one of the best-known examples of fossil Konservat-Lagerstätten in the world and a model formation for exceptional preservation conditions (Seilacher et al., 1985; Muscente et al., 2023). The Posidonia Shale spreads throughout south-west and north-east Germany, northern Switzerland, north-west Austria, southern Luxembourg, and the Netherlands (Muscente et al., 2023), featuring a wealth of exceptionally preserved fossil fauna, including numerous marine reptiles. The Posidonia shales, which formed under anoxic conditions during the Toarcian Oceanic Anoxic Event (Jenkyns, 1985, 1988, 2010; Schmid-Röhl, et al., 2002; Montero-Serrano et al., 2015; Muscente et al., 2023), include an preserved ancient fauna with exquisite detail. Those articulated structural fossils occasionally feature soft-tissue elements (e.g., Přikryl et al., 2012; van Loon, 2013; Lindgren et al., 2018; Jenny et al., 2019; Eriksson et al., 2022) providing an unusual insight into the palaeobiology of extinct organisms. The so-called 'deadfall communities' of fossils from the Posidonia Shale, which conserve biota associated with fallen large vertebrates, similar in nature to deadfalls of modern-day whales, are of particular interest to palaeontologists (Maxwell et al., 2022), because their preservation enables detailed studies of the taphonomic mechanisms to which the carcasses of both vertebrates and invertebrates are subject.

HISTORICAL BACKGROUND OF CEP-DG-7264-N

CEP-DG-7264-N (historically labelled *Ichthyosaurus communis*) was bought in 1850/1851 by the Jagiellonian University in Kraków, Poland (JU), Faculty of Mineralogy, Department of Natural Science (Collegium Phisicum, then located at 6 Św. Anny St., Kraków) and subsequently given the catalogue number 825, without information of from whom or at what cost the fossil was bought.

The first account of this specimen, along with specimen CEP-DG-775 (*Seiocrinus subangularis* plate figured by Kajdas et al., 2023) was by Alth (1864). While the specimen was bought by the Department of Mineralogy, after the Departments of Geology and Palaeontology were separated from it, the fossil became property of one of the new departments and at some point moved there (no information on this is available in historical documents). It was mentioned twice by Alth (1864) that the housing conditions of the specimen were suboptimal at best. Later, another mention of the specimen appeared in Szajnocha (1926), who noted that the slab was placed on the wall of the 6 Św. Anny St. staircase.

There is no exact record of the placement of the specimen between the years 1925 and 1975. Most peculiarly, during the long history of housing the specimen in the Collegium Phisicum building of the JU, it was covered in dark paint. There is no historical record of who painted the specimen with paint and why. A possible explanation is that this was an attempt to pass off the valuable specimen as a cast to hide it from invaders of the occupation forces during World War II, who would gladly acquire such a treasure. Another scenario, now considered to be the most likely, was that the specimen would look more aesthetically pleasing with a uniform cover of dark paint. There is also a possibility that the paint was applied as a conservation technique, as the bad housing conditions would have caused the weathering of the rock. The coat of paint hid the original

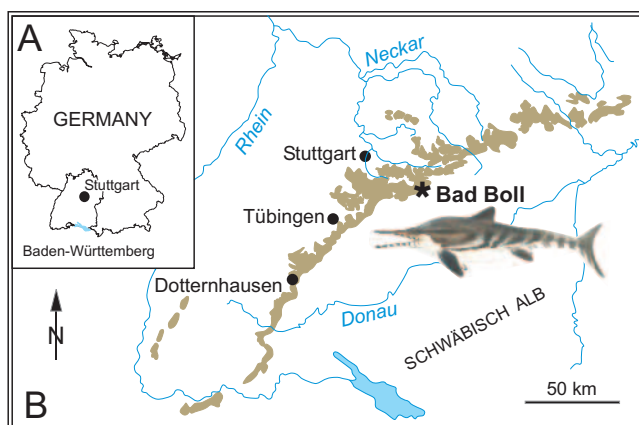


Fig. 1. Location of the site where CEP-DG-7264-N was found, and geological sketch map of south-west Germany

A – map of Germany with Baden-Württemberg land highlighted; **B** – location of find site – Bad Boll with highlighted outcrops of Posidonia Shale (coloured brown); redrawn and modified from Cooper and Maxwell (2023) and Cooper et al. (2024)

palaeontological specimen so well that with time its true nature was forgotten and the ichthyosaur skeleton was eventually assumed to be a mere plaster cast or a sculpture.

After 1951, the Faculties of Geology, Mineralogy, and Palaeontology were moved from the JU to the AGH University of Science and Technology in Kraków, Poland (AGH UST), but during the first six years, the faculties were still placed at 6 Św. Anny St. In 1957, the geological sciences returned to the JU. The Ministry abolished the Faculty of Physical Geology of the AGH UST and the Department of Geochemistry at the Faculty of Mineralogy and Petrography of the AGH UST. In their place, the new Faculty of Geology and Faculty of Mineralogy and Petrography were established at the JU, with both departments retaining their previous locations. However, the Faculty of Palaeontology was relocated, likely with the collections, to the AGH UST buildings. There are no records of the fossil's location during this period. The Department of Palaeontology at the Faculty of Geology of the JU would only be established in 1958.

The faculties were moved once again in 1962 to a new building of the Collegium Geologicum located at 2a Oleandry St. on the second campus of the JU. The new building housed the Faculty of Geology and the Faculty of Mineralogy and Petrography, both of which had been moved from the AGH UST. The Faculty of Palaeontology never returned to the JU, and in its place the Faculty of Paleozoology was formed, with Stanisław Geroch as the head (Morycowa et al., 1997).

It was not until 9 years after the move to 2a Oleandry St. that the collections from the Collegium Phisicum began to be unpacked in the new JU Geological Museum (Prochazka, 1980). In 1975, the ichthyosaur specimen, along the original *Seiocrinus* plate and four plaster casts of reptile tracks and marine reptile skeletons, was included in the collection '20P – Oryginały i odlewy liliowców, gadów i ślady stóp gadów' ('20P – Originals and casts of crinoids, reptiles, and reptilian tracks'). At the same time, the specimens from the 20P collection, once again covered with another layer of black paint (Fig. 2), were hung on the walls of the Collegium Geologicum staircase. At this point, black engraved plates with taxonomic identification and acquisition sites were placed on the specimens. CEP-DG-7264-N remained hanging on the staircase wall until the end of 2016.

By early 2017, the Institute of Geological Sciences of Jagiellonian University (ING JU) had once again changed its location from 2a Oleandry St. to 3a Gronostajowa St., which is a part of the '600th Anniversary Campus' of JU. Some of the casts and original specimens from the ING JU collection had been planned to be moved to the new building, but due to a lack of sufficient space, specimens were placed in the adjacent Nature Education Centre of Jagiellonian University in Kraków, Poland (NEC) in the museum collection, by agreement with Mariusz Kędzierski, the head of the ING JU.

Latterly, the true nature of the skeletal 'sculpture' of the ichthyosaur, which was still located at the ING JU at that time, was rediscovered. The specimen, which was long considered a gypsum model, was discovered to be an articulated, highly intact ichthyosaur fossil. The four layers of paint that covered it were removed and conservation work was undertaken on CEP-DG-7264-N.



Fig. 2. Archival photo from the collection of NEP JU documenting the process of covering *Stenopterygius quadriscissus* CEP-DG-7264-N in black paint, taken in 1974

METHODS

CEP-DG-7264-N (Fig. 3) has undergone wet cleaning of the black paint, and the frame itself was reinforced and renovated by the ICOS preparation company in Cholerzyn near Kraków during January–March 2023. The specimen was then digitized using a *Shining 3D EinScan Pro 2X 3D scanner* (*Handheld Rapid Scan*) with an *EinScan Pro 2X Color Pack* (texture scans) and *EXScan Pro 3.2.0.2* software. Snapshots of the model were captured in *MeshLab 2022.02* (Cignoni et al., 2008) using the *Save snapshot* tool in orthographic view and with the *Radiance Scaling (Lambertian)* shader enabled (Fig. 4B; Vergne et al., 2010). Additionally, an elevation map (Fig 4B) was generated in *ParaView 5.11.1* (Ahrens et al., 2005; Utkarsh, 2015). To better capture the details of the skull, including the right side, unreachable with the surface scanner, another, photogrammetric model was produced in *Agisoft Metashape 2.1.4*. The cranium model was based on photos taken by *Canon EOS M6 Mark II*.

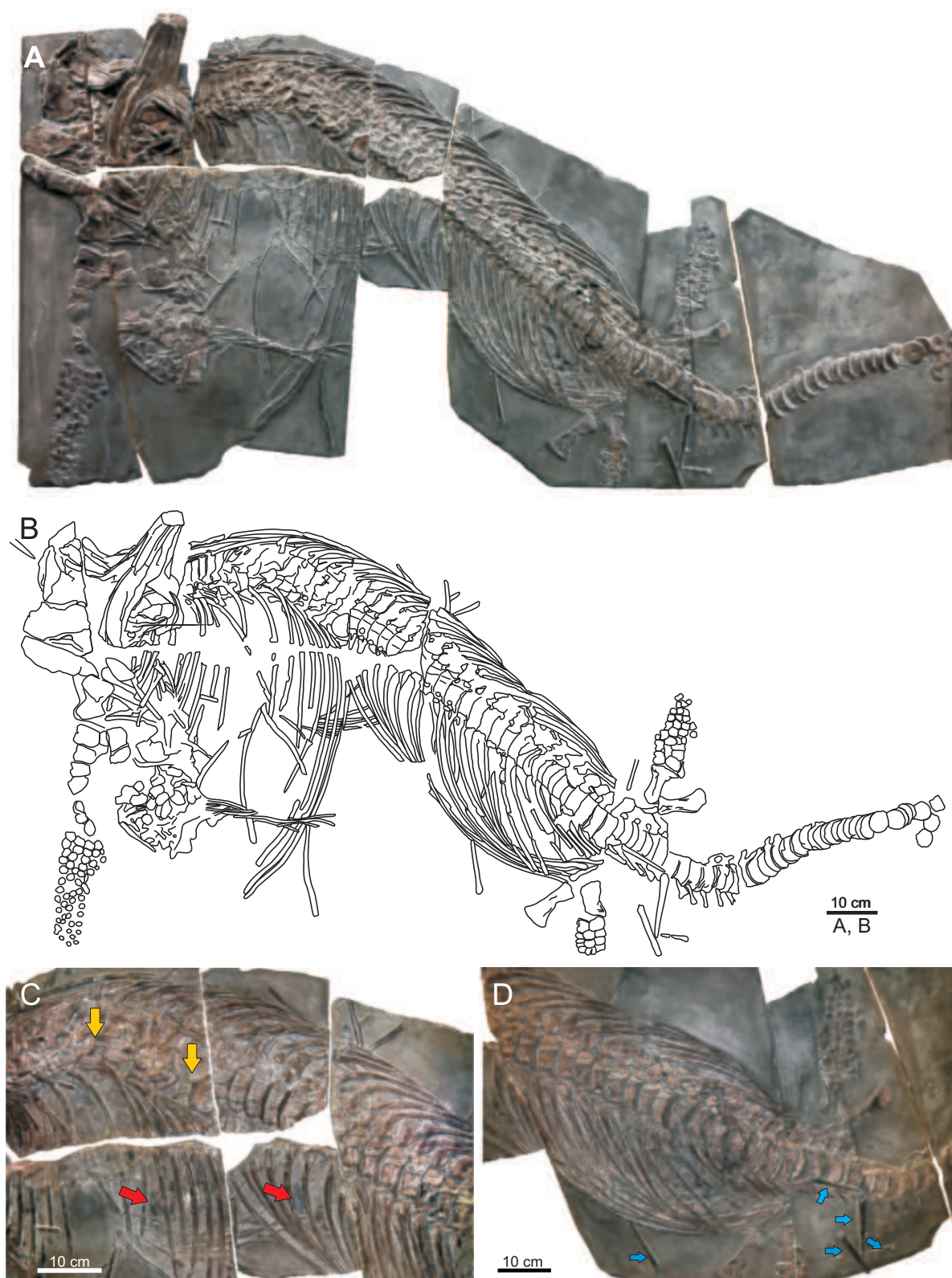


Fig. 3. Overview of the specimen CEP-DG-7264-N of *Stenopterugius quadriscissus* after restoration

A – overview of the fossil; **B** – schematic line drawing of the skeleton; **C** – dorsal portion of the axial skeleton showing exaggerated curvature indicated with yellow arrows and dark discolouration in thoracic area indicated by red arrows; **D** – lumbar and sacral section with preserved belemnite rostra highlighted with blue arrows

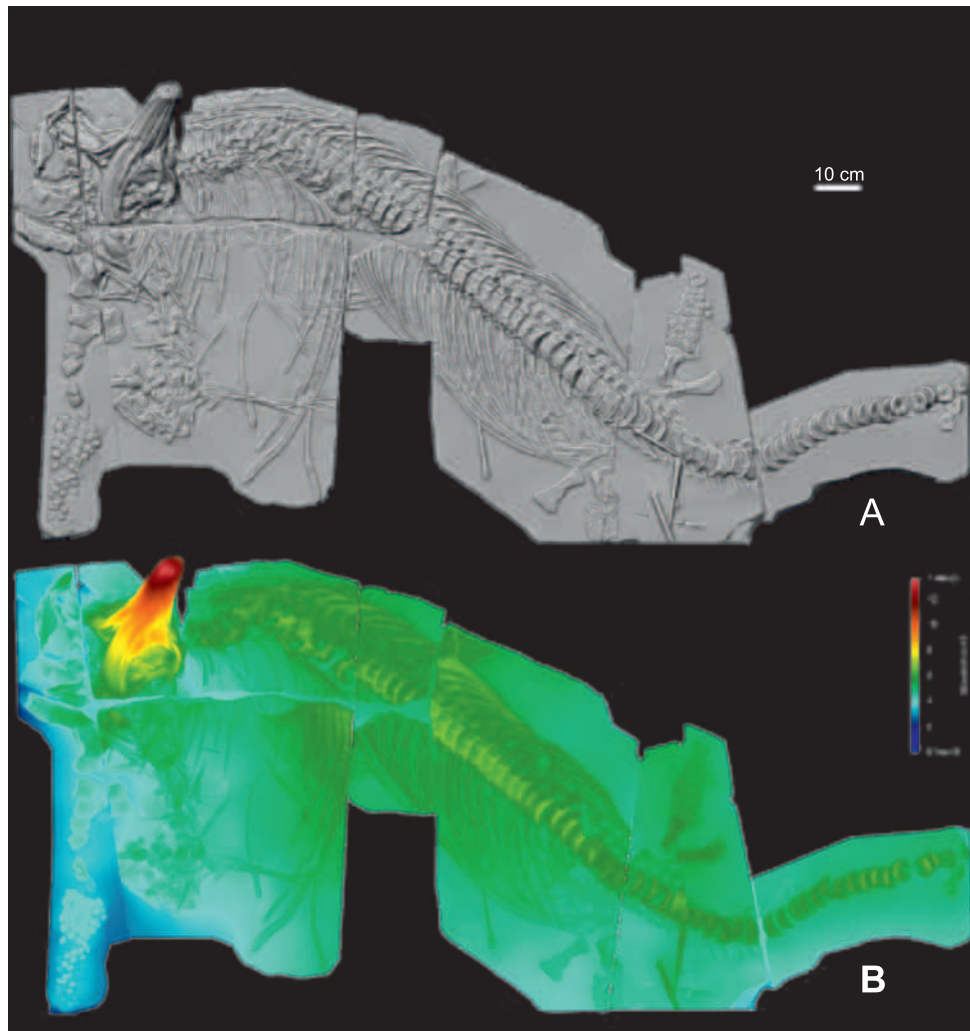


Fig. 4. 3D scans of *Stenopterygius quadriscissus* CEP-DG-7264-N

A – with Radiance Scaling (Lambertian) shader; **B** – an elevation map highlighting the rostral breakage, head rotation, and exaggerated spinal curvature in the anterior dorsal region

The virtual 3D scans of specimen CEP-DG-7264-N are available at MorphoSource:

<https://n2t.net/ark:/87602/m4/703704> (whole structured light body scan); <https://n2t.net/ark:/87602/m4/704670> (photogrammetry cranium scan).

SPECIMEN DESCRIPTION

Systematic palaeontology

Ichthyosauria de Blainville, 1835
 Neoichthyosauria Sander, 2000
 Parvipelvina Motani, 1999
 Thunnosauria Motani, 1999
 Stenopterygiidae Jaekel, 1904
Stenopterygius Jaekel, 1904
S. quadriscissus Quenstedt, 1856

Material. – CEP-DG-7264-N, mostly articulated, almost complete skeleton; missing: the anterior portion of the ro-

trum (anterior premaxillae and dentaries), distal parts of the anterior dorsal ribs, significant part of the gastralia, sections of the three dorsal vertebrae in central trunk, most of the distal caudal vertebrae of the ventral tail lobe, and distal phalanges of the left posterior limb (Figs. 3–7).

Location. – Posidonia Shale, Bad Boll (Germany).

Remarks. – (based mainly on Maisch and Matzke, 2000; McGowan and Motani, 2003; Maisch, 2008; and Maxwell, 2012 species discrimination characteristics): medium-sized (2 m as preserved, estimated ~2.5 m in-vivo length) thunnosaurian ichthyosaur showing typical diagnostic characters of *Stenopterygius*:

- slender premaxillae;
- maxilla extending as far posteriorly as lacrimal;
- angular exposure on posterior lower jaw extensive, but less so than in ophthalmosaurs;
- short mandibular groove;
- humerus with two distal facets;
- forelimb with 4 to 5 digits, with elements tightly packed proximally;
- intermedium appearing to be connected with III digit;

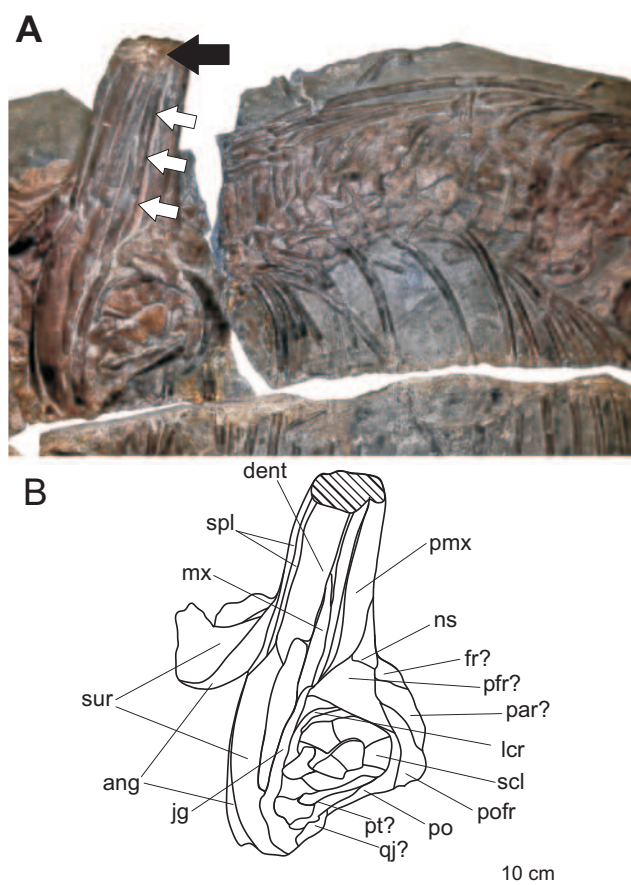


Fig. 5. Cranial anatomy of *Stenopterygius quadriscissus* CEP-DG-7264-N

A – with highlighted broken rostrum (black arrow) displaying the edentulous condition (white arrows) typical of ontogenetically adult *S. quadriscissus* specimens; **B** – interpretative drawing with highlighted bones; ang – angular, dent – dentary, fr? – frontal?, jg – jugal, lcr – lacrimal, mx – maxilla, ns – nasal, par? – parietal?, pfr – prefrontal?, pmx – premaxilla, po – postorbital, pofr – postfrontal, pt? – pterygoid?, qj? – quadratojugal?, scl – sclerotic ring, spl – splenial, sur – surangular; the hatched area indicates rostral breakage

- pelvic girdle bipartite;
- ischium and pubis fused (shared only with ophthalmosaurs);
- hindlimbs with 3 to 4 digits;
- forelimbs at least twice the length of hindlimbs, with humerus about 30% longer than femur.

Differs from the roughly coeval *Eurhinosaurus longirostris*, *Hauffiopteryx* spp., *Suevoleviathan* spp., and *Temnodontosaurus* spp. in the advanced fusion of the ischiopubis. Additionally, differs from *Hauffiopteryx typicus* in a shorter row of gastralia, from *Ichthyosaurus* spp., *Suevoleviathan* spp., and *Temnodontosaurus* spp. in a proportionally smaller head, from *Eurhinosaurus longirostris* and *Hauffiopteryx* spp. by no observable indications of overbite present; from *Ichthyosaurus communis* in narrower forefins; from *Suevoleviathan* spp. *E. longirostris* and *Temnodontosaurus* spp. in relatively smaller hindfins; from *Hauffiopteryx* spp. by orbit being only moderately large, yet larger than in *Ichthyosaurus* spp., *Suevoleviathan* spp. and *Temnodontosaurus* sp.; and from *Hauffiopteryx* spp. and *Temnodontosaurus* spp. in the lack of distal expansion of the humerus.

Additionally, CEP-DG-7264-N displays the following autapomorphies ascribed to *Stenopterygius quadriscissus*:

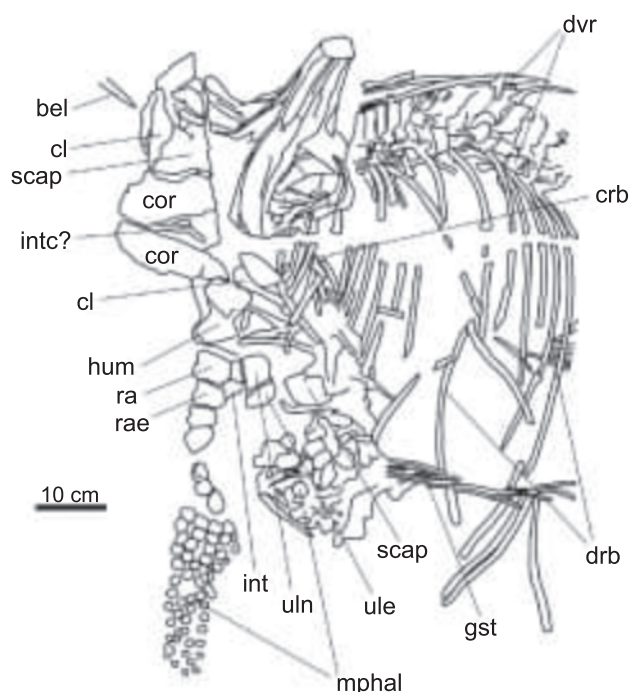


Fig. 6. Anterior part of *Stenopterygius quadriscissus* CEP-DG-7264-N with bones/features highlighted

bel – belemnite rostrum, cl – cleithrum, cor – coracoid, crb – cervical ribs, drb – dorsal ribs, dvr – dorsal vertebrae, gst – gastralia, hum – humerus, int – intermedium, intc? – interclavicle?, mphal – manus phalanges, ra – radius, rae – radiale, scap – scapula, uln – ulna, ule – ulnare

- edentulous jaws;
- antorbital segment of the skull moderately long;
- ischiopubis and femur robust;
- forefin with five digits;
- distal hindlimb short.

Cranium. In contrast to the postcrania (Figs. 3, 4, 6 and 7), the cranium (Fig. 5) is mostly three-dimensionally preserved, with the preorbital section (excluding the anterior end of the rostrum) and front half of the neurocranium intact, whereas the posterior neurocranium is laterally compressed like the postcrania. The right ramus of the mandible is deflected ventrolaterally to the point of breaking. In overall morphology, the cranium of CEP-DG-7264-N is proportionally small and gracile in the fashion typical of the genus *Stenopterygius*, which distinguishes it from the larger and more robust coexisting genera *Ichthyosaurus*, *Suevoleviathan* and *Temnodontosaurus* (see McGowan and Motani, 2003). The mandible and upper jaw appear to be in in-vivo position, while the lacrimal, prefrontals, postfrontals, frontal, parietal, postorbitals, quadrates, quadratojugs and likely squamosals are displaced. The skull is strongly projecting away from the slab (visible especially in the elevation map in Fig. 4B) and rotated dorsoventrally, with the neurocranium displaced ventrally from its original position. The anterior portion of the rostrum is missing (Fig. 5A), with the anterior parts of the premaxillae, dentaries, and splenials fractured, but the exposed right part of the skull has a well-preserved orbit, with the sclerotic ring intact. The orbit is only moderately large, which differs from the proportionally larger orbits of *Hauffiopteryx* spp. (see Maxwell and Cortés, 2020).

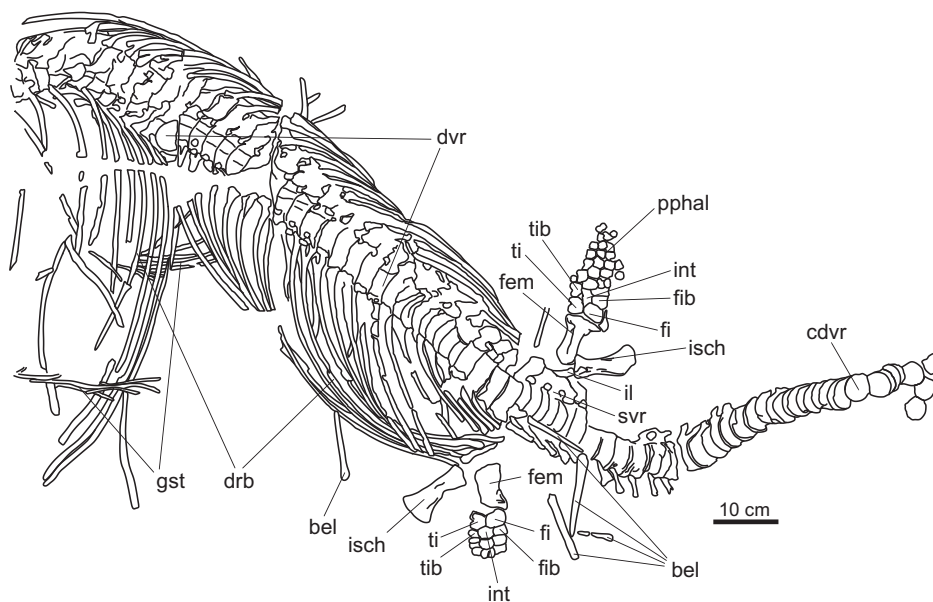


Fig. 7. Posterior part of *Stenopterygius quadriscissus* CEP-DG-7264-N with bones/features highlighted

bel – belemnite rostrum; cdvr – caudal vertebrae; drb – dorsal ribs; dvr – dorsal vertebrae; fem – femur;
fi – fibula; fib – fibulare; gst – gastralia; il – ilium; int – intermedium; isch – ischiopubis;
svr – sacral vertebrae; ti – tibia; tib – tibiale; pphal – pes phalanges



Fig. 8. Artistic reconstruction of *Stenopterygius quadriscissus* chasing its preferred prey, a cephalopod, by Bartosz Czader

Prior to its breakage, the rostrum was likely relatively long and slender, differing from the proportionally shorter and delicate rostrum of *Hauffiopteryx* spp. (Maxwell and Cortés, 2020) and the long, but robust rostra of *Suevoleviathan* spp. (see Maxwell, 2018), *Ichthyosaurus* spp. (see McGowan and Motani, 2003), and *Temnodontosaurus* spp. (see McGowan and Motani, 2003). The premaxillae are relatively long and gracile (with no indication of significant premaxillary elongation like in *E. longirostris*, see McGowan and Motani, 2003), in which they differ from the condition in other coeval ichthyosaur genera. Although the breakage of the anterior rostrum makes it impossible to measure the length of the antorbital segment/total mandibular length ratio, it appears that it was ~2:3, as characteristic of *S. quadriscissus* (see Maxwell, 2012). The maxilla is

exposed as a spindle-shaped band along the posterior part of the rostrum and does not reach the nostril.

The skull table and the posterior cranial bones are displaced, with part of the nasal, prefrontal, frontal, and parietal rotated laterally to the left and moved anteriorly, and the postorbital, quadrate, quadratojugal, and likely squamosal (on the slab the latter bone is not well-exposed) displaced strongly anteriorly. The lacrimal roughly occupies its original position, but is partially obscured by the neighbouring bones and may also be displaced to some extent. This also causes the outline of the external naris to be not traceable. As a result, the original extent of exposition and precise contacts between those structures cannot be reliably established. An elongated, gracile jugal is mostly intact but has been slightly displaced laterally. Due to the angle

at which the skull is positioned relative to the bedding plane, it is impossible to infer the shape of the supratemporal fenestrae, because they are placed within the slate.

The angular is prominent and well-exposed, as in *S. quadrisissus* (Maisch and Matzke, 2000; McGowan and Motani, 2003; Maxwell, 2012), and its prominence is especially visible due to the dorsal rotation of the cranium. The jaws of the specimen are completely edentulous (Fig. 5A), which is an important autapomorphy of adult *S. quadrisissus* in contrast to other species of *Stenopterygius* (Maxwell, 2012; Dick and Maxwell, 2015b). The mandibular alveolar groove appears to be short.

Postcrania. Generally, the body axis is rotated ventrolaterally in relation to the bedding plane (Figs. 3, 4, 6 and 7) with a visible rotation of the shoulder girdle, resulting in the placement of the right limb ventrally to the body axis and squashing its structure. The shoulder girdle itself (Fig. 6) has also been dislocated and is located anteriorly relative to its in-vivo position, whereas the limb bones of the right front limb are displaced and disarticulated. The distal ends of the anterior dorsal ribs are rotated anteriorly, while the distal ends of the posterior dorsal ribs are rotated posteriorly. The vertebral column is exposed in dorsolateral left view, with neural arches disarticulated from the centra and lying on their right sides. As preserved, the vertebral column is S-shaped, with the tail pointing in the opposite direction relative to the anterior dorsal region.

CEP-DG-7264-N has most of the axial skeleton preserved, missing only sections of the three dorsal vertebrae from the central trunk region and a significant number of the most distal caudal vertebrae that supported the ventral lobe of the tail. The cervical vertebrae appear to be obscured by the displaced cranium. The cervical vertebral centra are not detectable, but presumed cervical ribs are placed below the rotated cranium. *Stenopterygius quadrisissus* has 44–46 presacral vertebrae and >90 preflexural vertebrae (Maxwell, 2012), but due to the cranium obscuring the anterior cervical vertebrae and missing posteriormost caudal vertebrae from the tail lobe, it is difficult to confirm this condition in CEP-DG-7264-N. Nonetheless, ~66 vertebrae are exposed, of which 25 are caudal. The anterior dorsal portion appears to show an exaggerated curvature (Fig. 3C). In most cases, the anterior dorsal ribs are broken in distal parts, whereas the posterior dorsal ribs are mostly intact. Most of the preserved gastralia are dislocated and only the gastralia preserved close to their location in-vivo appear to be located in the anterior thoracic region below the spinal curvature (Fig. 6), transversely and ventrally away from their position in life. The gastralia do not appear to extend to the posterior dorsal region, which is different from *Hauffiopteryx* spp. (Maxwell and Cortés, 2020). Furthermore, adjacent to posterior abdominal and anterior caudal regions, along with a single occurrence near the skull, belemnite rostra can be observed (Figs. 3C, 6 and 7).

The entire shoulder girdle is displaced, as is the right forelimb, which is completely disarticulated. The left part of shoulder girdle is more clearly visible and discernible, due to the right half of the girdle being covered by the cranium and cervical vertebrae. The details of the shoulder girdle are not well-observable due to its displacement; thus, it is hard to observe the acromial and coracoid notch, which are also identifying characters for the genus. The front limbs (Fig. 6) are comparatively narrow (in contrast to *Ichthyosaurus communis* and later Ophthalmosauridae, see McGowan and Motani, 2003), and the humeri feature two observable distal facets for articulations with the ulnae and radii. The pectoral limbs of *Stenopterygius* spp. have 4 to 5 digits (Maxwell, 2012) and occasionally 6 digits according to McGowan and Motani (2003), while CEP-DG-7264-N has 5 digits, with three most proximal phalanges of digit V

preserved. The left front limb is semi-articulated with only the medial and distal phalanges disjoined from their in-vivo placement and the proximal carpals, humerus, ulna, and radius roughly retaining their relative positions. Most of the left paddle is disarticulated from the proximal part of the limb as a separate cluster and somewhat disarticulated distally, but retains its general pattern. The intermedium was connected to digit III as in *S. quadrisissus*. The preaxial notching is poorly marked and affects the radius and the anteriormost autopodial segments.

Hindlimbs (Fig. 7) of CEP-DG-7264-N are significantly smaller and less robust than forelimbs, and the forelimb-hindlimb length ratio is 2:1. The well-exposed left humerus is not only significantly more massive, but even with its slight ventral rotation it is about 1/3rd longer than the femora. The pelvis is bipartite, whereas the ischiopubis of the specimen is fused (which differs from the coeval *Hauffiopteryx* spp., *Eurhinosaurus longirostris*, *Suevoleiathan* spp. and *Temnodontosaurus* spp; see McGowan and Motani, 2003; Maxwell and Cortés, 2020), and rotated laterally from hindlimbs, the femur, tibia and fibula, as well as the tarsals and metatarsals are preserved and articulated, but in the left hindlimb the distal phalanges are missing. The right hindlimb has 3 digits, and two additional disjoined phalanges are adjacent to the 3th and 4th phalanges. The tibia and the subsequent three preaxial autopodial segments exhibit distinct notching. *Stenopterygius quadrisissus* can also be differentiated from *S. uniter* and *S. triscissus* by their proportionally robust ischiopubis and femur, and short distal hindlimb (Maxwell, 2012), which CEP-DG-7264-N appears to display.

DISCUSSION

TAPHONOMY

Based on our observations: head rotation, skull projection from the slab that differs drastically in angle from the rest of the body plane, and damage to the anterior part of the rostrum, we believe that CEP-DG-7264-N arrived headfirst on the seafloor after its death, similar to the condition observed in the *S. uniter* specimen SMNS 81719 studied by Maxwell et al. (2022). The skull has been fractured and dislocated due to the strong impact of landing, and the trauma has also flexed the spine in the cervical-thoracic region, possibly influencing the separation of the cervical region. The specimen landed on its right side, with its right front limb disarticulated and located underneath the body. As a result of spinal rotation, the front of the body is preserved on its side, while the posterior section is preserved more latero-dorsally. The anteriormost cervical vertebrae appear to be pressed into the back of the skull, similar to SMNS 81719. Furthermore, the observed flexure of the spine in the anterior section may have been enhanced by post-mortem rigor mortis relaxation.

We did not observe significant traces or signs of bioerosion or encrustation on the skeleton. There are six belemnite rostra (*Belmenitida* indet.) scattered near the skeleton: one located proximally, close to the head, and others located in the posterior abdominal and sacral region. The associated belemnite rostra located in the abdominal region could be interpreted as the remains of a meal from the animal's gastrointestinal tract. Post-mortem, the build-up of abdominal gases could lead to scattering of the rostra around the posterior trunk and anterior tail region. However, no crushing or superficial digestion/etching traces can be observed macroscopically. There are signs of

dark grey/brownish coloration inside the chest cavity (Fig. 3C), which be an organic residue from the animal's organs, though alternatively an artefact resulting from previous conservation works.

ONTOGENETIC STAGE OF CEP-DG-7264-N AND THE DIET OF *S. QUADRISCISSUS*

The ontogeny of *S. quadriscissus* has been extensively studied (Dick and Maxwell, 2015b; Dick et al., 2016; Miedema and Maxwell, 2022). *Stenopterygius quadriscissus* teeth are simple, conical, and without enamel ridges (Maxwell, 2012), and appear to exhibit few signs of wear (Dick and Maxwell, 2015b), suggesting that their role in food processing was not essential. Most importantly, many specimens of *S. quadriscissus* are edentulate (lack teeth) (Dick and Maxwell, 2015b; Dick et al., 2016), while some other species of *Stenopterygius* possess larger, unreduced teeth. Small juvenile specimens have been observed to have toothed mouths while larger specimens, interpreted as more ontogenetically mature, have very reduced dentition or toothless rostra (Dick and Maxwell, 2015b; Dick et al., 2016). Maxwell (2012) noted that edentulism is prevalent in specimens of *S. quadriscissus* that exceed 2 m in length, such as CEP-DG-7264-N. Dick et al. (2016) postulated that it appears that *Stenopterygius quadriscissus* experienced an ontogenetic change in diet, the young animals feeding primarily on small fish, while adults appeared to be exclusively teuthivorous, this being correlated with their ontogenetic loss of teeth. If this was the case, and also considering the size of the fossil (estimated 2.5 m in total length in vivo), CEP-DG-7264-N represents a mature specimen exhibiting an advanced stage of ontogenetic teeth reduction.

Dick and Maxwell (2015b) have proposed that *Stenopterygius* employed 'smash feeding' (Fig. 8), in which the high velocity and the sole impact of contact of the rostral bones with their preferred prey, belemnites, were sufficient to split the guard of the belemnite. The predator then consumed only the soft parts, representing a quite specific example of the 'Smash guild' of predatory marine reptiles of Massare (1987). In this scenario, the gastrointestinal tract would not come into contact with the hard belemnite rostra, and it has even been suggested that ichthyosaurs actively avoided the hard parts, spitting them out (Wursterberger, 1876; Pollard, 1968; Keller, 1976; Massare, 1987; Böttcher, 1989). Dick and Maxwell (2015a) noted that the ram feeding/raptorial teuthivore ecotype appears to have been a prevalent niche for ichthyosaurs throughout the existence of the group. Ontogenetic teeth loss is present also in other ichthyosaur genera (i.e. Sander et al., 2011; Martin et al., 2012), perhaps connected with this diet.

The skull of *S. quadriscissus*, among *Stenopterygius* species, appears to be especially adapted to feeding on cephalopods, because the rostrum is relatively shorter than in other species (Maxwell, 2012), and shortening of the rostrum together with dental reduction is considered an adaptation to specialization in feeding on cephalopods in ichthyosaurs (Sander et al., 2011). A large number of isolated belemnite rostra have

been found throughout the Posidonia Shale, that may be evidence of this kind of feeding behaviour among these animals (Seilacher, 1990; Etter and Tang, 2002).

In this light, it remains debatable whether the associated belemnite rostra are the result of the last meal, as Dick and Maxwell (2015b) suggest the active avoidance of this material by ichthyosaurs while feeding. Perhaps those belemnite remains were just deposited in close vicinity to the body of the animal. Dick et al. (2016) note that as yet, no belemnite rostra have been found in adult *S. quadriscissus* stomach contents. However, the large number of rostra in close vicinity should be considered, as it cannot be excluded that the rostra are indeed from the gastrointestinal tract and, perhaps by mistake, the specimen analysed had eaten the belemnites whole. The rostra are slightly dislocated posteriorly from the abdominal region, and if they are indeed the last meal, the likely cause of their position was post-mortem displacement by abdominal gases.

CONCLUSIONS

The fascinating history of the painting over of the ichthyosaur specimen CEP-DG-7264-N explains why it was considered a plaster cast for so long. However, due to the alertness and perseverance of the NEC staff, the true nature of the specimen was revealed.

The taphonomy of CEP-DG-7264-N suggests that it landed post-mortem on the sea floor on its rostrum, causing the breakage of the anteriormost fragments of the premaxillae, dentaries and splenials, and the impact probably also caused associated cranial and spinal dislocations.

Observable edentulism is a characteristic condition of ontogenetically mature specimens of *S. quadriscissus*, which was related to their belemnite diet, and leads us to believe that CEP-DG-7264-N was an adult. The associated belemnite rostra could likely be another example of the species' dietary preferences and may have possibly been the last meal of the animal, as they are located closely adjacent to the region of the gastrointestinal tract, even if *S. quadriscissus* typically avoided the hard parts of their cephalopod prey. However, it cannot be excluded that observed rostra may just have been deposited in close vicinity to the body during sedimentation.

Most importantly, CEP-DG-7264-N is another example of a perfectly preserved specimen of *S. quadriscissus*, expanding the future potential of the material to study population trends and other biological characteristics in these animals. CEP-DG-7264-N is now one of the centrepieces of the NEC collection.

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