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GIANT LATE TRIASSIC ICHTHYOSAURS FROM THE KÖSSEN FORMATION OF THE SWISS ALPS AND THEIR PALEOBIOLOGICAL IMPLICATIONS

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ABSTRACT—The Late Triassic was populated by the largest ichthyosaurs known to date, reaching lengths of over 20 m. Recent discoveries include the remains of giant ichthyosaurs from the Austroalpine nappes of the eastern Swiss Alps. The finds come from the lower two members of the Kössen Formation (late Norian to Rhaetian). The material consists of a very large tooth lacking most of the crown from the Rhaetian Schesaplana Member, a postcranial bone association of one very large vertebra and ten rib fragments also from the Schesaplana Member, and an association of seven very large vertebral centra from the upper Norian to lower Rhaetian Alplihorn Member. These associations represent the only published partial skeletons of large to giant ichthyosaurs younger than middle Norian. We compare the material with the two largest ichthyosaurs known from partial skeletons, *Shonisaurus popularis* (15 m) and *Shastasaurus sikkanniensis* (21 m) from the late Carnian (ca. 230 Ma) of Nevada and the middle Norian (ca. 218 Ma) of British Columbia, respectively. The incomplete tooth confirms that at least some giant ichthyosaurs had teeth. Based on their proportional differences, the two bone associations may represent two different taxa of *Shastasaurus*-like ichthyosaurs. The larger and geologically younger specimen may have been nearly the size of *S. sikkanniensis*, and the smaller that of *S. popularis*. These giant ichthyosaurs from the eastern Swiss Alps indicate that such ichthyosaurs also colonized the western Tethys. The finds also unequivocally document that giant ichthyosaurs persisted to the latest Triassic.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

Rebuilding of marine ecosystems after devastation at the end of the Permian ‘invited’ multiple lineages of reptiles to the marine habitat, leading to the well-known explosive radiation of marine reptiles in the Early Triassic and early Middle Triassic (Motani, 2009; Kelley and Pyenson, 2015). The record is found in lagerstätten, laminated, typically anoxic sediments that preserve complete or partial skeletons. Two major lineages of marine reptiles were part of this explosive radiation, the ichthyosaurs and the sauropterygians (Kelley and Pyenson, 2015). Ichthyosaurs early on colonized the open ocean, explaining their occurrence throughout the northern hemisphere. Ichthyosaurs also increased in body size amazingly fast, having evolved giant forms with a skull length of 2 m within 5 Ma after their first appearance, by the early Middle Triassic (Sander et al., 2021). Throughout the Triassic, ichthyosaurs appear to dominate the world’s ocean, showing high diversity and disparity (e.g., Fröbisch et al., 2013; Thorne et al., 2011; Kelley and Pyenson, 2015).

The two last stages of the Late Triassic, the Norian (19.5 Ma in duration) and Rhaetian (7 Ma in duration) account for over half

of Triassic time (35.5 Ma; Cohen et al., 2019) but have an exceedingly poor record of ichthyosaurs and other marine reptiles with few localities and poorly preserved and incomplete fossils. This situation is masked by simple qualitative tabulations, such as done by Bardet et al. (2014), and by binning at the stage level (Thorne et al., 2011; Moon and Stubbs, 2020) without correcting for uneven stage length. However, the pattern becomes easily apparent from the supplementary information of Bardet et al. (2014), where the tally for Norian named ichthyosaur taxa is six and for the Rhaetian is zero, compared with eight taxa for the Carnian and 23 for the Middle Triassic. For the entire Norian, there are only two marine reptile conservation lagerstätten known worldwide, in British Columbia (the Pardonet Formation) and Italy. Only the former preserves ichthyosaurs. No conservation lagerstätten are known for the Rhaetian, only concentration lagerstätten with abundant but disarticulated material. Apart from the Pardonet Formation, there are widely scattered reports of incomplete ichthyosaur fossils from the Norian and Rhaetian. These fossils mostly come from remote regions around the globe, as reviewed below.

The Late Triassic marine reptile record has a peculiar feature: ample but tantalizing evidence of giant ichthyosaurs. Focusing on the Carnian ichthyosaur record, this principally comes from the same regions that have yielded geologically older faunas, i.e., western North America (California, Nevada) and Guizhou Province, southwest China. Ichthyosaurs, and for the first and only

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time, thalattosaurs dominate the faunas from Carnian localities that record pelagic habitats in China (Wang et al., 2008). Giant ichthyosaurs from the Luning Formation at Berlin Ichthyosaur State Park (BISP) in central Nevada, U.S.A., are the foundation of the genus *Shonisaurus*, which reached a length of at least 15 m (Camp, 1980; McGowan and Motani, 1999). All of the large-bodied material from BISP probably pertains to a single species, *S. popularis* (McGowan and Motani, 1999). Several classical Late Triassic ichthyosaur taxa come from the Carnian Hosselkus Limestone of northern California (Merriam, 1908; McGowan and Motani, 2003). The greatest body size of the Hosselkus ichthyosaurs is seen in *Shastasaurus*, including some very large bones previously assigned to “*Shastasaurus*” *careyi* (Merriam, 1908) but more recently assigned to *Shonisaurus* (McGowan and Motani, 2003). Finally, there is a record of *Shonisaurus* from the Carnian of the Italian Alps (Dalla Vecchia and Avanzini, 2002).

The only Norian conservation lagerstätte with ichthyosaurs is the Pardonet Formation of northern British Columbia, Canada. The lagerstätte is of middle Norian age and has produced a wide array of ichthyosaurs (reviewed in McGowan and Motani, 2003), including the largest known ichthyosaur skeleton, the holotype of *Shonisaurus sikkanniensis* (Nicholls and Manabe, 2004). The specimen is estimated at 21 m in length. In some recent phylogenetic analyses (Sander et al., 2011; Moon, 2019), *Shonisaurus sikkanniensis* has been found to pertain to *Shastasaurus*. In other analyses (Bindellini et al., 2021), however, *S. sikkanniensis* forms a clade with the BISP *Shonisaurus* material. Another giant ichthyosaur from the Norian is *Himalayasaurus* from Tibet, sporting large cutting teeth (Motani et al., 1999). *Himalayasaurus* is known from the very fragmentary remains (a jaw fragment with teeth, a radius, a fin element, a cervical centrum) of a single individual. One of the few southern hemisphere records of Triassic marine reptiles consist of the scanty remains of very large ichthyosaurs from Norian-age rocks of New Caledonia (Mazin, 1985). These were assigned to *Shonisaurus* sp. Finally, indeterminate material of a large ichthyosaur and its gut contents comes from the Norian of the Brooks Range of northern Alaska (Druckenmiller et al., 2014).

There are two previous records of very large ichthyosaurs from the Kössen Formation of the Northern Calcareous Alps. A very large isolated dorsal centrum from the late Norian part of the Kössen Formation at Neumühle near Vienna, Austria, was described by Zapfe (1976) as *Leptopterygius* sp. However, Zapfe (1976) notes its similarity to *Shonisaurus* from Nevada. Karl et al. (2014) described a large caudal vertebral centrum from the Norian part of the Kössen Formation of the Bavarian Alps (Germany) and noted its similarity to *Shonisaurus* from Nevada. They confusingly identify the centrum first as a “presacral trunk” centrum but, in the next paragraph (Karl et al., 2014:195), correctly as a caudal centrum. This positioning is based on the hexagonal outline and the small round rib articular facets in the middle of the lateral surface of the centrum, as in the Nevada and British Columbia material of Late Triassic giant ichthyosaurs (Camp, 1980; Nicholls and Manabe, 2004). The height of the Bavarian centrum is 210 mm. However, the size of the animal is difficult to ascertain because of the posterior size decrease of caudal vertebrae.

As noted, no unequivocally Rhaetian marine reptile conservation lagerstätten are known. Also, no named genus of ichthyosaur is known that is exclusively and with certainty Rhaetian. Certain otherwise Jurassic taxa, e.g., *Whalisaurus*, *Protoichthyosaurus*, and *Leptopterygius*, have been reported from the Jurassic–Triassic boundary beds in England (Martin et al., 2015; Lomax, 2016; Lomax et al., 2017, 2018). However, the Triassic–Jurassic boundary has been notoriously difficult to place in these beds, hinging on whether the lowermost part of the Blue Lias Formation is latest Triassic or Hettangian in age, and we

thus cannot be sure whether the aforementioned finds are really Triassic. On the other hand, isolated bones and very fragmentary skeletons of unequivocal or putative large to giant ichthyosaurs occur in several unequivocally Rhaetian localities in central and western Europe, including the famous Rhaetic bonebeds of the U.K. (e.g., Huene, 1912; Storrs, 1994; Lomax et al., 2018) and Germany (Sander et al., 2016), and from French localities (Fischer et al., 2014).

Recently, a large and somewhat curved elongate bone fragment of 960 mm in length and some isolated bone shafts from the U.K. bonebeds, all of unequivocally Rhaetian age, have been interpreted to represent parts of the lower jaws, probably the surangular bone, of super-giant (at least 26 m in length) ichthyosaurs (Lomax et al., 2018). The isolated bone shafts had previously been interpreted as dinosaur leg bones (Redelstorff et al., 2014). It is uncertain whether these English super-giant ichthyosaurs had teeth, but it may be noteworthy that giant ichthyosaur teeth of the kind described in the current paper have not been reported from any of the UK and Continental Rhaetian bonebeds, which are otherwise rich in teeth. In summary, our understanding of the Rhaetian European finds outside of the Alps is greatly hampered by fragmentary preservation and often uncertain stratigraphic origin.

Finally, giant ichthyosaurs of late Norian to early Rhaetian age have been discovered at high-elevation localities in the Kössen Formation in the Canton of Grisons, eastern Swiss Alps (Furrer, 1993). The material was briefly mentioned by Callaway and Massare (1989). The Swiss Kössen Formation localities have also yielded undescribed remains of smaller ichthyosaurs (see Fig. S4A, Table S1), placodont remains (Neenan et al., 2014), saurosphargid remains (Scheyer et al., 2022), pterosaurs (Fröbisch and Fröbisch, 2006; Stecher, 2008), phytosaurs (Furrer, 1993), and actinopterygian and shark remains (Duffin and Furrer, 1981; Bürgin and Furrer, 1992, 1993). The material of giant ichthyosaurs from the Grisons has not been described in any detail and consists of fragmentary skeletons and a very large isolated, incomplete tooth, all from different localities (Furrer, 1993; this study).

It is thus clear that the Late Triassic global seas harbored whale-sized ichthyosaurs about which we know very little regarding their size, morphology, and lifestyle. Because of the incomplete preservation of most of these fossils of giant ichthyosaurs, their size (length and mass) is difficult to estimate. The next most complete material after the 21-m *Shonisaurus sikkanniensis* holotype are the skeletons from BISP. Camp (1980) estimates the length of specimen BISP A-5 (with the tail added from specimen BISP C) to have been 15.7 m. Kosh (1990) and McGowan and Motani (1999) agree and give estimates of 15 m. Body mass estimates have only recently been published by Gutarra et al. (2019) based on digital volume models, resulting in a mass of 29.7 metric tons for a *Shonisaurus popularis* of 15 m length. General size proxies are difficult to find for these giant ichthyosaurs because of our incomplete knowledge of their anatomy. Vertebral dimensions appear most suitable, but there is the caveat that vertebral numbers are high and variable in *Shonisaurus* and *Shastasaurus*. In fact, *Shastasaurus liangae* has over 80 presacral vertebrae and over 110 caudal vertebrae the highest number for any ichthyosaur (Sander et al., 2011) and, in fact, any non-serpentine tetrapod.

Some of the giant Late Triassic ichthyosaurs appear to be closely related, and *Shonisaurus sikkanniensis* was found to form a clade with *Shastasaurus pacificus* and *Shastasaurus liangae* (Sander et al., 2011; Moon, 2019; but see Bindellini et al. 2021). The phylogenetic position of *Himalayasaurus* is unclear, but affinities to *Shonisaurus* were proposed (McGowan and Motani, 1999). Phylogenetic analyses generally exclude this taxon because of the incompleteness of the material (e.g., Moon, 2019).

The feeding style of some of the giant Late Triassic ichthyosaurs is puzzling as well because the large skeletons at BISP, the *S. sikkanniensis* holotype, and the Rhaetian bonebed material appear to represent toothless forms which have been hypothesized to be suction feeders (Nicholls and Manabe, 2004; Sander et al., 2011; but see Motani et al., 2013). A much smaller fragmentary skull (RTMP 98.75.9; Figs. S1, S2) is known from the Sikkanni Chief River locality (Nicholls and Manabe, 2004) but cannot be assigned with any certainty to *S. sikkanniensis* (PMS personal observation; Figs. S1, S2) although it was interpreted as a juvenile of *S. sikkanniensis* by Nicholls and Manabe (2004). The presence of teeth in the large skeletons at BISP is somewhat equivocal. Whereas Camp in his posthumously published monograph (Camp, 1980; edited by J.T. Gregory) reported teeth in uncollected jaw fragments of large individuals (Camp, 1980:166) and reconstructed small teeth in the front part of the jaw, first-hand study of the material by other workers (Nicholls and Manabe, 2004; PMS personal observation) failed to reveal evidence of teeth. As for *S. sikkanniensis*, Nicholls and Manabe (2004) suggested that the juveniles of *S. popularis* had teeth, without addressing the possibility that the toothed material belongs to a different, smaller species of ichthyosaur.

Giant ichthyosaurs with teeth are thus unequivocally represented only by *Himalayasaurus* and the incomplete tooth described in this paper. It is the purpose of this paper to describe this tooth and two fragmentary skeletons from the Kössen Formation of the Grisons, Switzerland, and to compare them with other giant Late Triassic ichthyosaurs and their body size.

Geological Framework

The Kössen Formation is a widespread Late Triassic stratigraphic unit in the eastern Alps, ranging from eastern Switzerland in the west to eastern Austria in the east. The fossils described in this paper are from the western occurrences of the Kössen Formation, cropping out in various Austroalpine nappes of eastern and southeastern Switzerland (Canton of Grisons) and adjacent western Austria and northern Italy (Figs. 1, S3). In these western outcrops, the Kössen Formation is subdivided into five units (Furrer, 1985, 1993; Fig. S3). In ascending order, these are the Alplihorn Member, Schesaplana Member, Ramoz Member, Zirnenkopf Limestone (informal unit), and Mitgel Member (Fig. S3). The Alplihorn Member is 80–120 m thick. It mainly consists of dark gray shales, marls, and limestones. Occasionally, layers of oolitic limestone, siltstone, and dolostone are interbedded. The well-bedded, shallow marine sediments are often rich in bivalves. Bioturbation is common and disarticulated bones, teeth, and scales of fishes and reptiles can be found in tempestites (Duffin and Furrer 1981; Bürgin and Furrer, 1992, 1993; Furrer, 1993). Overlying the Alplihorn Member is the 25–90 m thick Schesaplana Member with well-bedded limestones and marls, rich in corals, brachiopods, and echinoderms, as well as scattered vertebrate fossils. Whereas giant ichthyosaur remains were only found in the lower two members (Alplihorn and Schesaplana), placodont reptiles (teeth, bones, and carapace remains of *Psephoderma alpinum*) and fish fossils were also discovered in the Ramoz Member. However, complete actinopterygian fish fossils are only known from the quarry of Lorüns, Vorarlberg, Austria (Bürgin and Furrer, 2004).

The exact age of the Kössen Formation in the Austroalpine nappes of Switzerland is not well constrained due to the absence of good index fossils such as conodonts, ammonoids, and palynomorphs. The upper boundary of the formation, exposed at Schesaplana Mountain on the border between Switzerland and Austria and in the adjacent region of Lorüns (Vorarlberg, western Austria), is the top of the late Rhaetian Zirnenkopf

Limestone (Furrer, 1993). This is overlain discordantly by the Schattwald Beds that include the Rhaetian–Hettangian boundary (Felber et al., 2015). Schesaplana Mountain and the region of Lorüns belong to the Lechtal Nappe, forming the western part of the Northern Calcareous Alps. This is the region where the global stratotype section and point (GSSP) for the base of the Jurassic has been defined by the International Subcommission on Jurassic Stratigraphy (Morton, 2008), specifically in the Kuhjoch Section in the Karwendel Mountains (central Northern Calcareous Alps, Austria). The Schesaplana, Ramoz, Zirnenkopf Limestone, and Mitgel members must be of Rhaetian age, as suggested by the Rhaetian foraminifers *Glomospirella friedli* and *Triasina hantkeni* in association with the bivalve *Rhaetavicula contorta* (Furrer, 1985, 1993). Based on the occurrence of *Rhaetavicula contorta* (Furrer, 1993; McRoberts, 2010), a late Norian to early Rhaetian age is likely for the Alplihorn Member.

The Kössen Formation with its vertebrate fossils represents shallow marine carbonate deposits at the northwestern margin of the Tethys ocean. Deposition was strongly influenced by fine siliciclastic sediments (clay and silt) from the intensely weathered Vindelician Land, separating the Kössen basin from the Germanic Keuper basin in the north. The Alplihorn Member was deposited in a very large shallow lagoon of the former Hauptdolomit carbonate platform. The Schesaplana Member similarly records shallow marine habitats but with a better connection to the open sea (Furrer, 1993).

Institutional Abbreviations—BISP, Berlin Ichthyosaur State Park, Nevada, U.S.A.; BMNH, Natural History Museum, London, United Kingdom; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NSM, Nevada State Museum, Las Vegas, U.S.A.; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Zurich, Switzerland.

MATERIAL AND METHODS

Material

The studied material was discovered by one of the authors (HF) and his associates during the summer months of the years 1976 to 1990 while mapping the Kössen Formation of Canton Grisons (Switzerland) and studying its facies (Furrer, 1993). The material comes from a number of widely spaced localities (Fig. 1), representing different tectonic nappes. The material consists of isolated bones and teeth as well as three bone accumulations (Table S1). However, only the specimens unequivocally pertaining to giant ichthyosaurs are described in this paper.

First, there is a very large tooth PIMUZ A/III 670 (Fig. 2), the only dental material to be described in this study. PIMUZ A/III 670 is incomplete in that it lacks most of the crown, although the root is well preserved. The incomplete tooth comes from the Rhaetian Schesaplana Member of the Kössen Formation at Chrachenhorn Mountain (elevation 2,891 m) near Davos-Monstein, Canton Grisons, Switzerland. It was discovered and collected by Daniel Wurster in 1990 (see also Wurster, 1991).

Two of the bone accumulations represent small parts of associated postcranial axial skeletons of giant ichthyosaurs (PIMUZ A/III 744 and PIMUZ A/III 1470). The third, PIMUZ A/III 4363, is an accumulation of teeth, vertebral centra, and other bones (Fig. S4A) that possibly belong to a single, but much smaller individual. However, the specimen is not described in any detail here because the vertebrae are too poorly preserved for comparison with the giant specimens. The isolated bones representing smaller ichthyosaurs are also listed in the Supplemental Material (Table S1). Two more specimens from the Kössen Formation probably pertaining to giant ichthyosaurs are a possible sacral rib or girdle bone (PIMUZ A/III 751) and a probable lower jaw fragment (PIMUZ A/III 4625). These large specimens are

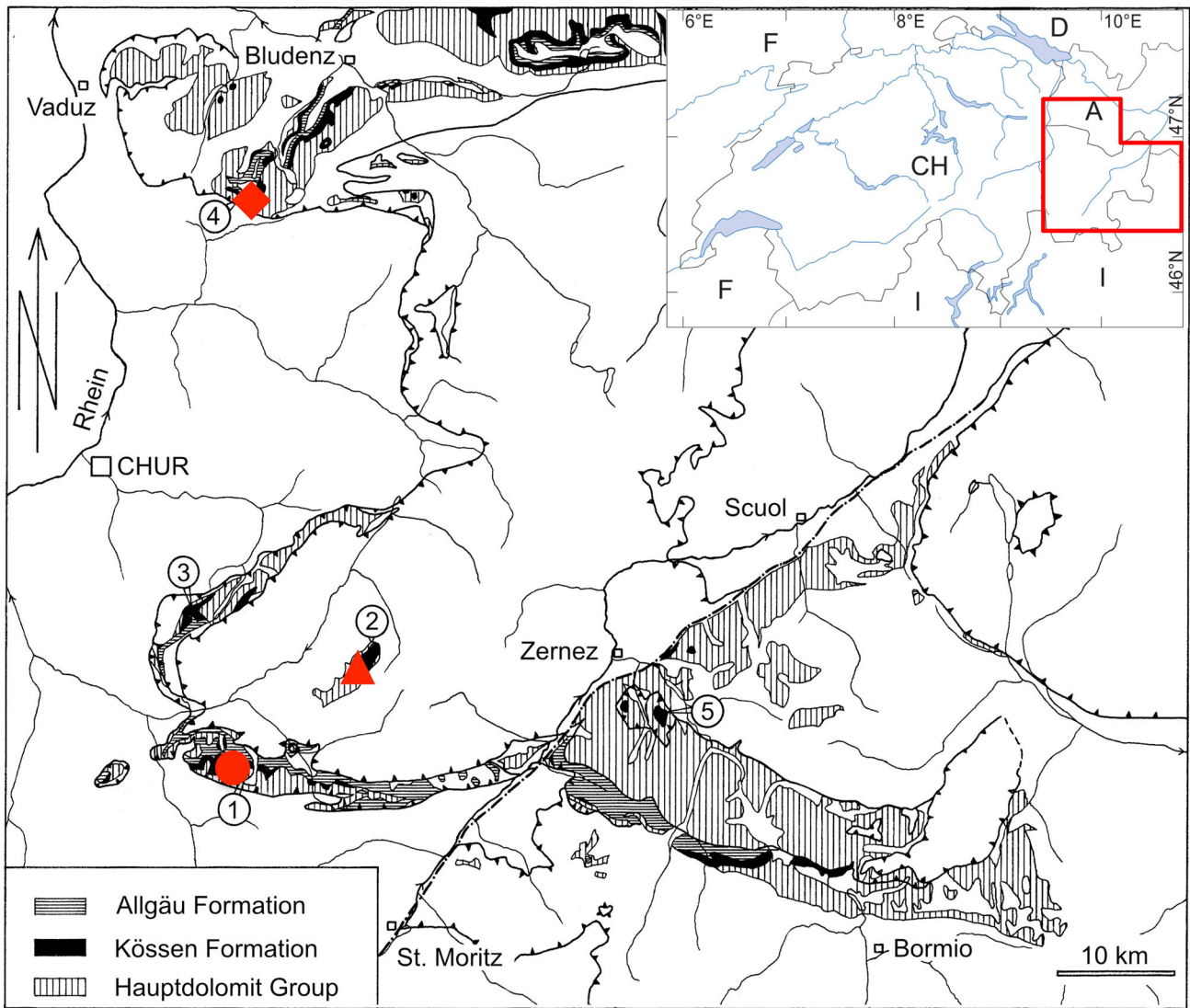


FIGURE 1. Geologic map of the Kössen Formation and its underlying and overlying units (Hauptdolomit Group and Allgäu Formation) in the most important tectonic units of eastern Switzerland, and localities of ichthyosaur fossils described in this paper. Key to units and localities: 1, Corn da Tinizong, Ela Nappe; 2, Alplihorn and Chrachenhorn mountains, Silvretta Nappe; 3, Ramoz, Arosa Dolomites; 4, Schesaplana Mountain, western Lechtal Nappe; 5, Murtèr, Terza Unit. The three important sites are highlighted by a triangle (Chrachenhorn Mountain), a circle (Corn da Tinizong Mountain), and a diamond (Schesaplana Mountain). Modified from Furrer (1993).

figured in the Supplemental Material (Figs. S4B, S5) but not discussed further because of their fragmentary nature and uncertain anatomical affinities. It is unclear how much of PIMUZ A/III 670, PIMUZ A/III 744, and PIMUZ A/III 1470 was lost to pre-burial destruction vs. the harsh erosional regime of the high Alps.

Specimen PIMUZ A/III 744 (Fig. 3) consists of a single dorsal vertebral centrum (Figs. 3, 4), eight associated fragmentary ribs that are proximally complete and preserve their shaft to various degrees, and two rib fragments (Figs. 3, 5). The specimen shows post-mortem deformation that is most obvious from the bilateral asymmetry of the vertebral centrum (Fig. 4). The specimen is from the Rhaetian Schesaplana Member of the Kössen Formation from the East side the Fil da Stidier ridge (elevation 2,825 m) northeast of Corn da Tinizong Mountain near Filisur, Canton Grisons, Switzerland. It was discovered by Arthur Rohrbach in 1975 and collected by one of the authors (HF) together with Arthur Rohrbach and Urs Oberli on July 21, 1976 (see also Rohrbach, 1976).

Specimen PIMUZ A/III 1470 is from the upper Norian to lower Rhaetian Alplihorn Member of the Kössen Formation at Schesaplana Mountain (elevation 2964 m), Seewis, Canton Grisons, Switzerland. Specimen PIMUZ A/III 1470 was found and excavated by HF in 1977 (Furrer 1993:fig. 14) and consists of seven dorsal vertebral centra lying flat on a bedding plane in a mosaic fashion with the posterior articular surface in field-top position (Fig. 6). This mosaic mode of preservation (but not necessarily in the same field-top orientation) is also observed in specimens of *S. popularis* remaining in the ground at Berlin Ichthyosaur State Park, Nevada, U.S.A. (Camp, 1976, 1980). The field-top faces are heavily eroded.

METHODS

Excavation and Preparation—The tooth and the bones were isolated completely or partly from their matrix in a combination

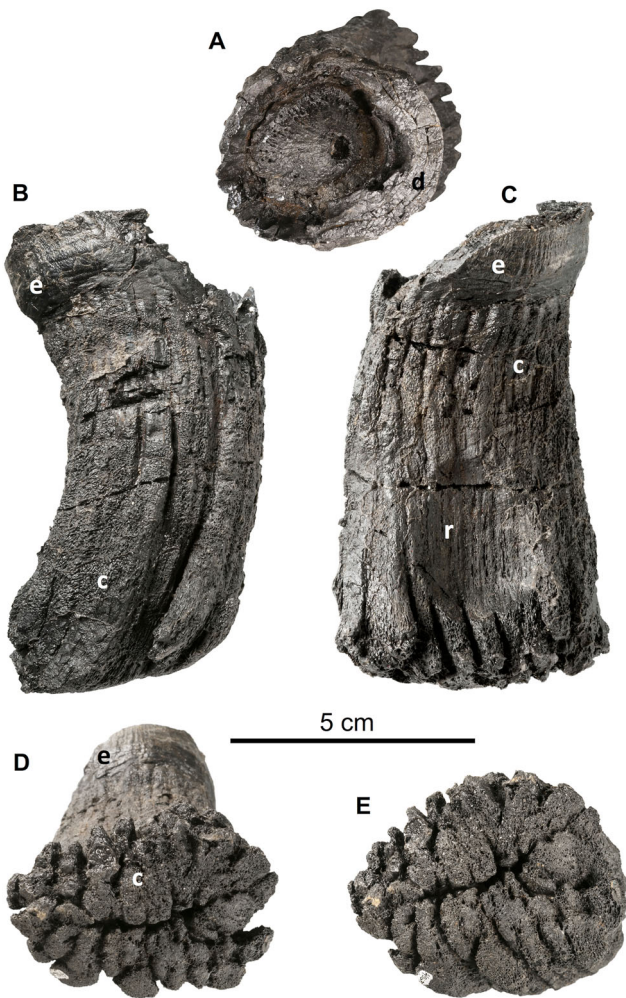


FIGURE 2. Ichthyosauria indet., tooth lacking most of the crown, PIMUZ A/III 670, Rhaetian Schesaplana Member, Kössen Formation, Crachenhorn Mountain, Davos-Monstein, Grisons, Switzerland. **A**, apical view; **B**, mesial or distal view; **C**, lingual view; **D**, oblique basal; **E**, basal view. **Abbreviations:** c, cementum; d, dentin; e, enamel; r, resorption pit.

of repeated mechanical preparation by air tool and chemical preparation with formic acid at PIMUZ.

Size Estimations—Body sizes were estimated by comparing measurements of comparable elements from more complete specimens. Measurements were selected for comparison with relevant studies (Camp, 1980; Kosh, 1990; McGowan and Motani, 1999; Motani et al., 1999; Nicholls and Manabe, 2004; Scheyer et al., 2014). Camp (1980) included several key measurements in his tables. Camp (1980) measured tooth height from the base to the tip, tooth base width, and tooth base diameter. In the vertebral centra, Camp (1980) measured anteroposterior length, dorsoventral height, and maximum width across the rib facets. Kosch (1990) and Nicholls and Manabe (2004) reported rib total length.

Our measurements were taken with a measuring tape and calipers. Tooth size was estimated graphically and in direct comparison with *Himalayasaurus* (Motani et al., 1999) (Fig. S6). Relative body size calculation was done based on vertebral centrum dimension, using the relationship between centrum length, width and height and total body length of the two sufficiently

known giant Late Triassic ichthyosaur species, *Shonisaurus popularis* (Camp, 1980; Kosh, 1990; McGowan and Motani, 1999) and *Shastasaurus sikkanniensis* (Nicholls and Manabe, 2004). Total body length of *Shonisaurus popularis* is estimated as 15 m (McGowan and Motani, 1999), and the holotype of *Shastasaurus sikkanniensis* is estimated at 21 m (Nicholls and Manabe, 2004). However, no complete skeletons are known for either taxon; the length estimate for *S. popularis* is based on a composite reconstruction and that of *S. sikkanniensis* on measurements in the field. Nevertheless, relative size estimates for the Kössen Formation giant ichthyosaur specimens are possible based on vertebral dimension, specifically anteroposterior length and transverse diameter.

Examination of Comparative Material—Between them, authors PMS and TW have personally examined all comparative ichthyosaur material discussed in this paper with the exception of the BMNH teeth discussed by McGowan (1996), the postcranial material of *Himalayasaurus* (Motani et al. 1999), and the dental material from BISP at NSM (Camp 1980). However, Dr. Nicole Klein (University of Bonn) examined the BISP material at NSM personally and provided extensive photographic documentation.

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA Blainville, 1835

ICHTHYOSAURIA indet.

(Fig. 2)

Material—One very large tooth lacking most of the crown, PIMUZ A/III 670.

Horizon and Locality—Rhaetian Schesaplana Member, Kössen Formation from Gretji, from scree 900 m southwest of Crachenhorn Mountain, Davos-Monstein, Canton Grisons, eastern Swiss Alps, Switzerland (coordinates 46.6850323N, 9.8036022E).

Description—The incomplete tooth is very large, being exactly 100 mm in length, and completely freed from the matrix. It is missing most of the crown, but the curved root is completely visible and well-preserved (Fig. 2). The curvature presumably is labiolingually. The length of the root is 90 mm, not measured along the curvature. The deeply infolded structure of plicidentin is well developed, and the pulp cavity at the base of the tooth root is closed. The cross section is oval, wider mesiodistally than labiolingually. The root is widest at its base, with a mesiodistal diameter of 60 mm and a labiolingual diameter of 46 mm. There is a distinctive resorption pit near the base of the lingual side of the root, indicating the development of a replacement tooth from the lingual side. The outside of the root shows a porous tissue, presumably cementum (Fig. 2).

The lower part of the crown is preserved along two-fifths of the tooth perimeter, mainly on the lingual side (Fig. 2). On the labial side, the crown is completely eroded, exposing a conical structure inside the crown base. The structure has a pit in the center, giving it the shape of a small volcano. The cone appears to consist of dentin, possibly representing the base of the crown. Typical dentin is also exposed in cross section on the fracture surface of the broken-off lingual part of the crown (Fig. 2).

The preserved height of the crown is 10 mm. The crown expands notably at its base as seen in many durophagous ichthyosaurs, but there is no indication of carinae. Assuming a regular conical shape for the crown of PIMUZ A/III 670, its height probably exceeded 60 mm (Fig. S6, Table 1; see Discussion section). The enamel at the crown base preserves fine longitudinal wrinkles as well as circumferential shallow ridges probably representing growth marks.

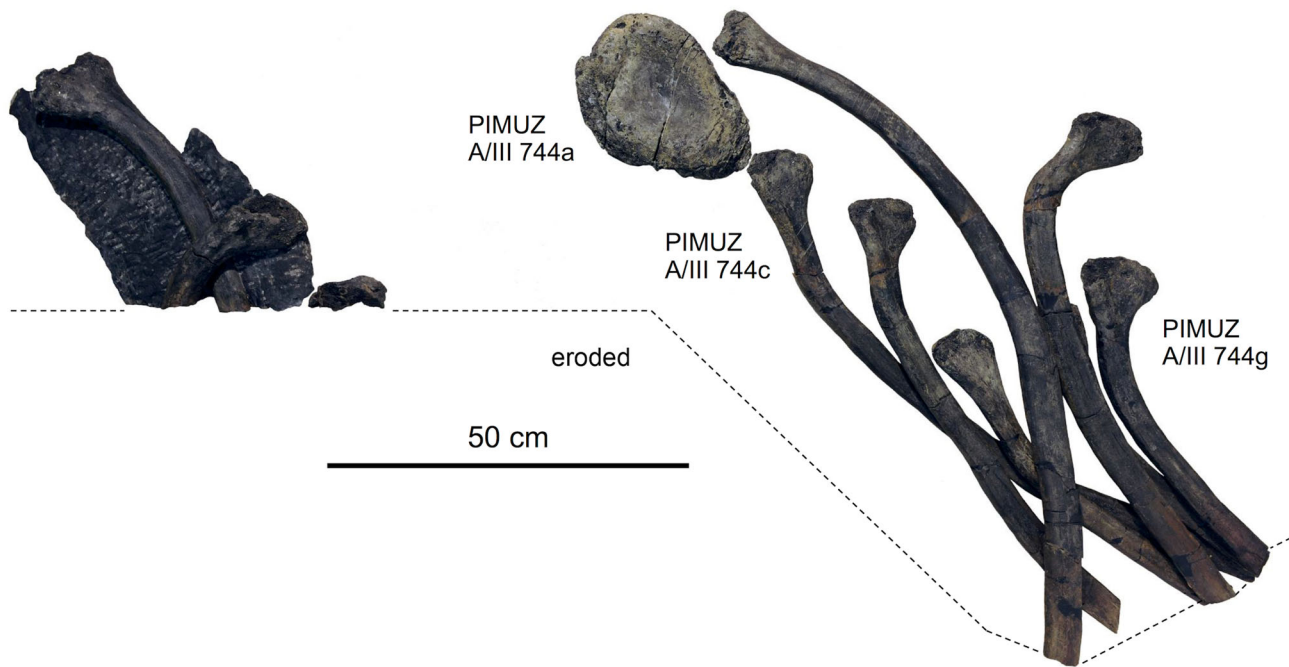


FIGURE 3. Reconstructed discovery situation (field top view) of partial incomplete skeleton of *Shastasauridae* sp. A, PIMUZ A/III 744, east side of Fil da Stidier ridge, Filisur, Grisons, Switzerland. The single large vertebra was exposed posterior face upward. Most of the associated ribs are right ribs and are seen in anterior view.

MERRIAMOSAURIA Motani, 1999

SHASTASAURIDAE Merriam, 1902 sensu Ji et al., 2016

Definition—The last common ancestor of *Shastasaurus* and *Besanosaurus*, and all its descendants (from Ji et al., 2016).

Apomorphy-based Diagnosis—See Ji et al. (2016).

SHASTASAURIDAE sp. A (Figs. 3–5)

Material—Specimen PIMUZ A/III 744, associated partial skeleton (Fig. 3) consisting of a very large anterior or middle dorsal vertebral centrum (PIMUZ A/III 744a) and eight distally incomplete dorsal ribs and two rib fragments (PIMUZ A/III 744b-l). The centrum is strongly tectonically deformed in the transverse plane. The ribs also appear tectonically deformed.

Horizon and Locality—Rhaetian Schesaplana Member, Kössen Formation. East side of Fil da Stidier ridge, Corn da Tinizong Mountain, Filisur, Canton Grisons, eastern Swiss Alps, Switzerland (coordinates 46.6204533N, 9.6816551E).

Remarks—We herein follow the phylogeny and systematic framework proposed by Ji et al. (2016) over that proposed by Moon (2019) because the former was designed to clarify the relationships of non-neoichthyosaurian ichthyosaurs which went extinct at the end of the Triassic. In addition, Moon (2019)

does not resolve many previously recognized clades of Ichthyosauria, including Shastasauridae. However, the Ji et al. (2016) matrix, which is a modified version of the Motani (1999) matrix, is not well suited because of its limited character sampling in the postcranial axial skeleton. This leaves as the only option a differential diagnosis to assign the Kössen Formation specimens to a taxon.

Differential Diagnosis—The dorsal vertebral centrum PIMUZ A/III 744a (Fig. 4) from the Kössen Formation differs in its large size from all other ichthyosaurian taxa except *Shastasaurus sikkanniensis*. PIMUZ A/III 744a and *S. sikkanniensis* share a uniquely large height and width (>220 mm) (Table 2). The Kössen Formation dorsal centrum PIMUZ A/III 744a differs from PIMUZ A/III 1470, *S. sikkanniensis*, and *S. popularis* in its shortness (unknown in *Himalayasaurus*). The height/length ratio average in all three of these taxa is around 2.5 (Table 2) compared with 3.16 in PIMUZ A/III 744a. The rib articular facets of these taxa are all of the elongate, anteriorly slanted “shastasaurid” type (unknown in *Himalayasaurus*). PIMUZ A/III 744a differs from *S. sikkanniensis* and *S. popularis* in the indistinct boundary between the periosteal bone and the endochondral bone of the articular surface (Figs. 4, S7). An indistinct boundary is also seen in some specimens of *S. popularis*, but this is due to pre-burial erosion of the upper side on the sea floor. PIMUZ A/III 744a differs from *S. sikkanniensis* (Figs. S7,

TABLE 1. Comparative measurements (in mm) of the largest ichthyosaur teeth known.

Specimen	Taxon	Age	Total height	Crown height	Max. crown diam.	Root height	Root diameter	Reference
PIMUZ A/III 670	indet.	Rhaetian	150 -160*	10**	~46	90	60 × 46	This study
IVPP V4300-1	<i>Himalayasaurus</i>	Norian	133	59.7	39.5	73.3	~30	Motani et al. 1999
BMNH 28283	indet.	Early Jurassic	116	33	-	83	-	McGowan 1996

*estimated; **as preserved.

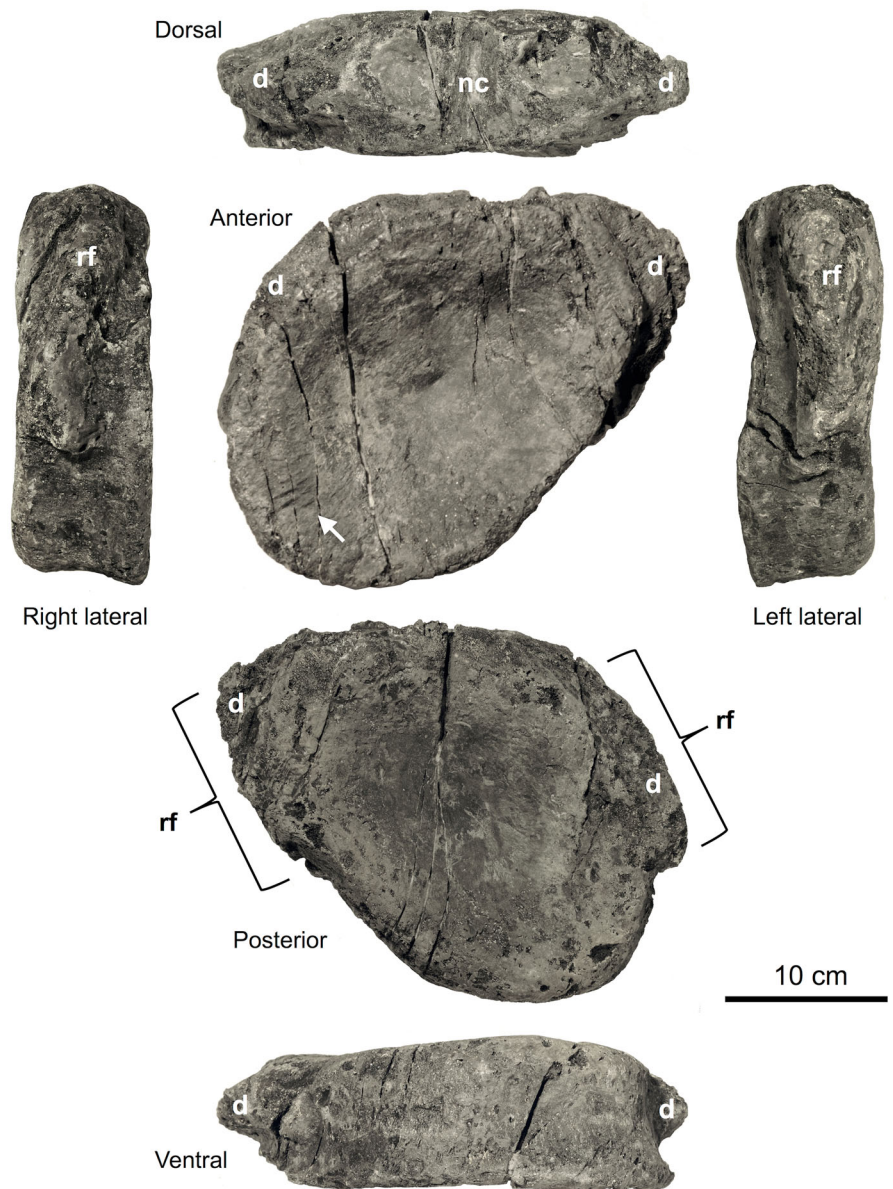


FIGURE 4. *Shastasauridae* sp. A., dorsal vertebral centrum, PIMUZ A/III 744a, Rhaetian Schesaplana Member, Kössen Formation, east side of Fil da Stidier ridge, Filisur, Grisons, Switzerland. **Abbreviations:** **d**, diapophysis; **nc**, neural canal; **rf**, rib articular facet. Arrow points to radial ridges on anterior face.

S8) and *S. popularis* (Fig. S9) in the presence of radial ridges on the articular surface of the centra (Figs. 4, S7–S9). The radial ridges are shared with PIMUZ A/III 1740. PIMUZ A/III 744a differs from *S. sikkanniensis* and *S. popularis* in the morphology of the proximal shaft of the dorsal ribs which only has an anterior groove as opposed to the figure-eight cross section in *S. sikkanniensis* and the wide-oval cross section in *S. popularis* as figured by Camp (1980, contra his text).

Description—Specimen PIMUZ A/III 744 (Fig. 3) represents an associated partial skeleton, although only a small part of the skeleton is preserved. The specimen consists of a single anterior or middle dorsal vertebral centrum (PIMUZ A/III 744a) and eight distally incomplete dorsal ribs and two rib fragments (PIMUZ A/III 744b-1). The specimen clearly was distorted by Alpine tectonics (see below). However, fracture surfaces of its ribs show a seemingly an intact trabecular architecture, indicating that the specimen was not deformed by sediment compaction. The posterior face (field top) of the centrum

is abraded (Fig. 4). In the field, seven ribs were located closely together on the anatomically left side of the centrum with all heads pointing towards the centrum; two short fragments and a truncated rib head were found at a distance of 40 cm on the anatomically right side of the centrum (Fig. 3). The ribs are all distally incomplete, having been truncated by weathering to lengths of 110 to 15 cm. All of the bones were originally embedded in a dark clayey limestone with scattered crinoid fragments and a few bivalves.

Vertebral Centrum—The centrum PIMUZ A/III 744a (Fig. 4) is strongly tectonically deformed in the transverse plane, distorting its bilateral symmetry. The anterior face was field bottom, being well-preserved as a result. The centrum is amphicoelous. The posterior face must have been exposed on the sea floor, leading to abrasion. The anterior face shows two distinctive features: low concentric rings and distinctive radial ridges. The rings are subtle and appear to be cyclical, with two more prominent ones being separated by several more indistinct ones. The

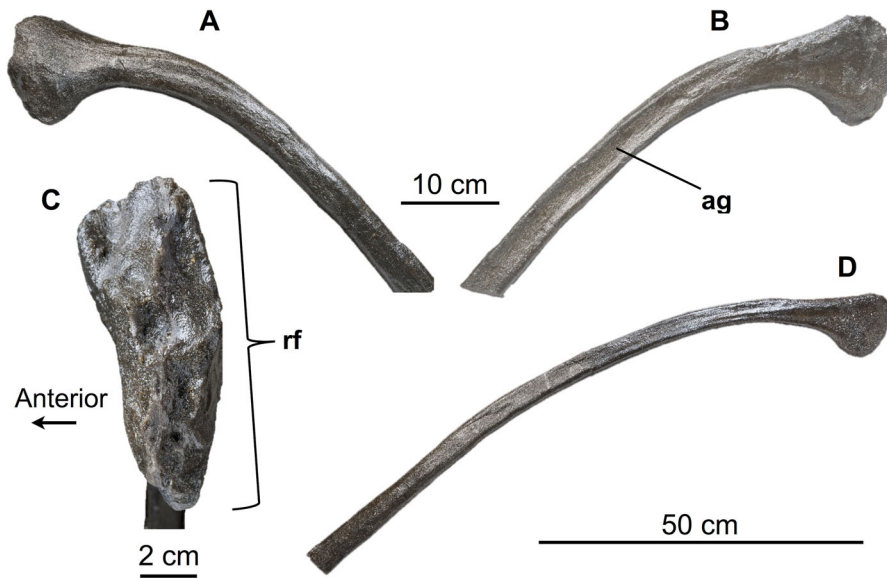


FIGURE 5. Shastasauridae sp. A, ribs, Rhaetian Schesaplana Member, Kössen Formation, east side of Fil da Stidier ridge, Filisur, Grisons, Switzerland. **A**, PIMUZ A/III 744 g (cast), incomplete right rib in posterior view; **B**, same in anterior view; **C**, PIMUZ A/III 744 g (cast), close-up of rib head in proximal view; **D**, PIMUZ A/III 744c, longest preserved rib (left) in posterior view. **Abbreviations:** ag, posterior groove; rf, rib articular facet. Arrow points to anterior.

radial ridges are most pronounced on the ventral part of the face, originating about halfway outward from the center of the articular surface and terminating in a point close to the margin, in the

region of the greatest anteroposterior length of the centrum. The ridges end in peripheral tips, giving them a flame-like appearance (Fig. 4). The periphery of the articular face of the centrum is

TABLE 2. Comparative measurements (in mm) and proportions of very large Triassic ichthyosaur vertebral centra.

Specimen/position	Anteropost. length	Dorsoventral height	Width across diapophyses	Height/Length
Shastasauridae sp. A PIMUZ A/III 744a	75	237	262	3.16
Shastasauridae sp. B				
PIMUZ A/III 1470b	62	-	198	
PIMUZ A/III 1470c	67	177	193	2.64
PIMUZ A/III 1470d	70	170	207	2.43
PIMUZ A/III 1470e	71	180	200	2.54
PIMUZ A/III 1470f	60	-	-	
PIMUZ A/III 1470g	68	172	187	2.57
Average	66.3	175	197	2.55
<i>Shonisaurus sikkanniensis</i> holotype (Nicholls and Manabe, 2004, appendix)				
6	95	210	220	2.22
14	83	220	224	2.65
25	99	-	233	
26	92	-	229	
27	109	-	191	
28	87	-	222	
34	93	-	239	
Presacral A	88	249	-	2.83
Presacral D	102	227	-	2.23
Presacral F	93	243	-	2.61
Average	91.6	230	223	2.51
<i>Shonisaurus popularis</i> specimen A of Quarry 5 (Camp, 1980:table 3)				
Anterior dorsal	75	220	-	2.93
Anterior dorsal	80	200	180	2.50
Middle dorsal	90	210	205	2.33
Middle dorsal	90	210	210	2.33
Middle dorsal	80	160	220	2.00
Posterior dorsal	75	200	-	2.66
Posterior dorsal	70	220	-	2.50
Average	80	202	204	2.46
<i>Himalayasaurus tibetensis</i> (Motani et al., 1999)				
Middle cervical	75	160	220	2.28
" <i>Leptoptygius</i> " (Zapfe, 1976)				
Dorsal	54	152	162	2.81

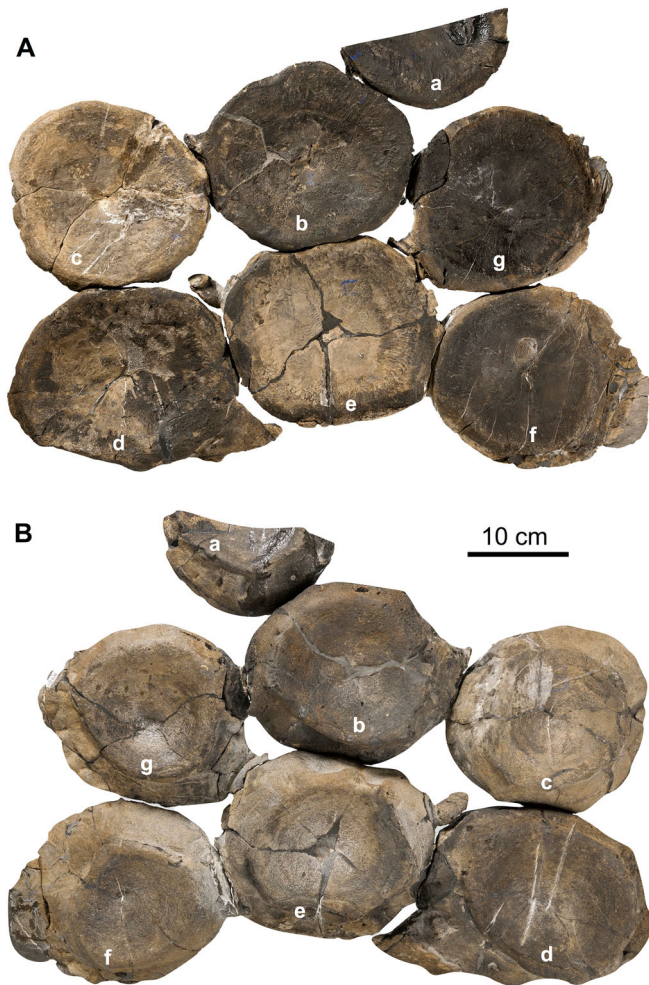


FIGURE 6. Shastasauridae sp. B, PIMUZ A/III 1470a to A/III 1470 g. Seven associated dorsal vertebrae in discovery position, upper Norian-lower Rhaetian Alplihorn Member, Kössen Formation, Schesaplana Mountain, Grisons, Switzerland. **A**, anterior view, field bottom; **B**, posterior view, field top. Note the strong erosion of the bone surfaces. Small white letters are last letter of specimen number.

smooth, lacking ridges. The transition from the endochondral bone of the articular face to the periosteal bone of the sides and ventral surfaces of the centrum is gradual, lacking a sharp demarcation. The floor of the neural canal is about 40 mm wide at either end and not much constricted in the middle. The suture facets for the neural arch are well defined and together with the floor of the neural canal represent the dorsal side of the vertebra. The rib articular facet can be discerned on both sides of the centrum. The facet is located on a raised ridge representing the diapophysis. The diapophysis extends from below the neurocentral suture facet ventrally to more than the mid-point of the vertebra laterally, being closer to the ventral side. In lateral view, the rib facet curves slightly towards anterior. The dorsal end of the ridge is not confluent with the neural arch facet, however. The space between the rib facet and the neural arch is narrow. These features (Fig. 4) allow positioning of the centrum along the vertebral column as a middle dorsal in comparison with other shastasaurids.

Ribs—Seven of the ten ribs (PIMUZ A/III 744b to 744i) are preserved in a cluster near the vertebral centrum, of which five show the same orientation (Fig. 3). These five are right ribs and

one, the longest preserved, is a left one. The seventh is too fragmentary for determination. The ribs have an expanded and anteroposteriorly flattened head with a single articular facet and a gently bent shaft (Fig. 5). The unfinished bone of the articular facet is pitted. This and the rounded shape of the head in anteroposterior view indicate the presence of a thick cartilage cap. The rib heads are dorsoventrally about 110 mm wide, commensurate with the length of the diapophysis (taken as the average between the two sides of the vertebral centrum). The rib heads differ, however, in that in some, the anterior face appears gently convex and the posterior one gently concave, whereas in others both are gently convex. This variation probably results from fossilization processes because adjacent ribs should not vary that much in shape. All ribs lack their distal end, and the maximum preserved rib length is 1100 mm in PIMUZ A/III 744b. The diameter of the shaft increases very gradually from the proximal shaft region distally (Fig. 5). The main difference between the ribs is the tightness and angle of the curvature just distal to the head, which ranges from 20–30° in six specimens and 40–60° in two specimens. While some of this variation may be anatomically positional, the strong curvature of 40–60° in two specimens must also be due to tectonic deformation given the obvious deformation of the vertebral centrum on the same bedding plane (Fig. 3). The anterior side of the shaft is characteristic in having a shallow groove running along the entire preserved rib from the head to the preserved distal end. On the posterior side, there also is a shallow groove that extends from the rib head to the middle of the longest preserved shaft and becomes less pronounced or disappears distally. As a result, the cross section of the distal-most part of the shaft is oval, as can be seen in the distal fracture surfaces. In its proximal part, the dorsal margin of the posterior groove is developed as a rounded crest.

SHASTASAURIDAE sp. B (Figs. 6, 7)

Material—Specimen PIMUZ A/III 1470, seven probable dorsal vertebrae (PIMUZ A/III 1470a–g), probably from a continuous series (Fig. 6). PIMUZ A/III 1470a was incomplete and sectioned for histology. The vertebrae were found arranged in mosaic fashion (Fig. 6), similar to specimens of *Shonisaurus popularis* at BISP (Camp, 1980; Hogler, 1992:fig. 5B; Fig. S9).

Horizon and Locality—Upper Norian to lower Rhaetian Alplihorn Member, Kössen Formation. Western flank of Schesaplana Mountain, Seewis, Canton Grisons, eastern Swiss Alps, Switzerland (coordinates 47.0518547N, 9.6983309E).

Differential Diagnosis—The vertebrae of PIMUZ A/III 1470 differ from PIMUZ A/III 744 in size and proportions. They are smaller and relatively longer. They are also smaller than those of *S. sikkanniensis* and *S. popularis* but share the same H/L ratio of about 2.5 with these two taxa (Table 2). PIMUZ A/III 1470 also differs from *S. sikkanniensis* and *S. popularis* in the indistinct boundary between the periosteal bone and the endochondral bone of the articular surface (Figs. 7, S7–S9). This feature is shared with PIMUZ A/III 744. An indistinct boundary is also seen in some specimens of *S. popularis*, but this is due to pre-burial erosion. PIMUZ A/III 1470 differs from *S. sikkanniensis* and *S. popularis* in the radial ridges on the articular surface of the centra, which are shared by PIMUZ A/III 744.

Description—As mentioned above, the vertebrae PIMUZ A/III 1470a–g were preserved as a mosaic lying on the sea floor, with the centra in close proximity. The centra were excavated in a way that preserved their relative position to each other, with the marly matrix still adhering to the fossils. This allowed reassembly of the field situation (Fig. 6). In all centra, all anatomical elements are difficult to detect due to

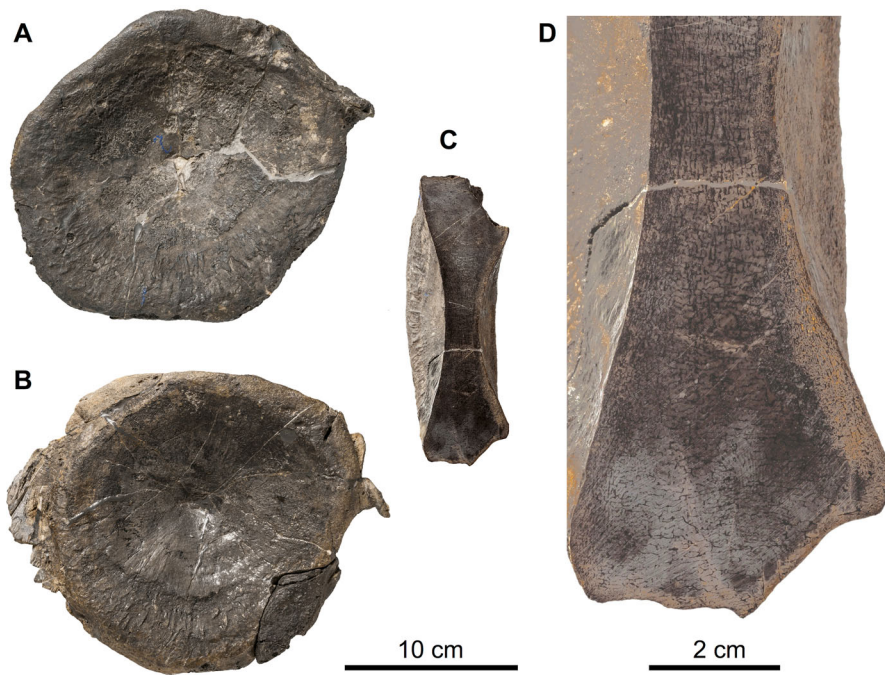


FIGURE 7. Shastasauridae sp. B, selected dorsal vertebral centra of PIMUZ A/III 1470, Upper Norian to lower Rhaetian Alplihorn Member, Kössen Formation, Schesaplana Mountain, Seewis, Grisons, Switzerland. **A**, PIMUZ A/III 1470b in field bottom view, neural canal is at the top; **B**, PIMUZ A/III 1470 g in field bottom view, neural canal is at the top; **C**, PIMUZ A/III 1470a in cross section. Note the very short anteroposterior length. **D**, close-up of **C**, the intact trabecular architecture indicates that the vertebra is uncrushed and the shortness is the original morphology.

the strong preburial corrosion of the vertebra, only leaving the field-bottom face untouched. However, the polished section across one centrum (PIMUZ A/III 1470a) indicates that the internal trabecular structure is intact (Fig. 7C, D) and that therefore no anteroposterior shortening of the centra by compaction occurred. The vertebrae PIMUZ A/III 1470a–g are clearly smaller than PIMUZ A/III 477a (see Table 2) and probably represent dorsal vertebral centra. However, the perimeter of the centra is too corroded to reveal the location of the facets for the neural arch and the rib articular facets to confirm this positioning in the column. The lack of rib articular facets also means that the anteroposterior orientation is not known. The well-preserved field-bottom articular faces show the same kind of sculpture of rings and radial ridges (Fig. 7) as PIMUZ A/III 477a. The proportions of the centra are different from this large centrum because they are relatively longer by about 25%, with a MD/L ratio of around 2.5 vs. 3.16 in the larger PIMUZ A/III 477a. This is a maximum value, of course, because of the loss of material due to corrosion on the field-top face. This difference in proportion could be positional or ontogenetic, although in the related taxa, the proportions are similar throughout the presacral vertebrae column. In addition, such distinctive proportional changes in an ontogenetic series of very large ichthyosaurs has not been observed before, a case in point being the study of Camp (1980) who did not note any proportional differences in all of his large-bodied specimens.

DISCUSSION

Giant Tooth Fragment: Affinity, Size Comparison, and Implications

As discussed above, many of the giant Late Triassic ichthyosaurs appear to lack teeth. The only certain exception is *Himalayasaurus* (Motani et al., 1999) and the tooth PIMUZ A/III 670 described in this study. There is no indication that PIMUZ A/III 670 represents a specimen of *Himalayasaurus* because

the root is larger in diameter than the crown (as opposed to *Himalayasaurus* with its labiolingually flattened, carinate crown). The nearly circular cross section of the crown base of PIMUZ A/III 670 (Fig. 1) suggests that the crown was not laterally flattened nor is there any indication of the mesial and distal carinae seen in *Himalayasaurus* (Motani et al., 1999) and *Thalattoarchon* (Fröbisch et al., 2013). In both of these taxa, the carinae extend to the crown base (Motani et al., 1999:fig. 4A, B; Fröbisch et al. 2013:fig. 1E–H; PMS personal observation) and very likely would be recognizable in a specimen similar in preservation to PIMUZ A/III 670. The incomplete tooth PIMUZ A/III 670 is distinctive in the labiolingually somewhat compressed root base and the labiolingual curvature of the root (Figs. 2, S4), neither of which are seen in standard conical ichthyosaur teeth. The curvature, however, could also indicate a posterior position in the jaws, as seen in Cretaceous platypterygiin ichthyosaurs (Fischer, 2016). These ichthyosaurs also have labiolingually compressed roots, although the compression may be diagenetic (Fischer, 2016). We refrain from erecting a new taxon for PIMUZ A/III 670 at this time because it would be based on a single incomplete tooth.

The strong curvature of the root is reminiscent of the teeth of large odontocetes, i.e., sperm whales and orcas, which have posterolingually recurved teeth. The curvature possibly indicates a raptorial mode of feeding or a diet of large coleoid cephalopods in the ichthyosaur species that PIMUZ A/III 670 belongs to. Alternatively, the curvature may be explained by a posterior position of the tooth in the jaw, as noted above.

The incomplete tooth PIMUZ A/III 670 is very large, and its root is the largest known for any ichthyosaur tooth. Next in line is the only complete tooth of *Himalayasaurus* (Fig. S6), and the Lower Jurassic teeth described by McGowan (1996) (Table 1). At 133 mm total height, the only complete tooth of *Himalayasaurus* is somewhat higher than what is preserved of PIMUZ A/III 670 (100 mm), but the latter lacks most of the crown. To exceed the value of 133 mm of *Himalayasaurus*, the crown of PIMUZ A/III 670 would thus have to be higher than 43 mm (Fig. S4). This appears likely because otherwise the

crown would be less high than its greatest diameter (ca. 46 mm). If the root/crown ratio of *Himalayasaurus* were to be applied to PIMUZ A/III 670, the latter would have been 163 mm high. However, this is probably an overestimate because *Himalayasaurus* has an unusually high crown. A graphical comparison of PIMUZ A/III 670 with the complete tooth of *Himalayasaurus* IVPP V4300-1 (Fig. S4) also suggests a total height of >150 mm. It thus is probably safe to assume that the tooth PIMUZ A/III 670 was between 150 and 160 mm high.

The largest of the Lower Jurassic teeth is BMNH 28283 from Lyme Regis (McGowan, 1996). The source beds are either Hettangian or Sinemurian in age. McGowan (1996) states that the entire tooth is 116 mm high but that the crown, which has sharp cutting edges, is only 33 mm high (Table 1). The root thus must be 83 mm high, compared with the 90 mm root height in PIMUZ A/III 670. Thus, PIMUZ A/III 670 is likely to have been distinctly larger than BMNH 28283.

The teeth assigned to *Shonisaurus* by Camp (1980:figs. 22, 23) are significantly smaller, as described by Camp (1980:166). Camp (1980) also figured some *Shonisaurus* teeth but did not provide a scale bar, only a magnification factor of questionable reliability. Indeed, later observers (Nicholls and Manabe, 2004; see above) question the presence of teeth in the large large in-situ skeletons altogether.

Morphology of Centra and Implications for Soft Part Anatomy

One feature of vertebral morphology shared by PIMUZ A/III 744 and PIMUZ A/III 1470 needs to be discussed against the background of taxonomy. This feature is the distinctive radial ridge sculpture on the articular surfaces of centra (Figs. 4, 7A, B). It clearly is not present in *S. sikkanniensis* (PMS personal observation, Figs. S7, S8) and not seen in the *S. popularis* specimens still *in situ* at BISP (PMS personal observation, Fig. S9). However, the radial ridge sculpture in these specimens potentially could have been destroyed by pre-burial erosion on the sea floor, because it is not seen on the field-top side of the PIMUZ material, either. The material in the NSM collections and figured by Camp (1980) lacks the radial ridges. The radial ridges are unlikely to be pathological in origin because they are present in all vertebrae of both PIMUZ specimens.

Presumably, the radial ridges reflect the nature of the intervertebral soft part anatomy. Ichthyosaurs were recently shown to have possessed an intervertebral disc (Wintrich et al., 2020). Possibly, the radial ridges thus could reflect the insertion of the fibrocartilage of the annulus fibrosus in the peripheral region of the articular surface (Wintrich et al., 2020). On the other hand, the ridges may be linked to a particularly thick cartilaginous endplate that was located between the endochondral bone of the centrum and the intervertebral disc. Such a thick cartilaginous endplate may also be indicated by a feature seen in both PIMUZ specimens (but absent in other ichthyosaur dorsal vertebra, including *S. sikkanniensis* and *S. popularis*; PMS personal observation, Figs. S7–S9), the indistinct boundary between the periosteal and endochondral domains. Thick cartilaginous endplates attached to the the bony centrum would have substantially lengthened the centrum. This would have brought the centrum proportions of the PIMUZ specimens and other very short Late Triassic ichthyosaur centra (Table 2, Fig. 8) more in line with normal ichthyosaur centrum proportions. Our hypotheses about soft part anatomy possibly could be tested histologically as shown by Wintrich et al. (2020) for intervertebral articulations in many fossil amniotes. A similar conclusion about soft part anatomy and vertebral spacing was reached by Massare et al. (2006) based two specimens of the Middle Jurassic ichthyosaur *Ophthalmosaurus natans*. In these specimens from the Sundance Formation of Wyoming (U.S.A.), there is wide vertebral spacing in the entire vertebral column and an indistinct

boundary between the periosteal and endochondral domains in the caudal column (Massare et al., 2006).

Affinities of the Two Partial Postcranial Skeletons

Several issues surround the taxonomy of the giant vertebrae and ribs from the Kössen Formation. First, do the two major finds, PIMUZ A/III 744 and PIMUZ A/III 1470, represent the same taxon? Second, can this taxon (or the two taxa) be assigned to a known species? Third, how does the material differ from other Late Triassic giant ichthyosaur finds? Named valid species are *Shonisaurus popularis*, *Shastasaurus sikkanniensis*, and *Himalayasaurus tibetensis*. Motani et al. (1999) had already noted that *S. popularis* and *Himalayasaurus* may be sister taxa based on the relative shortness of their centra, but this insight is superseded by the discovery of *S. sikkanniensis*. Even shorter but large ichthyosaur centra have been described particularly from late Norian and Rhaetian localities across Europe (Fig. 8), having been found in Austria (Zapfe, 1976), the U.K. (Storrs, 1994), France (Fischer et al., 2014), and most recently Germany (Sander et al., 2016). It thus is interesting to note that the unequivocally Rhaetian specimen, PIMUZ A/III 744, is also shorter than all the Norian or Norian/Rhaetian ones (Table 2). Possibly, this reflects a paedomorphic evolutionary trend to a reduced ossification of the vertebral column accompanied by an increase in cartilaginous endplate thickness.

The two PIMUZ specimens probably differ in body size, given that centrum length and height (to a lesser extent) are good proxies for total length. PIMUZ A/III 744 thus is larger than PIMUZ A/III 1470 (Table 2). The main difference, however, are the proportions, which would suggest that PIMUZ A/III 744 and PIMUZ A/III 1470 each appear to represent a distinctive taxon of giant shastasaurid. However, the proportional differences between the two specimens could be preservational or positional, and the size differences could be ontogenetic. Arguing against the two individuals representing an ontogenetic series is the marked degree of proportional difference of 20% combined with a limited size difference. Such strong ontogenetic proportional differences have not been reported for the only giant Late Triassic ichthyosaur, which shows a probable ontogenetic series, *S. popularis* (Camp 1980), nor other ichthyosaur ontogenetic series including presumable adults. Without directly investigating the internal trabecular structure of the larger vertebra, we cannot exclude the possibility that this centrum was shortened by compaction of the enclosing sediment. However, the ribs of the same specimen show no indication of compaction, as noted above.

Two characters unite the two PIMUZ specimens, however: the radial ridges on the articular faces of the centra and the gradual transition from the articular surface to the outer periosteal surface (Figs. 4, 7A, B), not seen in any of the named taxa. Nevertheless, these features are not enough to erect new species for the PIMUZ material.

In terms of morphology, the European isolated Norian and Rhaetian presacral vertebrae centra mentioned above are difficult to compare because of the lack of positional information within the vertebral column. Nevertheless, the Kössen Formation vertebra described by Zapfe (1976) has a bicipital rib articulation with very widely spaced articular facets, one near the dorsal margin and one near the ventral one. One Aust Cliff vertebra (Storrs, 1994) has a round single facet in a ventral position.

Size Comparison among Late Triassic Giant Ichthyosaurs

The Kössen Formation specimen described by Zapfe (1976) as well as the vertebrae from the epicontinental Rhaetian of the U.K. (Storrs, 1994), France (Fischer et al, 2014), and Germany (Sander et al., 2016) (Fig. 8) clearly represent smaller

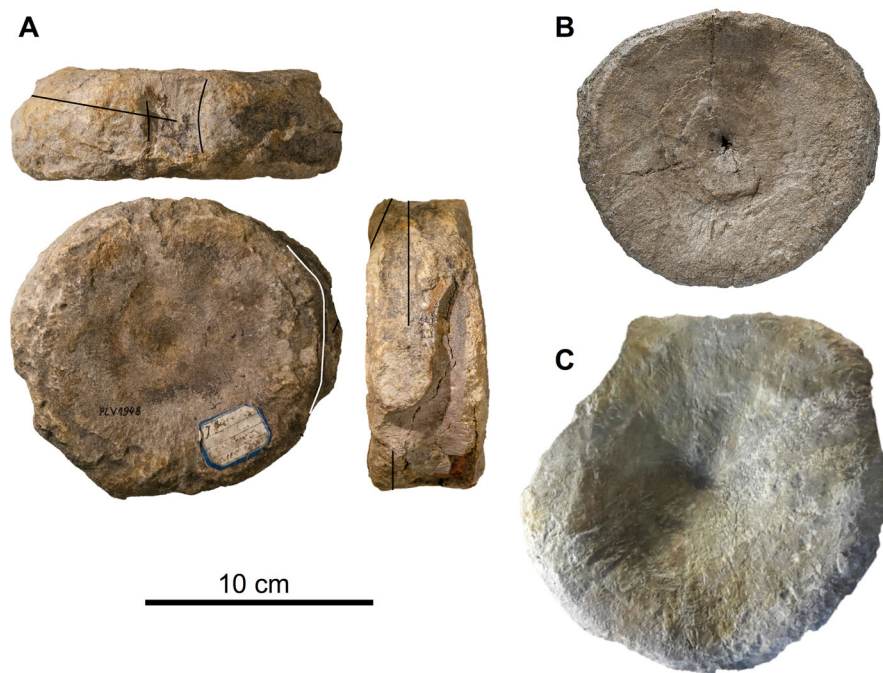


FIGURE 8. Various very large ichthyosaur vertebrae from the European Rhaetian. **A**, dorsal vertebra from the French Rhaetian near Autun in dorsal view (top), anterior view (bottom), and right lateral view (right; modified from Fischer et al., 2014); **B**, cervical or anterior dorsal vertebra from Bonenburg, Westphalia, Germany, in anterior view (modified from Witkowski, 2017); **C**, dorsal vertebra from Neumühle, Austria, in anterior view. Specimen of Zapfe (1976).

ichthyosaurs than *S. sikkanniensis* and the larger of the two PIMUZ finds, PIMUZ A/III 744. The largest of these other specimens has a centrum diameter of 20 cm (BRSUG 7007; Storrs, 1994), greater than the smaller of the two Swiss finds, PIMUZ A/III 1470. The Austrian centrum from the Kössen Formation of Neumühle (Fig. 8C) is 54 mm in anteroposterior length, 152 mm in dorsoventral height, and 162 mm in width (Zapfe, 1976). This is somewhat smaller than both PIMUZ specimens. The epicontinental Rhaetian finds from Germany are clearly smaller (Fig. 8B), but one of the French finds is the same size as the smaller Swiss one, the Cuers ichthyosaur (Fischer et al., 2014) (Fig. 8A).

The discovery of the large ichthyosaurian remains from the Kössen Formation of the eastern Swiss Alps raises the question whether this material could represent the remains of the largest ichthyosaurs that ever evolved. Body size estimates for the Kössen Formation material needs to be based on a comparison of the dimension of the dorsal vertebral centra, which are represented by PIMUZ A/III 744a, the somewhat smaller PIMUZ A/III 1470, the material of *S. popularis* and the holotype of *S. sikkanniensis*.

The overall width across the diapophyses (262 mm) of PIMUZ A/III 744a is greater than the widest *S. sikkanniensis* vertebra (240 mm). The highest *S. sikkanniensis* dorsal is 249 mm, whereas PIMUZ A/III 744a is slightly less high (237 mm). The greater width and lesser height of PIMUZ A/III 744a presumably results from post-mortem deformation. The greatest length of *S. sikkanniensis* dorsal vertebrae is 109 mm, but the average of the dorsal vertebrae (posterior to the 10th) is 93 mm (Table 2). PIMUZ A/III 744a is only 75 mm long. Thus, whichever comparative measure is used for dorsal vertebral dimension, the animal from which PIMUZ A/III 744a derives may have been the same size or only slightly smaller than the holotype of *S. sikkanniensis*. This conclusion is strengthened by probable presence of thick cartilaginous endplates in the two PIMUZ specimens, suggesting a similar segment length of PIMUZ A/III 744a and *S. sikkanniensis*. Both animals thus could have had a similar body size provided their vertebral counts were similar.

As for PIMUZ A/III 1470, its vertebral dimensions are clearly smaller than those of PIMUZ A/III 744a as well as of the holotype of *S. sikkanniensis*, a large specimen of *S. popularis* (specimen A from Quarry 5), and the holotype of *Himalayasaurus tibetensis* (Table 2), leading to a size estimate of well under 15 m for PIMUZ A/III 1470.

Nicholls and Manabe (2004) note in passing that isolated bones from the Pardonet Formation indicate larger individuals of *S. sikkanniensis* than the holotype. The only published evidence of significantly larger ichthyosaurs than the holotype of *S. sikkanniensis* and PIMUZ A/III 744a is a report of an ichthyosaurian vertebral centrum (now lost) from the Triassic of New Zealand (Hector, 1878). The specimen was reported in this scientific publication to have measured 457 mm in diameter (Hector, 1878). However, the specimen does not survive in any collection and thus its size cannot be verified today (Zammit, 2010). Other giant Late Triassic ichthyosaurs appear to be represented by very large probable jaw bones from the Rhaetian of the U.K. (Lomax et al., 2018). The existence of giant ichthyosaurs in the Late Triassic of the western Tethys realm is, of course, also documented by the large tooth PIMUZ A/III 670 discussed above (Fig. 1).

Ecological and Evolutionary Implications of Late Triassic Giant Ichthyosaurs

Named species of giant ichthyosaurs from the Late Triassic all derive from western North America and East Asia, but indications of their presence had also come from the European Norian and Rhaetian (Fischer et al., 2014; Lomax et al., 2018). The remains of giant ichthyosaurs from the eastern Swiss Alps now confirm these earlier reports based on unequivocally ichthyosaurian material and indicate that such ichthyosaurs also inhabited the western Tethys.

The paleoenvironment of the Alplihorn and Schesaplana members of the Kössen Formation, from which the Swiss material originates, is a very wide lagoon or shallow basin characterized by restricted circulation (Furrer, 1993), consistent with the finds of placodonts (Furrer, 1993; Neenan and Scheyer,

2014), pterosaurs (Fröbisch and Fröbisch, 2006; Stecher, 2008), and phytosaurs (Furrer, 1993), but inconsistent with the occurrence of giant ichthyosaurs. This suggests that these marine reptiles, which were adapted to a life in the open sea, sometimes strayed into the coastal basin of the northwestern Tethys ocean or that their carcasses were washed in.

These Late Triassic giant ichthyosaurs clearly were among the largest animals to ever inhabit our planet. Despite their global distribution in the Norian and Rhaetian marine habitats, we know next to nothing about their morphology, size, lifestyle, and feeding adaptations. Diversity in feeding adaptation is suggested by the seemingly toothless jaws of several finds, including the Norian *Shastasaurus sikkanniensis* (Nicholls and Manabe, 2004) and the Rhaetian probable ichthyosaurian jaw bones from France and the U.K. (Fischer et al., 2014; Lomax et al., 2018; see also Fig. S5). On the other hand, some of these giants had accordingly sized predatory teeth, as evidenced by *Himalayasaurus* (Motani et al., 1999) and the giant tooth described here (PIMUZ A/III 670).

Gigantism arose very early on in ichthyosaurs, only a few million years after the origin of the clade in the earliest Triassic (Sander et al., 2021). Body size evolution in ichthyosaurs is best described by an early burst model, and the giant Late Triassic ichthyosaurs discussed in this study are the result of this evolutionary trend (Sander et al., 2021). The importance of the new material is that it helps to characterize the final phase of ichthyosaurian gigantism. Because of its young stratigraphic age, i.e., Rhaetian, the tooth PIMUZ A/III 670 and the partial skeleton PIMUZ A/III 744 show that giant ichthyosaurs persisted close to the end of the Triassic. The putative giant ichthyosaur jaw material described by Fischer et al. (2014) and Lomax et al. (2018) is consistent with this observation. The finds from the eastern Swiss Alps thus strengthen the conclusion already reached by Thorne et al. (2011) and Fischer et al. (2014) of massive extinction among ichthyosaurs at the end of the Triassic. This is contrary to suggestions of more gradual extinctions (Martin et al., 2015) based on rather scanty evidence (see also Lomax et al., 2018).

CONCLUSIONS

The giant Late Triassic ichthyosaurs material described in this study comes from the Upper Triassic Kössen Formation in the Austroalpine nappes of the eastern Swiss Alps, Canton Grisons. The material was recovered from the two lower members of the formation, the Alplihorn Member (late Norian to early Rhaetian in age) and the Schesaplana Member (Rhaetian). The two partial skeletons may represent a single species or two species that existed at least from the late Norian to the Rhaetian. The giant tooth from the Schesaplana Member cannot be assigned to the same taxon as the postcranial material with any certainty. As for size of the two partial skeletons, the larger one rivals the largest in ichthyosaurs known in vertebral diameter but not in vertebral length. Uncertainties regarding the thickness of the intervertebral disk and the number of presacral vertebrae make total body size estimates difficult for the Swiss material.

There are several implications of specimen PIMUZ A/III 670: for one, it represents the currently known upper limit of tooth size in ichthyosaurs. Second, together with the scanty but morphologically different dental material of *Himalayasaurus*, the tooth suggests the existence of a diversity of giant tooth-bearing ichthyosaurs in the Late Triassic. These must have been the size of the very large odontocetes and inhabited the world's ocean as macropredators, coexisting with toothless giants. Third, the find underscores the notion that the Late Triassic ichthyosaurs were distinctly larger than the more familiar Jurassic forms. The fossils described in this paper also underscore

the global distribution and ecological diversity of giant Norian and Rhaetian ichthyosaurs and the profound faunal turnover among ichthyosaurs at the end of the Triassic.

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