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Research paper

A reassessment of the geochemical, phylogeny, morphology, and taxonomy of two crocodilian jaw remains of Paleogene from central Europe (Germany and Austria)

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Abstract

Crocodiles are a conservative group of reptiles regarding their morphology and behaviour. Available Fossils are hence important to be studied for phylogeny, taxonomy and morphology. A fossil fragmentary crocodilian skull was found in lignite clay in the Paleogene sedimentary area from the Middle Oligocene Epoch of Sieglitz near Camburg at Saale river in Central Germany. This 20th century discovery documents a new species of *Diplocynodon* (*Diplocynodon Haeckeli*, described by Seidlitz in 1917). Another crocodile fossil was unearthed in 1878 from the Eocene Epoch, of Haunsberg near Sankt Pankraz in the province of Salzburg in Austria, which had been missing since 1970 and was recently rediscovered and identified. This rediscovered specimen, representing a crocodile mandible and an isolated tooth, which could belong to *Asiatosuchus* and not *Diplocynodon*. However, the morphology of isolated tooth is not a reliable source to identify it up to the generic level, so open taxonomy is used here for identification, it may be associated to the same or a new species. The new discoveries of fossils provide new characters enhancing our knowledge on a particular taxon and on the whole group.

Keywords: *Taxonomy; Archeozoology; Preparation; Principles; Crocodilian jaws; Paleogene; Central Europe.*

1. Introduction

Crocodilian fauna are ancient group of emblematic reptiles in terms of conservative tendencies of their phylogeny and physiognomy, which conveys a high level of adaptations for a particular type of food and prey access. They hunt their prey by using different techniques, as their prey being diversified and having different size and behaviours. Crocodiles gained different types of adaptations in the past geological time, the refinement of these ones assuring a remarkable continuity of the group's geological existence (They appeared first in the Triassic period, at 228.7 Ma.). Despite the significant number of papers published on different aspects like morphology, taxonomy and phylogeny of eusuchians in the last three decades, a few taxa are still poorly known and their phylogenetic relationships remain controversial or yet untested. A good example is represented by the Asiatosuchus-like taxa that were discovered and described from several localities from Asia, Europe and North America and whose age ranges from the Late Cretaceous to the early Oligocene (Delfino et al. 2017). A single fossil of jaw of Palaeogene crocodile from Germany have been reported and published several times (Karl 1989, 1990, 1991, 1994, 2007, 2017, 2018, 2020; Karl & Müller 2008; and Karl & Tichy 2004, 2019). Complete fossil specimens of same taxa are only known from the Eocene Geiseltal Fossil-Lagerstätte near Halle (Haubold 1989; Kuhn 1938), Eocene Messel Fossil-Lagerstätte near Darmstadt (Berg 1966) and the reptilian fauna from the Eocene Bolca Fossil-Lagerstätte in Italy (Seghetti et al. 2022).
Stratigraphically, the type material of Diplocynodon Haeckeli is related to the Middle Oligocene as described by Karl (1990, 1991, 2007, 2020) and Karl & Müller (2008). The locality is related to the area of the Weißelster basin as Palaeogeographically.
Another almost complete fossil discovery from Sieglitz, would have been available. But the condition of the preserved fossil, in especially its geochemical conditions, did not allow it to be passed on.
Special care is require in preparation and storage of fossils, composed partialy or completely of marcasite and pyrite. Moisturize and oxygenatiom can cause a decay process quickly. The decay of sulphadized fossils, especially in clay, bituminous, or calcareous matrix, is a common problem in paleontological collections. Reference is made to the work "Pride, Preparation, Principles and Prejudices, etc." by Liston (2020).

2. Material and methods

The material refers to a bioclastic limestone tile, shaped through cutting. The counterpart of the limestone plate which most likely contained the dorsal continuation of the specimen was never recovered from the scraps. A fossil's remains of crocodilian jaw was found in lignite clay in the Paleogene sedimentary area from the Middle Oligocene of Sieglitz near Camburg at Saale river in Central Germany. Another crocodile fossil was unearthed in 1878 from the Eocene, of Haunsberg near Sankt Pankraz in the province of Salzburg in Austria, which had been missing since 1970 and was recently rediscovered and reidentified.The limestone slab which contains the fossil remains was slightly processed in the laboratories.

Fossil material 1 (From Germany): Holotype of Diplocynodon Haeckeli Seidlitz 1917, rostrum fragment with remains of the nasals, premaxillae dex. and maxillary dex. now lost or missing due to geochemical erosion. Origin 165 fragments from all body regions, including fragments of dermal placoids, remains of extremities and vertebrae. The whereabouts of all the material is unknown, probably originally from the collection of the former Institute for Geology and Paleontology of Friedrich-Schiller-University in Jena (Fig. 1 - 3).

Fig. 1: Geological Map of Prussia and the Thuringian States (Central Europe), Location of Discovered Materials 2 & 3 = Sieglitz (Germany) and Haunsberg (Austria).

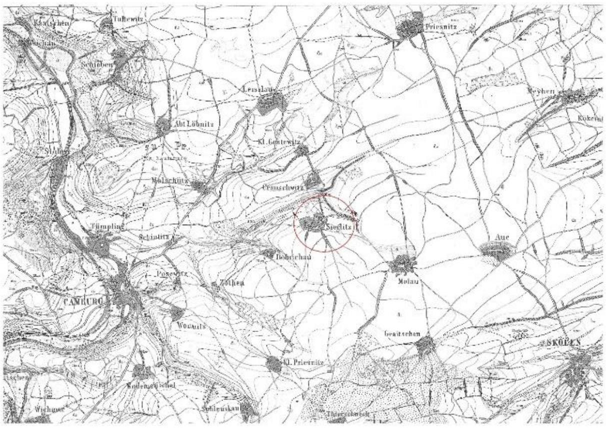

Fig. 2: Geographic Map of Central Europe (Germany), Location of Discovered Material 1 = Sieglitz.

Fossil material 2 (From Austria): Another crocodile remain from the Hansberg near Sankt Pankraz has only recently turned up in Professor Berg's estate and has been returned to the palaeontological collection of the Haus der Natur in Salzburg. Miss Dr. Anna Bieniok, curator of geosciences at the Haus of Natur, infomed that they had surprisingly gotten back the crocodile jaw that had been found before 1878 in the St.Pankraz quarry on the Haunsberg. In 1970, Rudi Vogeltanz sent the jaw fragment to Prof. D. E. Berg in Mainz for determination. The current curator, Prof. Dr. Kerstin Grimm, found it among D. Berg's old documents and sent it back to Salzburg. Vogeltanz gave the only reference to the determination in 1970 in his publication on the sedimentology of the Helvetic in a footnote that Berg had assigned the jaw to a form close to the genus Crocodylus Laurenti, 1768. According to Prof. Grimm, Berg would not have published anything else about it. But Vogeltanz had already suspected as much. Vogeltanz then assigned the teeth to a crocodile and therefore 1970 D. E. Berg contacted. A postcard from Vogeltanz was found with the remains of the pine tree, in which he mentions that he will only include Berg's determination as a footnote in the manuscript from 1970 that has already been submitted. Nothing is known of a publication by Berg on the remains of the pine. In addition to the jaw, there is also a single tooth in the Haunsberg display case, which is designated a crocodile tooth. In the old Fugger catalogue, on the other hand, there are a total of 5 entries for "dinosaur teeth" from St. Pankraz (Fig. 2 & 3).

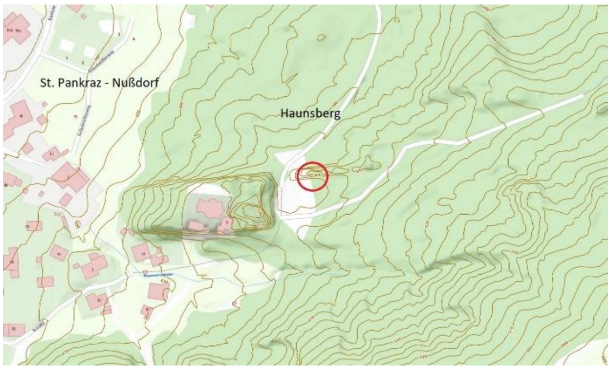

Fig. 3: Geographic Map of Central Europe (Austria), Location of Discovered Material 2 = Haunsberg.

3. Systematic paleontology

Class Sauropsida Huxley, 1864; Subclass Diapsida Osborn, 1903; Infraclass Archosauromorpha von Huene, 1946; Supraorder Crocodylomorpha Hay, 1930; Order 1842 Crocodylia Gmelin, 1789; Suborder Eusuchia Huxley, 1875; Suprafamily Crocodyloidea Fitzinger, 1826; Family Crocodylidae Cuvier, 1807.

1) Gen et spec. indet.

Synonym: Diplocynodon Haeckeli Seidlitz 1917

Locus types: Sieglitz (Könnern) between Halle (Saale) and Bernburg (Saale) in the Fuhne lowlands in middle Germany. The Sieglitz material is geographically and stratigraphically related to the Weißelster basin (Karl 2007), Karl (2020) and Karl & Müller (2008).

Stratum typicum: Lignite clay, Middle Oligocene.

Diagnosis: According to Seidlitz (1917) similar to Diplocynodon darwini Ludwig 1877 from Middle Eocene of Messel in Hessonia.

Taxonomical notes: Diplocynodon darwini is the most common of the many crocodile species in the Messel Pit and Geiseltal basin (Berg 1966; Kuhn 1938). The genus name is due to the pair of fangs in the upper and lower jaws, which can be clearly seen from the side. This is in contrast to most crocodiles where only one tooth is enlarged. The teeth are pointed. Karl & Tichy (2019) list and depict on (Fig. 4), such a pointed tooth from the St.Pankraz quarry on the Haunsberg as Diplocynodon cf. hantonensis (Wood 1846), collected by Rudolf Waldhör, Salzburg. According the revised diagnosis by Martin (2010) and Rio et al. (2020) Diplocynodon hantoniensis (Oligocene) can be diagnosed by a unique combination of characters, e.g. premaxillary surface posterolateral to naris with a deep notch (Rio et al. 2020). These features cannot be represented according to the original illustrations of "D. haeckeli".

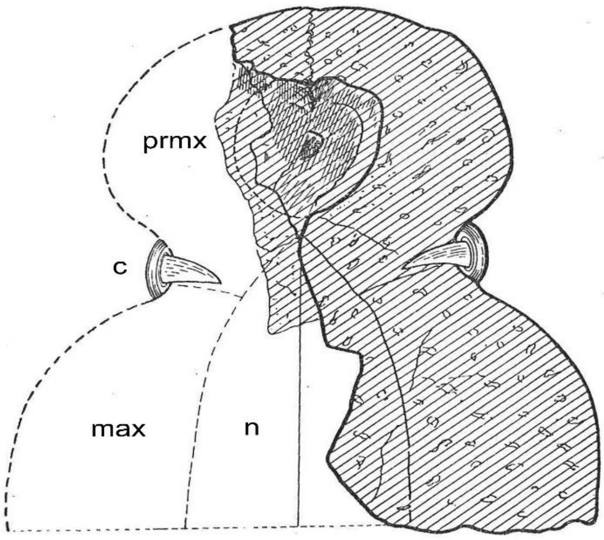

Fig. 4: Reconstruction of the Dorsal Rostral Region of "Diplocynodon Haeckeli" (Seidlitz, 1917): Prmx = Premaxillary Bone, C = Fang or Canine Tooth, Max = Maxillary, N = Nasal Bone.

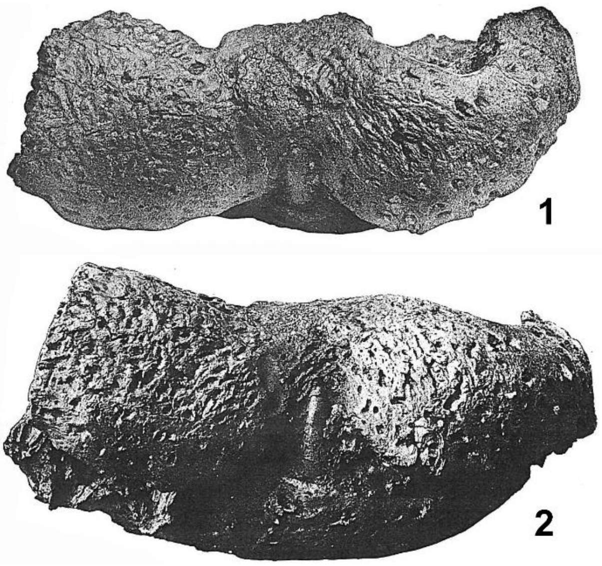

Plate 1: 1 = Dorsal View and 2 = Right Lateral View of the Lost Holotype Specimen of “Diplocynodon Haeckeli“ (Seidlitz, 1917).

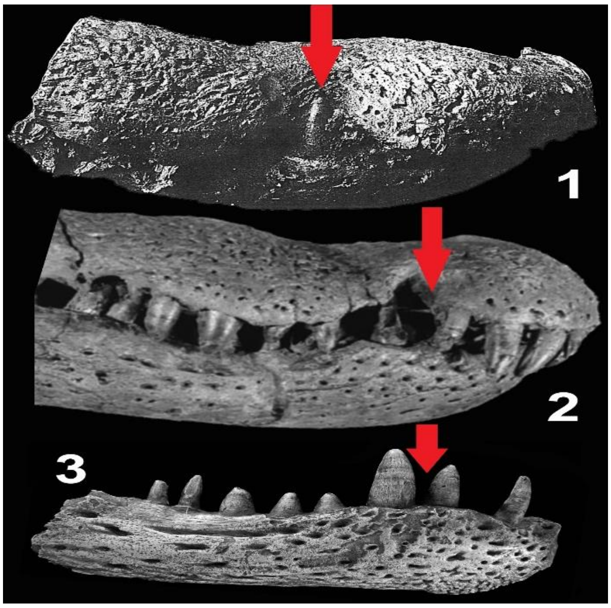

Plate 2: 1: Front Fragment of A Crocodile Snout of Dyplocynodon Haeckeli (Seidlitz, 1917). 2: Anterior Region of A Crocodile Skull of Asiatosuchus Germanicus. 3: Right Front Region of A Crocodile Mandible of Dyplocynodon Hantonensis.

1) Gen et spec. indet.

The fragment of the mandible contains three teeth in origional position. The cross-sections are longitudinally oval, slightly incurved, longitudinally scored, and provided with anterior and posterior longitudinal ridges. The tooth measurements are as follows:

Measuring distances in mm	root length	crown length	crown width at the base
Tooth 1	-	8,84	6,17 x 3,43
Tooth 2	25,19	16,84	10,74 x 7,64
Tooth 3	(18,42)	-	18,29 x 14,42

Locality: The remains of the jaw already have an old inventory number and are already mentioned in the Fugger catalog from 1878 as: dinosaur teeth Mayermelnhofbruch St. Pankraz, found before 1878 in the St.Pankraz quarry on the Haunsberg. Old inventory numbers are 29958 and P-00437 (Plate: 1- 3).

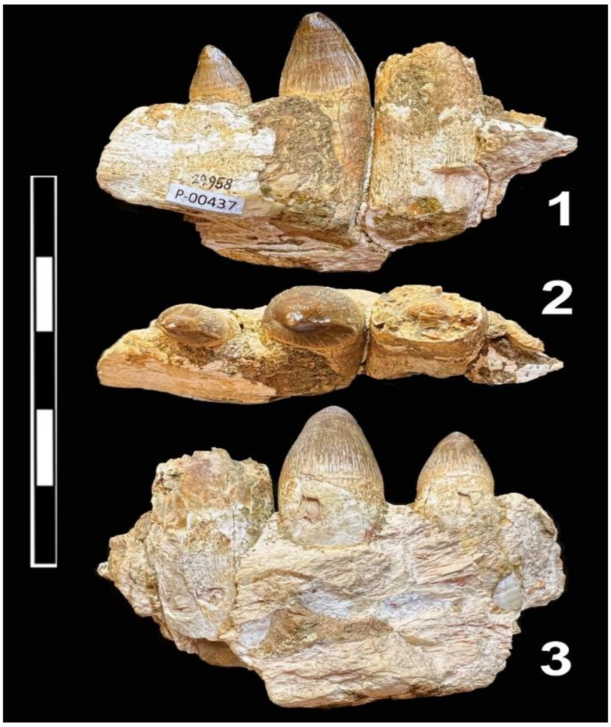

Plate 3: View 1: Inner Region of A Crocodile Mandible Fragment from the Mayermelnhofbruch St. Pankraz. View 2: View from the dorsal side of the crocodile teeth from the Mayermelnhofbruch St. Pankraz. Viewe 3: view from outer side of the crocodile mandible fragment from the Mayermelnhofbruch St. Pankraz.

Horizon: Vogeltanz, 1970 worked on a fossil of red ore layer Ro 1 a in nummulite calcarenite, and described it as a) Biogenic - tribe Vertebrata. Nummulites are large lenticular fossils, characterized by its numerous coils, subdivided by septa and into chambers. These are the shells of the fossil and present-day marine protozoan Nummulites, a type of foraminiferan rhizopodes and calcarenite is the carbonate of sandstones.

Taxonomical notes: Asiatosuchus is an extinct taxon of crocodiles that lived in Eurasian regions during the Paleogene period. Many crocodile's fossils of this period which were discovered from Eurasia have been attributed to genus "Asiatosuchus". The genus name was proposed in 1940. The species of Asiatosuchus have generalized morphology of crocodiles notified by flat and triangular skull. The distinguishing feature of this genus is a broad connection/symphysis between the two halves of the mandible. Latest studies of the phylogeny of the early group of crocodiles fossils suggest that only the first named species of Asiatosuchus is A. grangeri of Mongolia from the Eocene Ephoc, belongs to this genus as a solo secies. Most species are now regarded as "dubious names", meaning that their type specimens lack the unique anatomical features necessary to justify their classification as distinct species. Some other species like A. germanicus and A. depressifrons are still considered valid species of this geus, but they still lack phylogenic grouping with A. grangeri that would confirm theses species to be placed together in the genus Asiatosuchus (Delfino & Smith 2009). A partial skeleton of a crocodyloid from the Sulaiman Mountains of Pakistan was tentatively attributed to Asiatosuchus. The fossil was found in the Middle Eocene Drazinda Formation, a marine deposit which has also preserved the remains of archaeocete whales. The presence of a possible specimen of Asiatosuchus in marine deposits suggests that these crocodilians could have tolerated prolonged periods of time in the ocean, an ability that would have aided in the dispersal of early crocodyloids across Eurasian regions.Well-preserved fossil remains of crocodyloid were firstly described from Germany and France in 1966 and placed these in a new species of genus Asiatosuchus as A. germanicus. The German remains came from the Messel Pit quarry, a fossil site that has preserved many forms of life that inhabited a series of anoxic lakes and surrounding subtropical forests during the Eocene. Of all the species that have been assigned to Asiatosuchus, A. germanicus is known from the most complete fossil's material (Angielczyk & Gingerich 1998). A relative twisting analysis was used by Hastings & Hellmund (2017) to quantify and compare the shape of skulls, revealing Allognathosuchus and Boverisuchus to be very distinct from each other as well as from Diplocynodon and Asiatosuchus. According to them the overlaping in shape is present between some sspecies of Diplocynodon and Asiatosuchus, but still there was a size difference in adult form. Berg (1966) gives the following characteristics as a generic description for Asiatosuchus: This genus had the characteristics of an outwardly open maxillary niche for the fourth mandible tooth; the maximum dentition in maxillae are 19 teeth; the central bending of the inner edge of the angulare and the fifth maxillary tooth is bigger than the fourth one.

According Brochu (2013), two Lutetian species formerly known as Pristichampsus can be identifed recently as Boverisuchus magnifrons in Germany and other parts of Europe, and Boverisuchus vorax, in western North American locaities. The snouts of these differ from the holotype of haeckeli in their slender outline and the non-separated nasal ball. Eusuchians with deep snouts and labio-lingually compressed teeth are known from the Palaeogene of Laurasia. These are usually known as Pristichampsinae.

In the case of fragmentary materials, dermal plates and teeth, allopathic facies genesis can be assumed for the identification and description of these fossils of crocodiloids. Scherer (1979) published and described a crocodilian fossil's remains from the Miocene Lignite of Viehhausen near Regensburg (Bavaria, Germany) as Diplocynodon huetikonensis (Meyer, 1854). This extinct species identification was evidence of another crocodile from Viehhausen, based on a maxillary fragment with rounded posterior teeth. With a small left maxillary fragment (no. 101/69) with 10 densely packed teeth that the posterior teeth are broadly rounded. This finding is an indication that another crocodile lived in the area of Viehhausen in same era. As a result of all these current and previous findings, two types of crocodiles were found in the Central European Tertiary, *Diplocynodon* and *Asiatosuchus*.

Asiatosuchus has a generalized crocodilian skull like most of other Paleogene crocodyloids, that is triangular in shape when viewed from dorsal side. Asiatosuchus have teeth in the maxillae that completely overlap the teeth in the mandible, giving them overbites. An overbite is a primitive feature among crocodyloids because modern crocodiles have teeth in the upper and lower jaws that interlock with each other with little overlap. Asiatosuchus can be distinguished from other early crocodyloids by its extended mandibular symphysis, the region where the two halves of the lower jaws connect. In many crocodyloids this joint is formed from two pairs of bones, the dentary bones and the splenial bones, but in *Asiatosuchus* it is only formed by the dentary bones.

Sources and the condition of the materials

Seidlitz (1917) gives a clear description of this. Thereafter, the pieces were surrounded by gray clay, which was difficult to remove. Some parts, especially the cranial cavities, were filled with a mixture of pyrite and bituminous masses, partly in crusts or pillar formations. The color of the bone remains was greenish-brown, that of the clay masses blackish-grey. The described state of preservation is known to be extremely critical. The preparation method used is all the more strange. Accordingly, the bone fragments were boiled and soaked in a diluted glue solution. The remains of the skull were treated in the same way after the examination, before they were glued together with plaster of paste solution and the bone cavities filled with it. Only individual remains relevant to identification were prepared, the larger part was only to be re-prepared after new finds.

4. Geochemical and preparatory background

The carcasses of many marine reptiles often became highly enriched in the iron sulphide pyrite after they sank to the sea floor. Pyrite and marcasite are common on the exterior of fossils. In sediments, pyrite is always initially precipitated as amorphous iron monosulphide (FeS) through the metabolic activity of sulphate-reducing bacteria under anaerobic conditions, it can also precipitate directly, even in the water column is common sea basins like the Black Sea dissolved sulphate ions are always present in sufficient concentrations in seawater. However, the process can also be take place in soil if sulphate-rich groundwater is present, for example in the vicinity of gypsum deposits. This is abundant in the Camburg region in the Triassic underground. The predominantly amorphous iron monosulphide reacts, among other things with sulphur that is also microbially precipitated, to form iron disulphide (FeS_2), which crystallizes as pyrite or marcasite. The pyrite contained in the lignite is one of the sources of acidification in open cast mines. Pyrite develops predominantly idiomorphic crystals in the shape of cubes or pentagon dodecahedrons. Octahedrons and disdodecahedrons are also common, as well as combinations of these forms. Marcasite mostly develops tabular, pyramidal or prismatic crystals. Exposed to atmospheric oxygen, i.e. oxidizing conditions, marcasite weathers faster than pyrite via several intermediate stages to iron oxide hydrate (limonite or brown iron ore) FeO•OH, with the sulphur being oxidized to sulphuric acid, which in turn accelerates decomposition. Pyrite is chemically stable. In the pyritized fossil i. i.e. R. also the chemically unstable marcasite present. Both minerals are chemically identical. The difference lies in their crystal structure. When marcasite decomposes, sulphurous acid and various sulphates are formed. At a relative humidity of 60%, iron sulphate can react to form melanterite, the sevenfold hydrate of iron sulphate and thus achieve a volume expansion of over 250% of Sulphurous acid is hygroscopic and is also hydrolyzed by atmospheric moisture. Especially when clay minerals are almost always present, aluminum sulphates are also formed in addition to iron sulphates, which are also hygroscopic and continue to react when they absorb moisture from the air. An autocatalytic reaction sets in, attacking not only the remaining marcasite but also the chemically stable pyrite. For some particularly susceptible fossils, a relative humidity of 30% is sufficient. For comparison, it should be pointed out that a normal relative room humidity is between 40% and 50%. In calcitic fossils, the sulphurous acid reacts not only with the pyrite but also with the calcite to form gypsum. This means that not only the aluminum and iron sulphates but also the large volume of gypsum can be involved in the blasting of the fossil. In the past, aging paints were often used, which decomposed over the years and damaged the fossil material with their decomposition products. Today it is known that shellac, nitrocellulose varnish (e.g. zapon varnish) or wood glue have no place on fossils and cause lasting damage. Some of the paint undergoes a chemical transformation, becomes insoluble, brittle and puts stress on the surface, which can then crack and flake off. Bonded areas become unstable and break. Different materials were often used together or applied one on top of the other so that the surfaces of the originals are no longer recognizable. The interactions between the individual components are the real problem. Traditional glues consist of nitrogenous, animal substances that are insoluble in cold water but swell. They only become soluble and develop their adhesive strength when they are subsequently heated, hence the term warm glue. When they cool down, they gel into an elastic mass, the jelly. Today almost only the gelatine is known. Gelatine consists mainly of glutin, which gives its name to the group of glutin glues. In the case of gelatine, attention is paid to the ability to gel, while in the case of glue, the adhesive strength. The different names of the glues partly come from the raw products such as bone, skin or leather. Cold liquid glue used to be created by adding acetic, hydrochloric or nitric acid, which led to an aggressive course of the reaction. All of these chemical milieus irretrievably destroy fossil bones. In contrast, vertebrate fossils in calcareous sediments show a much better preservation. The jaw fragment from Haunsberg shows all the details of the tooth morphology.

Acknowledgements

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