SHORT COMMUNICATION

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Bernhard Peyer and his discoveries of Triassic vertebrates in Switzerland

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Abstract

Bernhard Peyer (1885–1963) was a prominent Swiss vertebrate palaeontologist and anatomist at the University of Zurich. In 1919, he discovered the occurrence of Middle Triassic (Anisian–Ladinian) ichthyosaurs, sauropterygians, and other reptiles at Monte San Giorgio on the border between Switzerland and Italy. Starting in 1924, Peyer, and later his student and successor Emil Kuhn-Schnyder, worked tirelessly to excavate and collect material from fossil-bearing deposits in this region. The discovery of an articulated skeleton of a long-necked reptile in 1929 allowed Peyer to solve the riddle of unusually elongate bones from the German Muschelkalk, which, he demonstrated, were cervical vertebrae of the extraordinarily long-necked reptile *Tanystropheus*. As a student in 1919 and later in 1942, Peyer explored a Rhaetian bonebed close to his native town of Schaffhausen. Processing the sediment, he recovered numerous small bones and teeth of vertebrates, among which teeth of diverse stem-mammals are of particular importance.

Introduction

The recognition of the world-famous Middle Triassic (Anisian–Ladinian) marine biota at Monte San Giorgio is due to the efforts of the Swiss palaeontologist and zoologist Bernhard Peyer (1885–1963). It is therefore appropriate to present a brief biography of this remarkable scientist and scholar in this Special Issue dedicated to the UNESCO World Heritage Site Monte San Giorgio. A leading expert on the Monte San Giorgio fauna, Rieppel (2019) published a richly illustrated book on the Triassic fossils from Monte San Giorgio and their discovery. Furrer (this issue) provides a detailed history of the collecting activities at Monte San Giorgio.

This biographical sketch is based on information from an obituary published by H. Peyer (1963) a biography by Schlatter (2007), and the historical background of

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the research at Monte San Giorgio in Rieppel (2019). H. Peyer's (1963) article also includes a complete list of Bernhard Peyer's publications.

Bernhard Peyer (Fig. 1) was born in Schaffhausen on July 25, 1885, as the son of Sophie (née Frey) Peyer and the textile manufacturer Johann Bernhard Peyer. Even as a young pupil he distinguished himself with his phenomenal memory and remarkable gift for languages. In high school, Peyer developed a deep interest in the natural world under the tutelage of one of his teachers. He also met and worked with the geologist Ferdinand Schalch (1848–1918; Fig. 1), a Schaffhausen native who studied and mapped the geology of the region around the city.

Given his linguistic abilities and classical humanistic education, Peyer could have chosen an academic career as a philologist, but his love of nature and the outdoors won out and led him to pursue studies in the natural sciences. Peyer studied at the universities in Tübingen, Munich, and Zurich. In Zurich, he earned his doctorate under the supervision of the zoologist Arnold Lang (1855–1914) with a study on the cranial development of the asp viper, *Vipera aspis* (Peyer, 1912). Following the completion of his studies, Peyer joined the primatologist and anatomist Hans Bluntschli (1877–1962; Fig. 1) on an expedition to the upper reaches of the Amazon



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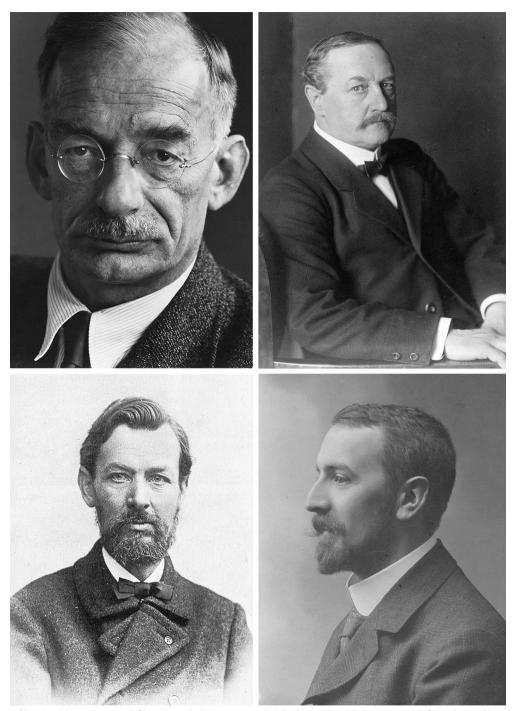


Fig. 1 Portraits of Bernhard Peyer (top row, left), Karl Hescheler (top row, right), Ferdinand Schalch (bottom row, left), and Hans Bluntschli (bottom row right). Portrait of Bernhard Peyer from author's collection; all other images sourced from Wikipedia

and Argentina to collect monkey embryos. After returning from his trip to South America, Peyer went to Munich again to attend lectures by the renowned vertebrate anatomist Richard von Hertwig (1850–1937) who, together with his brother Oscar, had developed

the germ layer theory. While there, he formed lifelong friendships with the palaeontologists Ferdinand Broili (1874–1946) and Ernst Stromer von Reichenbach (1870–1952), both of whom became leading authorities in the field in Germany.

At the University of Zurich, Lang's successor, Karl Hescheler (1868-1940; Fig. 1), had taught courses in palaeontology since 1903. He encouraged Peyer to seek a faculty position in palaeontology and comparative anatomy. Peyer's Habilitation project (a second thesis required for teaching at universities in the Germanspeaking countries) examined the structure of the fin spines in various catfishes and carps (Peyer, 1922). He became a Privatdozent and introduced systematic palaeontology at the university. His inaugural lecture was entitled "Wesen und Ziele der Paläontologie" (The nature and aims of palaeontology). At the beginning of Peyer's university career, the collections of fossil vertebrates housed in Zurich were inadequate. Thus, he embarked on a new research program to build up these holdings. As detailed below, his efforts were aided by a serendipitous discovery in southern Switzerland.

At the University of Zurich, Peyer was promoted to Associate Professor (Extraordinarius) for Palaeontology in the Department of Zoology in 1930, appointed Director of the Museum of Zoology in 1940, and, in 1943, Professor of Palaeontology and Comparative Anatomy in the Department of Zoology. He also served as Dean of the Philosophical Faculty II of the University of Zurich (1940-1942). Peyer retired in 1955 and never returned to the museum due to a dispute with a former student. He passed away after a long illness in uZurich on February 23, 1963.

Peyer's scientific achievements were recognized by his election to the Kaiserlich Leopoldinisch-Carolinisch Deutsche Akademie der Naturforscher (1936; now Deutsche Akademie der Naturforscher Leopoldina) and as 'Correspondant' of the Académie des Sciences in Paris (1957). He was also active in various Swiss academic societies. A man with a great sense of humor, he delighted members of the Schweizerische Naturforschende Gesellschaft by twice staging sketches at meetings. Peyer would use his fluency in English, French, Italian, and Spanish at international conferences to facilitate conversations between attendees from different countries. In 1967, the town of Meride posthumously made him an honorary citizen and named the street in his honor, Via Bernardo Peyer.

In 1926, Peyer married Hildegard Amsler, the widow of his cousin Hans Hermann Peyer. He named one of his first major finds from Monte San Giorgio, the armored placodont Cyamodus hildegardis, in her honor (Peyer, 1931b). The couple had a son and a daughter in addition to a son and two daughters from the wife's first marriage.

Peyer and Monte San Giorgio

After attending the 1919 annual meeting of the Schweizerische Naturforschende Gesellschaft in Lugano, Peyer decided to prospect an outcrop of Middle Triassic bituminous shales of the Grenzbitumenzone (now Besano Formation) quarried for oil extraction. This was at Monte San Giorgio, near the town of Meride in the Canton Ticino and operated by the Società Anonima Miniere Scisti Bituminosi di Meride e Besano. The first fossil fishes from their mine Cava Tre Fontane had already been acquired by the Museum of Zoology in 1916. Correlative oil shales in northern Italy had previously yielded fishes and various marine reptiles during the nineteenth century (Bassani, 1886; Stoppani, 1863).

The oil-extracting company allowed him to search spoil heaps of shale, and Peyer almost immediately found the well-preserved forefin of a small ichthyosaur. Encouraged by this discovery, he extended his search to spoil heaps of bituminous shale material at the mine Cava Tre Fontane, which is located on the western flank of Monte San Giorgio. There Peyer recovered only fragmentary remains because the shales were quarried by mining operations that included blasting. Peyer realized that the collection of better material would require exposing large individual bedding planes of fossil-bearing rock.

Returning from his trip, Peyer showed his finds to his friend and supervisor Karl Hescheler, who immediately grasped their importance. He offered financial support and urged his young colleague to apply for funding from a newly established Swiss foundation, the Georges and Antoine Claraz Stiftung. Peyer's application was successful, and he started fieldwork in 1924 after receiving permission from the Miniere Scisti Bituminosi di Meride e Besano to collect fossils at two sites. Peyer had to pay a substantial fee to gain access to and dig at Cava Tre Fontane and in Val Porina, a valley along the southern slope of Monte San Giorgio. In return, the company provided two workers to assist in exposing a large area of bedding planes of dolomite and black shale. The hard physical labor was rewarded by finds of fishes and complete skeletons of ichthyosaurs and several taxa of sauropterygian reptiles. This success spurred Peyer to return to the site in 1925. Systematic excavation layer by layer continued to yield spectacular finds. Peyer decided to extend the scope of his fieldwork to areas not worked by the oil-extracting company. His reconnaissance led to the discovery of fossils not only in the Grenzbitumenzone but also in the overlying lower beds of the Meride Limestone. Peyer and his crew would return annually to work these sites between 1927 and 1933 and again in 1937 and 1938.

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One discovery, made by Peyer at Val Porina in 1929, proved to be particularly important. He found an articulated, nearly complete skeleton of an unusually longnecked reptile. Peyer immediately noticed that the neck vertebrae of this specimen matched peculiar elongate bones first reported from the Middle Triassic Muschelkalk near Bayreuth, Germany. The German palaeontologist Hermann von Meyer (1801–1869) described these elements and placed them in a new taxon, Tanystropheus conspicuus in his classic monograph on Middle and Late Triassic tetrapods from Central Europe (Meyer, 1847-1855). He interpreted them as caudal vertebrae but left their zoological affinities unresolved. In 1886, the Italian paleontologist Francesco Bassani (1853–1916) reported (without illustrations) on a curled-up skeleton of a smallsized reptile, which he named Tribelesodon longobardicus in reference to its three-cusped teeth and classified as a pterosaur (Bassani, 1886). This fossil was recovered from bituminous shales of the Besano Formation above Besano in Italy, a short distance from the border with Switzerland and close to Monte San Giorgio. Many years later, Bassani's purported pterosaur attracted the interest of the Austro-Hungarian palaeontologist Baron Franz von Nopcsa (1877–1933). Nopcsa (1922) accepted Bassani's interpretation of Tribelesodon longobardicus as a pterosaur and interpreted elongated bones of the original specimen as elements of a long wing finger, a diagnostic feature of pterosaurs. Peyer's discovery finally solved the long-standing mystery of these bones-they were vertebrae forming a greatly elongated neck (Peyer, 1931a). Peyer published a detailed anatomical study of Tanystropheus and established that Tribelesodon was a subjective junior synonym of the former taxon.

The wealth of recovered fossils posed a challenge for preparation and research. Back in Zurich, Peyer decided to proceed systematically, with projects on specific taxa rather than attempt an overall review of the vertebrate assemblages. He meticulously prepared many specimens himself using sharpened gramophone needles to free the bones from the enclosing sediment. Many fossils were also X-rayed at a local hospital. Peyer planned a series of monographs on the Triassic marine fauna, which were issued under the serial title "Die Triasfauna der Tessiner Kalkalpen" (The Triassic fauna of the Ticino limestone Alps) and published starting in 1931. He also provided a general review of the geology and fossil content of the localities at Monte San Giorgio (Peyer, 1944).

His student and eventual successor Emil Kuhn (1905–1994) first joined Peyer in the field in 1925. For his doctorate (awarded in 1932), Kuhn examined vertebrate remains recovered from the prehistoric lake dwellings (7000–3000 years BCE) of Switzerland while working as a

high-school teacher (Kuhn, 1932). He then accepted a job as a research assistant working with Peyer at the Zoological Museum of the university. In 1947, Kuhn presented a monograph on the thalattosaur Askeptosaurus italicus for his Habilitation (Kuhn-Schnyder, 1952). (Kuhn changed his surname to Kuhn-Schnyder following his marriage in 1952.) After Peyer's retirement, he was appointed Director of the newly founded Palaeontological Institute at the University of uürich in 1956. Kuhn-Schnyder led largescale excavations at a locality named Point 902, near Mirigioli on Monte San Giorgio, with tremendous success every summer from 1950 to 1968, amassing a huge collection of Middle Triassic marine vertebrates. This collection remains an invaluable resource for researchers. Doctoral students supervised by Kuhn-Schnyder published several important monographs on fishes (Schwarz, 1970) and reptiles from Monte San Giorgio (Krebs, 1965; Wild, 1973).

Given the enormous number of collected fossils and limited resources for preparation, much of the material long remained unprepared and unstudied. Starting in the 1980s, there has been a resurgence of interest in these important fossils, and investigations continue to this day (e.g., Lautenschlager & Desojo, 2011; Rieppel, 1985, 1987, 1989; Spiekman et al., 2020). The international importance of the classic fossil locality Monte San Giorgio, situated at the southern border of the Alps, was highlighted by its designation as a World Heritage Site by UNESCO in 2003 (Felber et al., 2004). Since 2012, the new Museum of fossils from Monte San Giorgio and visitor center in Meride has been open to the public (Furrer & Vandelli, 2014).

Peyer's other research interests

In addition to his work on the Monte San Giorgio reptiles, Peyer also studied other vertebrate fossils from Switzerland, including giant late Miocene tortoises from the vicinity of Zurich (Peyer, 1942) and the Oligocene alcediniform bird *Protornis glaronensis* from the Canton Glarus (Peyer, 1957). The most important study in this area of his research interests was an exquisitely illustrated monograph on teeth of latest Triassic (Rhaetian) mammal relatives from a locality close to his birthplace Schaffhausen (Peyer, 1956). Peyer's work on these tiny fossils dated back to his fieldwork with Schalch in his youth. In 1915 Schalch had explored a temporary exposure of Rhaetian-age strata at Bratelen (also known as Hallauerberg), a small mountain ridge above the village of Hallau near Schaffhausen. He dug a shaft to expose a bonebed, which yielded small vertebrate remains when the matrix was washed and sieved (Schalch & Peyer, 1919). In 1942, Peyer sank another shaft near Schalch's original site and recovered over eight tons of sediment, which he processed and picked for fossils. His efforts yielded teeth of dipnoans, various sharks, and actinopterygians, teeth and bone fragments of temnospondyls and reptiles, and occasionally teeth of the enigmatic cynodont Tricuspes and of haramiyid and morganucodontid stem-mammals. Clemens (1980) restudied the latter as well as additional fossils that a private collector had donated to the museum in Zurich in 1955. He recognized three new taxa of morganucodontid stem-mammals, with two species names honoring Peyer and Schalch, respectively. Most recently, Whiteside et al. (2017) identified several taxa of rhynchocephalians, including one new taxon, in the Hallau fossil

Aside from his wide-ranging studies on fossil vertebrates, Peyer also maintained a lifelong interest in the structure and evolution of hard tissues in vertebrates, especially teeth. In addition to detailed studies on the dentition in various vertebrate taxa (e.g., Peyer, 1929), Peyer published major reviews on integumentary hard tissues in vertebrates (Peyer, 1931c) and on teeth and dentitions (Peyer, 1937), respectively. Just weeks before his death, his popular introduction to the diversity and evolution of vertebrate teeth appeared in print (B. Peyer, 1963). Starting around 1960, Peyer had worked on a book-length comparative survey of vertebrate dentitions but passed away before he could see it to completion. His former student Rainer Zangerl, then a curator at the Field Museum of Natural History, edited the unfinished manuscript and translated it into English (Peyer, 1968). Peyer (1950a) also authored a well-written introduction to the history of animal life for general audiences.

Peyer never neglected his humanistic interests. As a researcher in a historical science, it was only natural that he should develop a keen interest in the history of biology and medicine. His remarkable linguistic facility allowed him to read ancient texts in their original languages and proved to be a great asset for his historical work. Peyer's publications include a study of the zoological works by Aristotle (Peyer, 1946a), an essay on the Swiss physician and anatomist Johannes von Muralt (Peyer, 1946b), and another essay on Goethe's theory of the vertebrate skull (Peyer, 1950b). He also authored a study on the life and work of one of his distinguished ancestors, the physician and anatomist Johann Conrad Peyer (1653–1712) (Peyer, 1932), and co-authored a major review of medical information contained in the works of the Roman poet Martial (Peyer & Remund, 1928). Peyer's studies in the history of science show the same meticulous attention to detail that characterized his scientific publications.

Conclusion

Peyer was one of the world's leading vertebrate palaeontologists during the first half of the twentieth century, and his discoveries of Triassic vertebrates at Monte San Giorgio represent a major milestone in the history of palaeontology. Today Peyer's scientific contributions are often overlooked since almost all of his papers were published in German. It is to be hoped that the resurgence of scientific interest in the UNESCO World Heritage Site Monte San Giorgio will draw renewed attention to his foundational work.

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