

# Rare pterosaur remains tentatively referred to *Dorygnathus banthensis* (THEODORI, 1830) from the Lower Jurassic (Posidonia Shale) of Schandelah (Lower Saxony, Germany)

## Seltene Flugsaurier-Fossilien cf. *Dorygnathus banthensis* (THEODORI, 1830) aus dem unterjurassischen Posidonienschiefer von Schandelah (Niedersachsen)

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### Summary

The Posidonia Shale (Lower Toarcian, Upper Lias) is famous for its fossilized vertebrates. Since the beginning of the excavations of the State Museum of Natural History in Brunswick in 2014, a number of isolated bones of pterosaurs have been unearthed and tentatively referred to *Dorygnathus banthensis* (THEODORI 1830). The findings of pterosaurs are a curiosity in northern Germany, as they are usually known from famous sites in southern Germany. Using 3D scans, sketches and high-resolution photographs, the bones are analyzed individually and compared to findings described in the literature. Based on the dentition and proportions of the lower jaw, the proportions of the humerus, the lengths of the flight finger phalanges and on the lower leg with adhered tibia and fibula, most of the bones seem to belong to small, probably juvenile, individuals of *Dorygnathus banthensis*. The characters of the humerus and the phalanges of the flight digit suggest that flight in *Dorygnathus banthensis* was possible. Furthermore, the remains of teeth yield information about the cycle of tooth replacement.

## 1 Introduction

The descriptions of pterosaur remains from the Early Jurassic of the Posidonia Shale of Germany reach back to the early 19th century, more precisely to the 1820s (PADIAN 2008b). Most of these specimens originate from northern Bavaria, although the majority of specimens found in Germany altogether are from Holzmaden, Baden Württemberg, where also the most complete pterosaur remains were unearthed (PADIAN & WILD 1992). Since the early 20th century, there have been findings from the Posidonia Shale of northwestern Germany (STIELER 1922). Only the two pterosaur genera *Dorygnathus* and *Campylognathoides* are known from the Lower Toarcian of German deposits (PADIAN & WILD 1992; PADIAN 2008a, b; RIEGRAF et al. 1984; URLICHS et al. 1994). The earliest found remains of pterosaurs in German Liassic deposits were collected in Banz, Germany, in 1828, even before the earliest findings of Liassic pterosaur remains from Lyme Regis in England in December 1828 (PLIENINGER 1894). The latter

were labeled as *Pterodactylus macronyx* by Buckland and later as the genus *Dimorphodon* by Owen (citing from PLIENINGER 1894).

The German findings have not been recorded until the work of MÜNSTER 1830 (citing from PLIENINGER 1894; PADIAN & WILD 1992). At that time, every pterosaur fossil was assigned to the genus *Pterodactylus* (PADIAN & WILD 1992). In the same year, THEODORI (1830) was the first to describe the lower jaw holotype with the inventory number PSB 757 of the pterosaur currently known as *Dorygnathus banthensis* in the “Petrefakten-sammlung Banz”, as well as the slab PSB 758, which is associated to it and contains further skeletal remains. Because of the long jaw, THEODORI (1830) assigned it to *Pterodactylus*’ subgenus *Ornithocephalus*. Furthermore, THEODORI (1830) described the slabs PSB 770, which show several wing bones of one individual, and PSB 76x (last number illegible) with further wing bones. On basis of the ratios among them, it is unlikely they even belong to *Dorygnathus* (PADIAN & WILD 1992). The morphology of the lower jaw and the ratios between the lengths of the wingbones in the slabs PSB 76x and PSB 770 from the “Petrefaktensammlung Banz” led THEODORI (1830) to the cognition that the specimen represents a new taxon, which made him label it as the new species “*banthensis*”. One year later, in 1831, *Ornithocephalus* Soemmering (1812) turned out to be just a juvenile specimen of *Pterodactylus* Cuvier (1809), so the specimen got the label *Pterodactylus banthensis* (citing from PADIAN & WILD 1992).

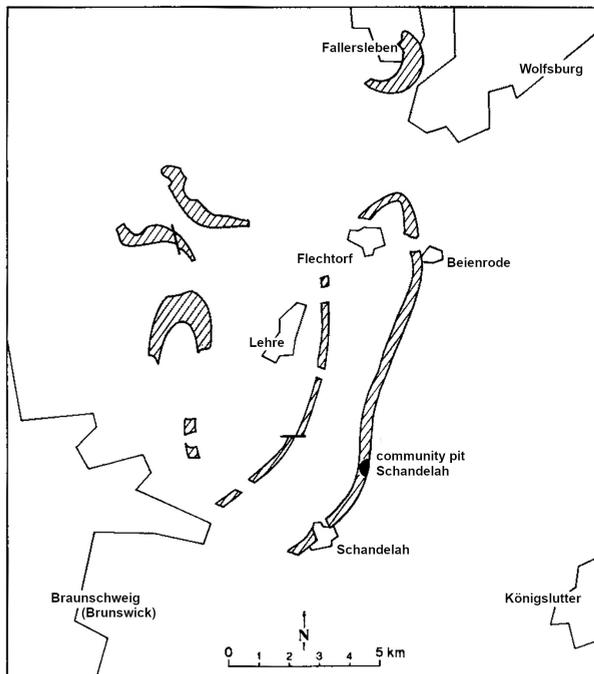
In 1831, MEYER considered the German and English findings to be of the same species and assigned them to *Pterodactylus macronyx* Buckland (1835, citing from PLIENINGER 1894) first and later to *Rhamphorhynchus macronyx* (citing from WAGNER 1860; PADIAN & WILD 1992). But in 1859, skull remains were found in Great Britain, which showed an unusual dentition so that Owen established “*Dimorphodon*” as a new genus for the British material (citing from WAGNER 1860; PADIAN & WILD 1992). Finally, in 1860, WAGNER established “*Dorygnathus*” as a new genus for the German Liassic pterosaurs, based on the ratios of the lengths of the limbs. Meanwhile, the German pterosaurs were considered as “*Dimorphodon banthensis*” (OWEN 1861). This identification is invalid, as *Dimorphodon* from Great Britain is from Hettangian deposits, not from Toarcian as *Dorygnathus* and *Campylognathoides* (PADIAN 1983, 2008). There were no findings of a complete skeleton of *Dorygnathus* until the beginning of the 1900s (PADIAN & WILD 1992).

The first description of what is currently known as *Campylognathoides*, is the holotype GPIT 9533 by QUENSTEDT (1858), a slab with a number of “post-cranial bones”, assigned to *Pterodactylus liasicus* (citing from PLIENINGER 1894; PADIAN 2008a). By reference to their proportions, QUENSTEDT (1858) noticed that the specimen is different from *Ornithocephalus* (now *Dorygnathus*) *banthensis*. He classified the specimen, devoid of a tail, to *Pterodactylus*, which was common for all forms with short tails during those days, whilst long-tailed ones were referred to *Rhamphorhynchus* (PADIAN 2008a). The short-tailed forms were thought to go along with a longer metacarpus, which QUENSTEDT (1858) assumed in this specimen, because of its shorter forearm that he thought would imply a shorter coracoid and therewith a longer metacarpus. There have been no more reports of this species for the entire century (PADIAN 2008a). In 1894, PLIENINGER established the taxon *Campylognathus zitteli* on the basis of the large

“skull and skeleton” SMNS 9787 from Holzmaden, found in 1893. In 1928, “*Campylognathus*” became “*Campylognathoides*” (STRAND) (citing from PADIAN 2008a). In 1901, PLIENINGER found out that “*Pterodactylus*” *liasicus* was actually assigned to the genus “*Campylognathus*” (citing from PADIAN 2008a). In 1974 and 1980, JAIN described pterosaur material from India as “*Campylognathoides indicus*” (citing from PADIAN 2008a).

In 1801, GEORGES CUVIER was the first to realize that *Pterodactylus* from the late Jurassic of Eichstätt was a flying reptile (citing from WELLNHOFER 1991). However, pterosaurs likely differ from the characters of a reptile in their presumed endothermy (WELLNHOFER 1991). Because of the high energy demand, that is necessary for flight, they also must have needed a higher metabolic rate than other reptiles, which can only be sustained by endothermy (WELLNHOFER 1991). This hypothesis is supported by indications of fossil hair covering (YANG et al. 2019). Even so, they still are classified to the group of reptiles. They are assigned to the Archosauria based on the fact that in addition to their diapsid temporal fenestra in the skull, there is another aperture between orbita and nasale, the preorbital fenestra (WELLNHOFER 1991).

Pterosaur findings from northern Germany are not common. STIELER (1922) reported on postcranial skeleton remains from the Posidonia Shale of Schandelah-Flechtorf, namely *Dorygnathus banthensis* (THEODORI 1830) recovered from a nodule in the upper “capellinum-Zone”. WELLNHOFER & VAHLDIK (1986) described a pelvis from the same region, which is the first one unearthed of a pterosaur from the northwestern German Posidonia Shale, and which these authors assigned to *Campylognathoides* sp. The specimen is kept in the “Bayerische Staatssammlung für Paläontologie und historische Geologie, München”, Germany (PADIAN 2008a).



In this article, the isolated pterosaur remains from Schandelah (fig. 1) in Lower Saxony, Germany, excavated since 2014, are described, discussed and assigned systematically.

**Fig. 1:** The outcrop of the Posidonia Shale in the east of Brunswick, Germany, and the locality of the findings, “Geopunkt Jurameer von Schandelah” (community pit Schandelah), modified after WELLNHOFER & VAHLDIK 1986, after LOOK 1984.

## 2 Geological Background

In the Jurassic, middle Europe was dominated by subtropical climatic conditions, and the continent was covered by a shallow intracontinental shelf sea, which was influenced by sea level changes (ZELLMER 2014). Using ammonites, the Lower Toarcian (Lias  $\epsilon$ ) of southwestern Germany is subdivided biostratigraphically into the *tenuicostatum*-zone, *bifrons*-zone and the *falciferum*-zone. The latter is furthermore subdivided into the *elegantulum*-, *exaratum*-, *elegans*- and *falciferum*-subzones (RIEGRAF et al. 1984).

The dark, fine-grained sediments of the Lower Toarcian are named Posidonia Shale based on the common occurrence of the bivalves that were classified as *Posidonia*, but later renamed and divided into the two genera *Bositra* and *Steinmannia* (URLICHS et al. 1994; PADIAN 2008b). The Posidonia Shale is famous for its well preserved fossils of extinct vertebrates like ichthyosaurs, plesiosaurs and marine crocodiles, as well as pterosaurs, remains of a sauropod dinosaur, extinct sharks and bone fish, crinoids, crabs, ammonites, squids, insects and plant residues, like petrified tree stems and conifer twigs and branches (ZELLMER 2014). The Posidonia Shale is a dark, finely bedded sediment, which is, besides the fossils, also rich in bitumen (URLICHS et al. 1994). Its formations are linked with a distinct negative organic carbon isotope excursion (RÖHL et al. 2001; SCHOOTBRUGGE et al. 2018). This is explained by an elevated supply of organic matter during low sea levels and a high redox boundary within the water column. In the middle Lias  $\epsilon$ , horizons of marl are intercalated, which strongly froth in reaction with hydrochloric acid (URLICHS et al. 1994). The Posidonia Shale deposits originate from sapropel that formed on the bottom of an epicontinental sea, which was connected to the ocean by shallow seaways (SEILACHER 1990).

At first sight, the Posidonia Shale seems to show no traces or residues of benthic organisms like snails or brachiopods, that would be expected to be living on the bottom, but of both planktonic and nektonic pelagic organisms instead (URLICHS et al. 1994). Also, the preservation of the fossils is extraordinary, considering for example ichthyosaurs with preserved skin (ZELLMER 2014; SEILACHER 1990). This leads to the cognition that there was a lack of scavengers (URLICHS et al. 1994). The sediments show fine lamination and a high amount of organic matter of up to 16% (RÖHL et al. 2001) and pyrite (URLICHS et al. 1994). Findings of fossilized insects indicate terrestrial vicinity (URLICHS et al. 1994), and findings of iron ore confirm that their genesis is caused by pH-elevation in regions of iron-rich, acidic freshwater inflow (ZELLMER 2014). The occurrence of iron-rich ooids suggests agitated, shallow water (ZELLMER 2014). The characteristics of the sediments, solely regarding the state of preservation, bitumen content, to great parts the lack of epi- and endobenthic organisms and the fine bedding, are similar with those from the modern Black Sea (URLICHS et al. 1994; SEILACHER 1990). The Black Sea displays a stratification of the water column with a boundary layer between an upper and a lower body of water (URLICHS et al. 1994), that allows no vertical water exchange (SEILACHER 1990). The latter has a higher salinity, a lack of oxygen and contains toxic hydrogen sulfide, as a result of the oxidation of dead organisms sinking to the ground (URLICHS et al. 1994; SEILACHER 1990). The lack of oxygen in the lower water column does not allow the development of metazoan life, which

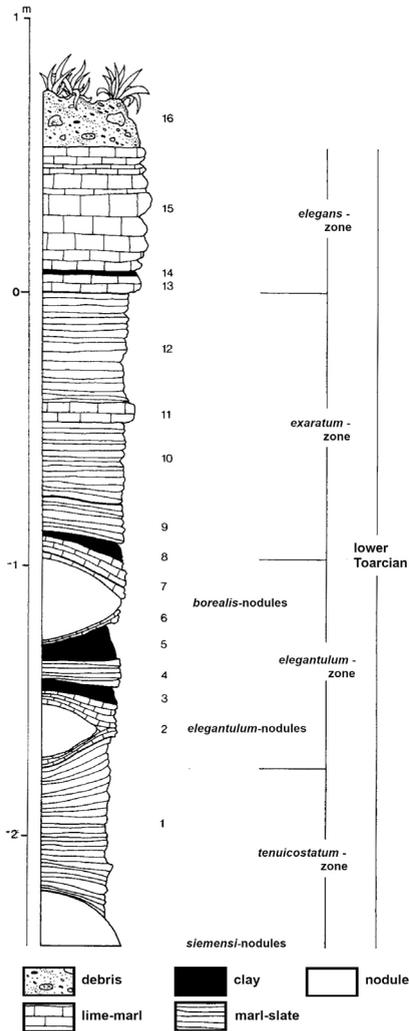
is why there are no scavengers thriving to consume descending dead organisms and decomposition only takes place partially (URLICHS et al. 1994). Differences between the Posidonia Shale and the Black Sea include shallow water depths and weak currents on the bottom, indicated by mass accumulations of ammonites, belemnites and bivalves that are oriented to the current (URLICHS et al. 1994; SEILACHER 1990). In some layers at Schandelah, fish remains are oriented in one direction as well (observations of RK). This phenomenon could have been caused by storms (SEILACHER 1990), which may also explain the distribution of bone material, so that no articulated pieces of pterosaurs are recorded in northern Germany, yet. Another peculiarity of the Posidonia Shale are horizons between the fine laminated layers, that show burrow structures, foraminifera and ostracods, as well as endo- and epibenthic bivalves (URLICHS et al. 1994). This leads to the cognition that there was no permanent boundary layer, but in phases a non-divided water-column (URLICHS et al. 1994). The anoxic benthic environment in the early Jurassic was likely interrupted by long- and short-term oxygenated periods (RÖHL et al. 2001). The long-term fluctuations were caused by sea-level changes and the short-term fluctuations were seasonal (RÖHL et al. 2001). At high sea level, the intracontinental shelf sea was in active water exchange with the Tethys and thus characterized by mixing of the water column, which interrupted the anoxic period at the bottom of the water body (RÖHL et al. 2001). The summer was characterized by monsoon rainfall, fluvial runoff, estuarine circulation, strong primary production and thus, oxygen consumption and an anoxic environment in the bottom waters (RÖHL et al. 2001). In winter, there was a strong evaporation, an interruption of stratification and only local areas of anoxic bottom waters (RÖHL et al. 2001). At low sea level, there was a restricted water exchange between the epicontinental shelf sea and the Tethyan Ocean (RÖHL et al. 2001). In summer, the outflow of the epicontinental shelf sea was stronger and the inflow weaker, than at high sea level (RÖHL et al. 2001). There was a permanent stratification that could not be interrupted by the minimized anti-estuarine circulation in winter.

The salt in the bottom body of the sea water likely originated from Permian salt stocks of northwestern Germany (URLICHS et al. 1994). Differences in thickness are caused by the syndepositional subsidence of the basement in the course of soaring salt (URLICHS et al. 1994). Salt tectonics, which lasted from the Mesozoic to the Pleistocene, is also the reason why the Jurassic strata in the wider study area has been displaced and rotated, and is now at the earth surface (GEHRT 2014).

### **3 Material and Methods**

#### **3.1 Material**

All bones were found isolated and at different depths, since the beginning of the excavations in 2014. Some are embedded in sediment, others were freely prepared. Many are dented in a certain range, due to the onload of the sediment and their hollowness. Some of the delicate long bones are broken and only fragmentarily preserved. The value of the depth of the findings is correlated with the borealis-nodules (fig. 2). They are located about 200 cm underneath the soil horizon at the location of Schandelah.



The material studied here is composed of the right lower jaw SNHM-3038-R, the vertebral body SNHM-2833-R, the ribs SNHM-2918-R, and SNHM-3158-R, the humerus SNHM-2911-R, the complete phalanges SNHM-2390-R, SNHM-2972-R, SNHM-2365-R, and SNHM-2910-R, the incomplete phalanx SNHM-2909-R, and the bone fragment SNHM-2919-R (fig. 3).

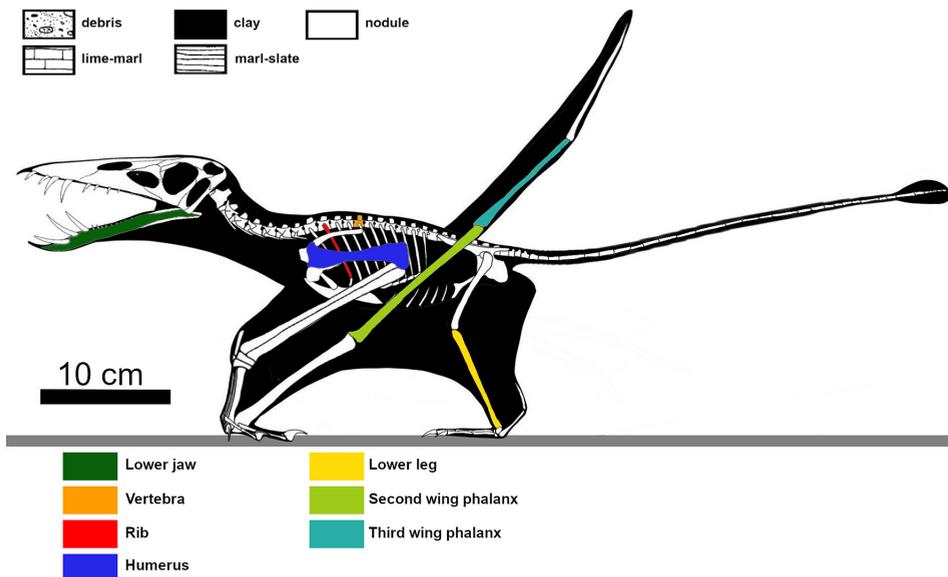
### 3.2 Methods

The lower jaw SNHM-3038-R and the lower leg SNHM-2972-R were photographed at high resolution to be able to take a closer look at the details as the jaw is a very small bone and the details are poorly visible to the unaided eye. For this purpose, the KEYENCE digital microscopes “VHX-6000” with a 20- to 200-fold optical magnification for the lower jaw, and “VHX-5000” with a 100-fold optical magnification for the lower leg, were used in combination with the software package “VH-Z 20T”. The photograph of the rib SNHM-2918-R was taken with a reflex camera.

Additionally, sketches of the lower jaw SNHM-3038-R, the vertebral body SNHM-2833-R, the humerus SNHM-2911-R, the lower leg SNHM-2972-R, and the phalanx SNHM-2390-R were drawn with rapidograph pens and

◀ **Fig. 2:** Stratigraphic profile of the Lias ε of Schan-delah (modified after WELLNHOFER & VAHLDIK 1986).

▼ **Fig. 3:** Bone material studied in this work (modified after D. SCHNABEL / deviantart).



a grease pencil on special paper with a structured surface. For that, a camera lucida mirror mounted at a binocular microscope in a 45-degree-angle was used to virtually trace the original on the paper. The microscope with 12-fold optical magnification was used for the vertebral body SNHM-2833-R, respectively the one with 6-fold magnification for the rest. Later all the sketches were post-processed with the program “Gimp”.

Furthermore, the lower jaw SNHM-3038-R and the humerus SNHM-2911-R were 3D-scanned, because these bones are separated from the shale matrix. For that purpose, the “HP 3D-Scanner” was used in combination with the program “HP 3D Scan Pro 5.6.0”. Later, the scans were edited with the program “MeshLab”. In sum, there were 24 individual photographs taken for one 3D-projection. The object had to be put down in three different positions. In one case, the bone was deposited on the anterior side, so that the posterior side was up. Afterwards, it was laid down on the posterior side so that the anterior side showed up. At last, it was leaned against a box, so that it stood on either the proximal or the distal end of the bone. In each position it was turned around seven times at an angle of about 45 degrees and was photographed and 3D-scanned at least eight times. That way two sequential pictures overlap for a certain range, which is important for the software when it puts all the pictures together in a further step.

Before the start of the scanning process, the scanner had to be adjusted to the size of the object and the distance to it, and the projector had to be calibrated.

Also, length measurements were taken of all bones. Ratios could not be calculated, because none of the bones are articulated and no potentially connected bones can be recomposed.

## 4 Results: Description of the pterosaur remains

### 4.1 Right lower jaw

SNHM-3038-R is the right ramus of the mandible and exhibits a length of 70.2 mm. But it is incomplete both anteriorly and posteriorly. The jaw consists only of the dentary, where the teeth are located. Sutures and coronoid process are not clearly noticeable. It was found isolated in a depth about 45 cm underneath the borealis-nodules. At the proximal side, the bone is collapsed in the vicinity of Meckel’s canal. The apical part with the four anterior teeth is slightly twisted to the labial side and strengthened by a broadening on the lingual side. There is more space between the second and third alveole than between the first and second and the third and fourth alveole. From labial view, the narrow bone is shaped slightly concave and from lingual view slightly convex. In the vertical axis, the mandible is straight.

There are 18 alveoli visible altogether (fig. 4). The first to fifth, seventh, twelfth, fifteenth, and sixteenth alveoli are empty, whilst there are teeth left in the alveoli six and eight. The ninth, tenth, eleventh, thirteenth, fourteenth, seventeenth, and eighteenth alveole are not clearly identified. The alveoles 1–4 are significantly enlarged.

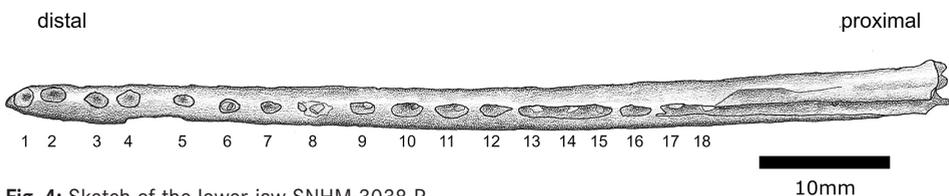
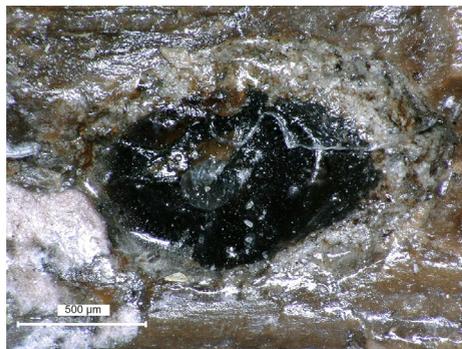


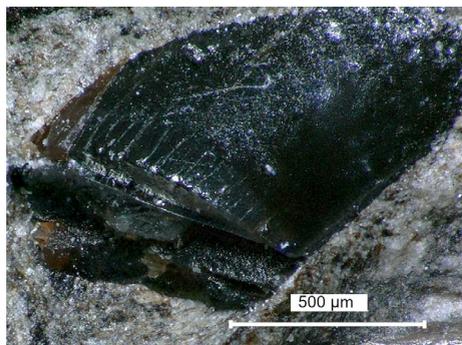
Fig. 4: Sketch of the lower jaw SNHM-3038-R.



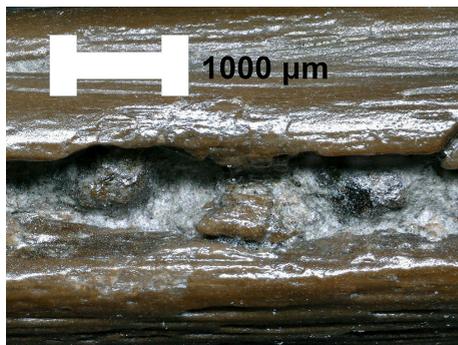
**Fig. 5:** High-resolution photograph of the embryonic tooth in alveole 6 from dorsal view. Photo: M. TOLLKÜHN.



**Fig. 6:** High-resolution photograph of the tooth in alveole 8 from lingual view. Photo: M. TOLLKÜHN.



**Fig. 7:** High-resolution photograph of the tooth in the alveole 8 from dorsal view. Photo: M. TOLLKÜHN.



**Fig. 8:** High-resolution photograph of alveoli 17 (left) and 18 (right) from dorsal view. Photo: M. TOLLKÜHN.

The teeth in the alveoli six (fig. 5) and eight (fig. 6) are broken off and show their cross sections. The tooth in alveole eight is overturned to the lingual side. In both teeth the tooth neck is exposed. That way, the pulp cavity is noticeable. The one in tooth number eight has a slightly oval shape. The pulp cavity of the embryonic tooth in alveole six is almost circular. There are no more structures like dentinal tubules or striations in the dental enamel visible (cf. PLIENINGER 1894).

The tooth in alveole eight shows its lingual side, which has a scratched surface (fig. 7) that might remind of a striation, as observed in the teeth of crocodiles. They are not present at the apex of the tooth and could also be scratches caused by corrosion due to the replacement process, when the new tooth rubs against the old one. About 13 scratches are clearly visible. Their spacing varies slightly.

The alveoli 9, 10, 11, 13, 14, 17, and 18 (fig. 8) show black, shining, shapelessly round nuggets, that could be component units of teeth, but they do not clearly exhibit the shape of teeth.

## 4.2 Vertebra

The only preserved pterosaur vertebra SNHM-2833-R (fig. 9) is 7.6 mm long from the prezygapophysis to the neuropophysis. There is no information of the depth it was unearthed from, because it was found coincidentally on the overburden. It is nestled in sediment, so that its left side is covered. The anterior side of the vertebral body is concave and the posterior side convex. This type of vertebral body is called “procoelous” and occurs in the cervical spine or as one of the front thoracic vertebrae in pterosaurs (HAECKEL 1895). The vertebra shows no diapophyses (Processus transversus) and postzygapophyses (Processus articulares caudalis). Both prezygapophyses and the neuropophysis are noticeable (cf. BUCHMANN & RODRIGUES 2019).

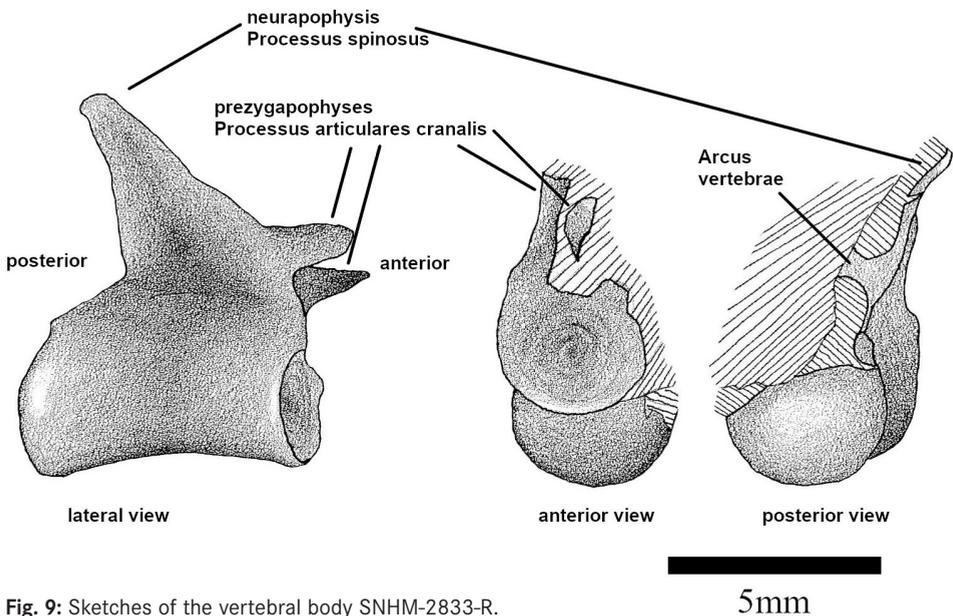


Fig. 9: Sketches of the vertebral body SNHM-2833-R.

## 4.3 Ribs

The rib SNHM-2918-R (fig. 10) consists of four disrupted pieces. After they were glued together, they are 65 mm long and a bend is clearly visible. They were unearthed from a depth of about 76 cm above the borealis-nodules. In cross section, the pieces are oval to flattened. There are no capitulum or tuberculum present at the wider, proximal end (cf. ARTHABER 1921). The rib is two-headed (cf. ARTHABER 1921). As the rib is proportionally long and only the thoracic ribs are ossified, in contrast to the ventral ribs and the middle sections (STARCK 1979), it is most likely a thoracic rib. The cranial thoracic ribs are two-headed, but they become more and more one-headed to the caudal direction (WELLNHOFER 1975; ARTHABER 1921), which makes the rib SNHM- 2019-R most likely one of the caudal thoracic ribs.



Fig. 10: Rib SNHM-2918-R. Photo: A. RITTER.

The bone fragment SNHM-3158-R is 28 mm long and was unearthed from a depth of about 87 cm above the borealis-nodules. It is one end of a long bone, but just a stump with no structures visible. At the other end, the bone is fractured. It might be a rib as well. The stump may be the one-headed proximal end of one of the caudal thoracic ribs.

#### 4.4 Humerus

The right humerus SNHM-2911-R (fig. 11) was unearthed from a depth of about 175 cm above the borealis-nodules. It is 57.6 mm long, 22.4 mm wide at the proximal end and 17.1 mm wide at the distal end. From anterior view, the bone is slightly convex-shaped and from posterior view concave. The distal end is bent forwardly and downwards. At the proximal end on the ventral side, the wide process of the deltopectoral crest is identifiable, which provides an attachment for a strong musculature necessary for flight (WELLNHOFER 1991; WILD 1971). Also, at the proximal end on the dorsal side, the greater tuberosity is preserved. The caput humeri (= head of humerus), which would be located between the greater tuberosity and the deltopectoral crest (cf. PADIAN 1983; cf. WELLNHOFER 1991), is missing, and thereby also the neck, the gap between the head of humerus and the greater tuberosity.

At the distal end of the humerus, the Processus supracondyloideus lateralis (1 in fig. 11), the Epicondylus lateralis (2 in fig. 11), the Trochlea radialis (3 in fig. 11), where the radius is attached, the Vallis intertrochlearis (4 in fig. 11), the Trochlea ulnaris (5 in fig. 11), where the ulna is attached, the Epicondylus medialis (6 in fig. 11), the Tuberculum supracondyloideum mediale (7 in fig. 11), and the Fovea supratrochlearis ventralis (8 in fig. 11) are identifiable (cf. PADIAN 1983; PLIENINGER 1907). There are no Foramina pneumatica present.

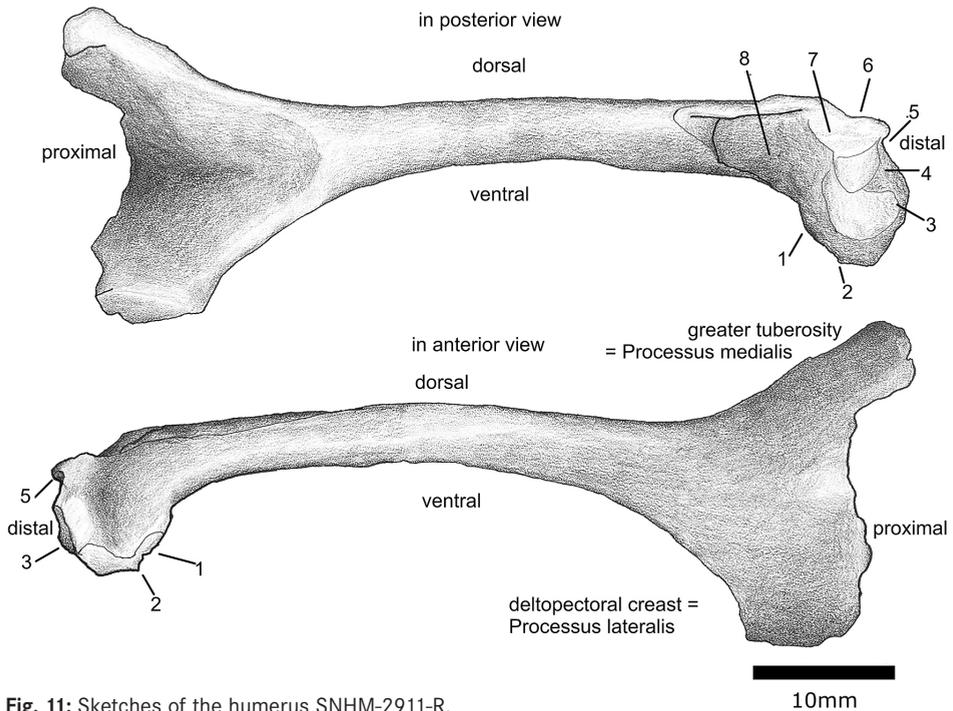


Fig. 11: Sketches of the humerus SNHM-2911-R.

#### 4.5 Lower Leg

The lower leg SNHM-2972-R (fig. 12) is 60.1 mm long, including a gap of 4 mm length. Along the proximal half of the tibia, there is an off-standing bone, the fibula, which is grown together with the tibia in the distal two thirds. The tibia is 6.2 mm wide at the proximal end and 4.8 mm wide at the distal end. It is the left lower leg, exposed in posterior view (cf. BUFFETAUT et al. 2010). There is no information of the depth it was unearthed from. At the distal end, it seems to be slightly concave and is more broadened in one direction, the proximal end is broadened and the fibula stands off of it. In the proximal half of the tibia, it is collapsed in the longitudinal axis, which indicates that it has been hollow (PLIENINGER 1894; cf. BUFFETAUT et al. 2010). The tibia gets thinner from the proximal end in distal direction and exhibits a plain joint surface at the proximal and a condyle at the distal end (PLIENINGER 1907). There are no pneumatic foramina present and no sutures noticeable. The process at the proximal end of the tibia, which towers above the knee joint (PLIENINGER 1894), is missing.

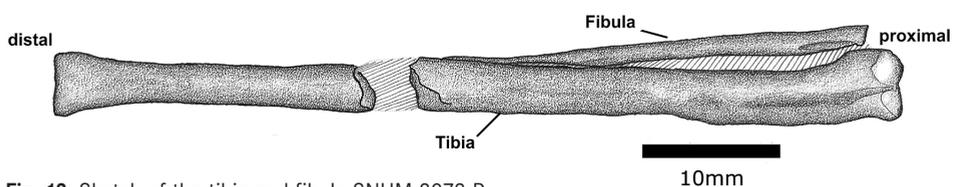


Fig. 12: Sketch of the tibia and fibula SNHM-2972-R.

## 4.6 Finger Phalanges

The phalanx SNHM-2390-R (fig. 13) is 56.8 mm long, 4.9 mm wide at the distal end and 6.1 mm wide at the proximal end. It was unearthed from a depth of about 45 cm above the borealis-nodules. The distal end of the phalanx is convex and broadened in one direction, the proximal end slightly concave and broadened in two directions. It has no olecranon-like process at the proximal end like the first wing phalanx. It is too compact to be the third wing phalanx and it is not thinned at the distal end as the fourth wing phalanx, which leads to the conclusion that it might be the second wing phalanx (cf. PADIAN 2008b; WELLNHOFER 1975).

The phalanx SNHM-2365-R is 49 mm long, 2.5 mm wide at the distal end and 4.0 mm wide at the proximal end. It was recovered from a depth of about 12 cm above the borealis-nodules. The distal end of the phalanx is convex and broadened, the proximal end slightly concave and appears to be broadened, also. Because it is more gracile than the phalanx SNHM-2390-R, it should be a third wing phalanx (cf. WELLNHOFER 1975). It is dented along the longitudinal axis.

The phalanx SNHM-2910-R is flattened, but nearly complete with a length of 51.1 mm, a width of 5.1 mm at the incomplete distal end and a width of 6.95 mm at the incomplete, proximal end. It was unearthed from a depth of about 32 cm above the borealis-nodules. At the proximal end, it is broadened and concave. The distal end is incomplete in its width, but still broadened and it seems slightly convex. There are no Foramina pneumatica present, but since the bone is dented, it might have been hollow inside (PLIENINGER 1894).

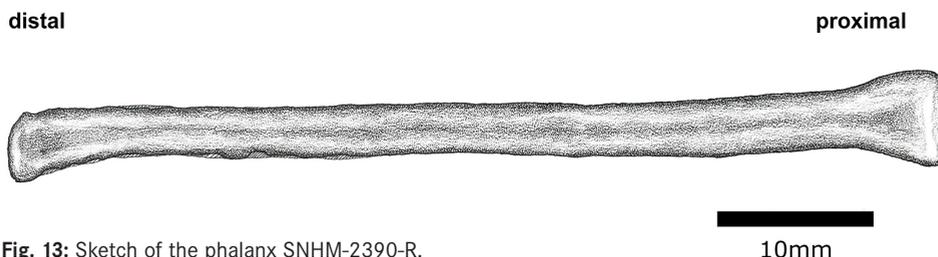


Fig. 13: Sketch of the phalanx SNHM-2390-R.

## 4.7 Fragmentary bones

The incomplete long bone SNHM-2909-R has a length of 69.6 mm and was unearthed from a depth of about 80 cm above the borealis-nodules. It lacks both ends and is strongly flattened.

The bone fragment SNHM-2919-R is 19.7 mm long and was extracted from about 53 cm above the borealis-nodules. It is the middle part of a long bone. In cross section it is almost circular. Also, in cross section the compacta is visible, which forms the wall of the bone. Inside of the compacta, there is a lighter colored circle, filled with sediment.

## 5 Discussion

### 5.1 3D-scanning

While there are numerous self-evident advantages of 3D-scanning of fossil remains, there are also some downsides. The disadvantage of a 3D-scan of a very delicate bone – like the right lower jaw – is that certain details possibly cannot be depicted. On the 3D-scan of the right lower jaw (fig. 14, compare fig. 4), the alveoles 6 and 8, where embryonic teeth are located, are not notable as alveoles, because there is no depth that could be gathered by the scan. Furthermore, the alveole 18 is just insinuated.

Another problem are fine cavities in the bone, like dental foramina, which are tried to be compensated by the software. This is why on figure 14, there is a bulge, marked with “A”, where actually a small hole is located in the bone. The bulge marked with “B” by contrast, is actually there and better noticeable on the 3D-graphic than on a photograph.

Less delicate bones, like the humerus, can be 3D-scanned successfully and reflect the original accurately (fig. 15).

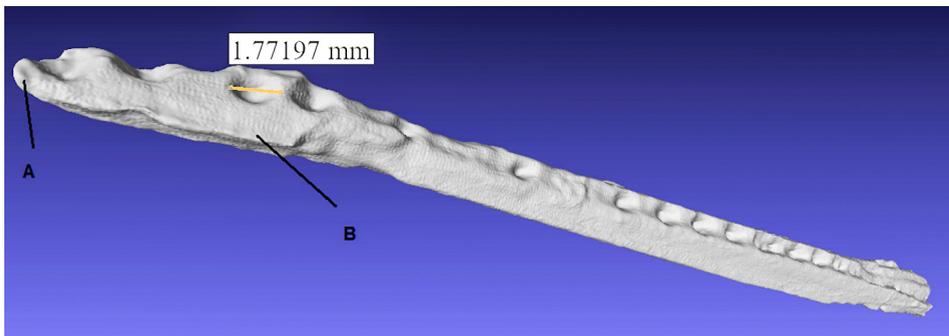


Fig. 14: 3D scan of the lower jaw SNHM-3038-R.

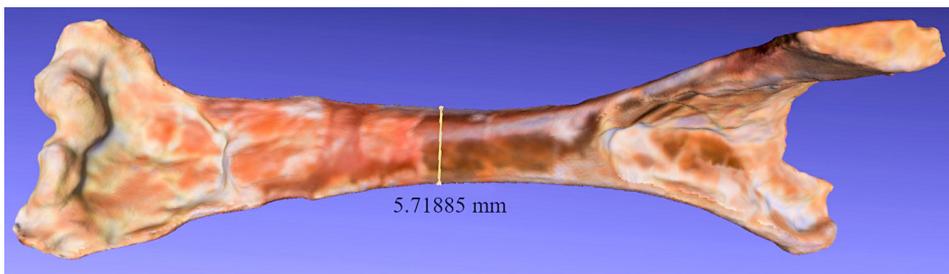


Fig. 15: 3D scan of the humerus SNHM-2911-R.

## 5.2 Tooth replacement

As the structure of the surface of the tooth in alveole eight (fig. 7) is induced by scratches, it cannot represent striae, because striation is built up of bulges of enamel (LIGGETT et al. 2005). Furthermore, the scratches do not show up at the tip, as striae would (LIGGETT et al. 2005). However, scratches can be caused by the tooth replacement process that is made up of erosion of the current tooth by a replacement tooth from the distolingual side (FASTNACHT 2008). Because the visible side of the tooth in alveole eight is also its lingual surface, they really seem to be caused by corrosion due to the tooth replacement.

The teeth of the early pterosaurs were replaced continuously, like they are in crocodiles today, following a certain pattern (EDMUND 1960, 1962). In the process of being replaced, the teeth get depletion textures as a result of the new tooth scraping along the distolingual side of the current tooth (FASTNACHT 2008). To analyze the tooth replacement, a replacement index can be calculated by taking the ratio of the height of the replacement tooth and the height of the functional tooth (FASTNACHT 2008).

The tooth replacement is a cycle that features four different stages (FASTNACHT 2008). In the first stage, the replacement index has a value of 0.6 to 0.9, so the current tooth is not yet full-grown. A completely erected tooth with no replacement tooth, yet, has a replacement index of 1.0. With a replacement index of 1.1 to 1.3, there is already a new tooth visible interiorly that starts the resorption of the base of the current tooth. In the fourth stage, the new tooth (replacement tooth) becomes visible from outside and goes on depleting the current tooth from the distolingual side. When the latter is vanished completely, the index of the replacement tooth reaches a value of 0.6 to 0.9 and this tooth becomes the next current tooth.

The teeth ordered in the diagonal, are called “Zahnreihen” (EDMUND 1960). As the rate of tooth formation is about the same as the rate of its resorption, the “Zahnreihen” in pterosaurs only consist of about three teeth (FASTNACHT 2008). So called “Z-spacing” describes the disparity between two neighboring “Zahnreihen”, which means the higher the Z-spacing, the lower is the rate of tooth replacement (FASTNACHT 2008). This mechanism is tried to be explained with the image of an impulse, which is released throughout the whole life of a pterosaur with the same time lag and causes consistently new “Zahnreihen” to generate (EDMUND 1969).

The way the replacement index reveals the stage of the replacement cycle, the replacement wave shows the pattern with which all teeth in the jaw are replaced (EDMUND 1962). The replacement takes place from posterior to anterior and one replacement wave consists of every second tooth (EDMUND 1962). In fact, the replacement process is phase-shifted so that no neighboring teeth are in the same replacement stage at the same time (FASTNACHT 2008). Also, the replacement indices of the teeth on the left and on the right side are alternating and differing by a value of 0.5 (FASTNACHT 2008).

### 5.3 Flight

The wide proximal process of the humerus is called *Processus deltopectoralis* or *deltopectoral crest* and offers an extensive surface for strong flight muscles to insert (WELLNHOFER 1991). Those conditions for such a strong musculature lead to the cognition, that early pterosaurs were actively flying, not gliding, like larger pterosaurs, which appeared later in the fossil record (WELLNHOFER 1991). The *scapulocoracoid* usually serves as a joint surface for the humerus (WELLNHOFER 1991), but there was none among the finds from Schandelah.

There are two muscle groups (fig. 16) that worked together for flight (WELLNHOFER 1991). The group to move the wing downwards is called *depressor-muscles*, the one to move the wing upwards *elevator-muscles* (WELLNHOFER 1991). The most prominent flight muscle is the *M. pectoralis*, as one of the depressor muscles (WELLNHOFER 1991). The elevator-muscles consist of the *M. deltoideus*, that inserts at *scapula* and *notarium* and moves the humerus upwards, and one muscle that inserts at the *sternum* and *coracoid*, the *M. supracoracoideus* (WELLNHOFER 1991). The latter is located underneath the humerus, but still moves it upwards as it pulls a tendon that is attached to the dorsal side of the humerus (WELLNHOFER 1991). The arm of a pterosaur is much stronger than its leg (PLIENINGER 1894). Rising from the *Musculus extensor digiti* of the humerus, a strong extensor tendon ranges to the front of the metacarpal and a big process at the front of the joint of the flight digit (WELLNHOFER 1991). As a requirement for propulsion, the humerus was able to “rotate around its longitudinal axis”, during wing movement (WELLNHOFER 1991). The pterosaurs were not able to fold their wings as tight as birds and to hold the humerus at the body like birds do in resting position, because relative to the horizontal, they could move their humerus no more than 20° downwards (WELLNHOFER 1991). The forwardly, outer bent, distal end of the humerus makes it possible to flap the wings together (WIMAN 1923). To stabilize the wing against the air pressure during flight, there are strong protuberances at the front edge of the phalanges, close to their distal and proximal ends, to serve as an insertion for ligaments (STIELER 1922). Since there is no movement possible at the ends of the phalanges, there was no muscle inserting at the protuberances, like ARTHABER 1921 considered possible (STIELER 1922). Despite the stiffness of the connection of the flightfinger phalanges, flexibility was reached in a certain range by layers of cartilage between them, to prevent bone fracture (STIELER 1922).

Like birds, pterosaurs had air sacs (WELLNHOFER 1991). In large pterosaurs, excrescence of the air sacs could get into the bones through tiny holes, called *Foramina pneumatica*, primary situated in the walls of long bones, to create pneumaticity for flight (WELLNHOFER 1991). In the bones from Schandelah, no *Foramina pneumatica* could be identified. Instead, the bones are nearly hollow (PLIENINGER 1907), disregarding the spongy ends of the bones, where the joints are located and a higher level of stress was exposed to them (WELLNHOFER 1991).

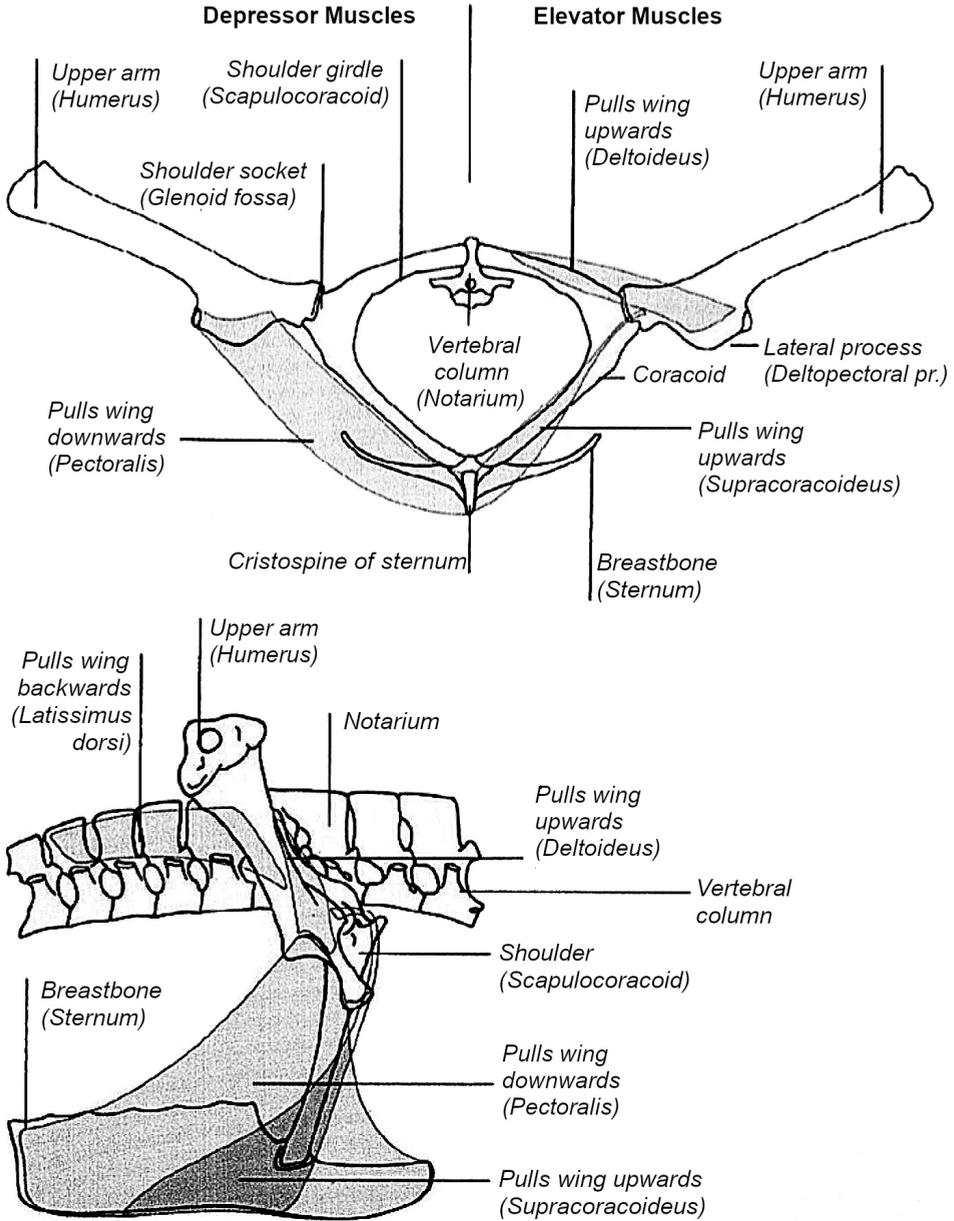


Fig. 16: The muscle groups necessary for flight (WELLNHOFER 1991).

## 5.4 Endothermy

To allow flight, high energy expenditure is needed, which includes an increased metabolic rate and can only be provided by endothermy (WELLNHOFER 1991). In 1927, hair covering of *Dorygnathus* was detected by BROILI, which is a strong indication of endothermy, because it apparently had an isolating function to keep the body continuously warm, while the flight membrane was spared (citing from WELLNHOFER 1991). Furthermore, appropriately preserved pterosaurs mostly show no stomach content, which is a characteristic of a fast digestion, resulting in a high energy expenditure and typical of endothermy (WELLNHOFER 1991). Also, Foramina pneumatica not only worked uplift-generating and weight-reducing, but also to cool down the body due to warmth, generated by the high activity of the flight musculature (WELLNHOFER 1991). Pneumatic foramina primarily appear in the larger pterosaurs of the Cretaceous (WELLNHOFER 1991). The material from Schandelah does not show any of these indications of endothermy.

## 5.5 Systematics

The short neck vertebrae relative to the tail vertebrae and the existence of teeth are typical for early pterosaurs of the Triassic and Early Jurassic (WELLNHOFER 1991).

### 5.5.1 Right lower jaw

The mandibles of the lower jaw of *Dorygnathus* are fused together at the mandibular symphysis (WIMAN 1923). By contrast, the mandibles of *Campylognathoides* are not grown together (PLIENINGER 1894). The lower jaw of *Dorygnathus* is straight, up to the symphysis, whilst the anterior third of the lower jaw of *Campylognathoides* is curved downwards (PLIENINGER 1894). In *Campylognathoides*, the dorsal margin of the tip of the mandible is straight and the ventral margin slightly curved upwards (PLIENINGER 1894). The mandibular symphysis of *Dorygnathus* is elongated forward and curved upwards (PADIAN 2008b). The tip of the lower jaw of *Dorygnathus* has no teeth (WELLNHOFER 1993) and is about 15 mm long (WIMAN 1923). The tip of the mandibles of *Campylognathoides* is short and toothless as well (PLIENINGER 1894). But unlike *Dorygnathus*, *Campylognathoides* has no long, dagger-like process without teeth at the symphysis and the mandibles of the lower jaw also are not broadened where the enlarged teeth are located (PLIENINGER 1894). Apart from that, the labial side of the lower jaw of *Campylognathoides* unlike *Dorygnathus* is recessed at the proximal end, it is almost plane and the proportions are more compact than those of the very gracile lower jaw of *Dorygnathus* (PLIENINGER 1894).

The most anterior alveole of the lower jaw of *Dorygnathus* is twisted to the labial side (cf. WIMAN 1923). There are three or four enlarged anterior fangs on the dentary and eight to eleven smaller teeth posteriorly (PADIAN & WILD 1992; PADIAN 2008b). *Campylognathoides* has two enlarged anterior fangs with a “prey-grabbing” function (UNWIN 2006; PLIENINGER 1894). Each mandible in *Campylognathoides* has 15 smaller

teeth behind the anterior fangs (PLIENINGER 1894). So *Campylognathoides* has a higher number of smaller teeth behind the fangs than *Dorygnathus* (PLIENINGER 1894) and the teeth, in general, are smaller than in *Dorygnathus* (PLIENINGER 1894; WELLNHOFER 1991). The latter has more dagger-like, piscivorous teeth than *Campylognathoides* (STIELER 1922), whose teeth are blunter, indicating an insectivore nutrition (URLICHS et al. 1994). The lower jaw of *Campylognathoides* with lengths around 11.5 cm (PLIENINGER 1894) is shorter than the one of *Dorygnathus* (PLIENINGER 1894), which exhibits lengths between 13 cm and 17 cm (PLIENINGER 1894; PLIENINGER 1907; WIMAN 1923).

As the right lower jaw SNHM-3038-R is very gracile and straight and consists of four anterior alveoles, it features characteristics of the genus *Dorygnathus*. Its short length of 70.2 mm compared to the length of the mandibles of specimens of the genus *Dorygnathus*, where the mandibles are between 13 cm and 17 cm long and the symphysis represents 35 mm of these lengths (WIMAN 1923; PLIENINGER 1894; PLIENINGER 1907), can be explained by the missing toothless anterior part and the broken off posterior part and possibly also by the fact that it was a juvenile individual. Exclusively the number of posterior teeth is extraordinarily large, by *Dorygnathus*-standards (cf. PADIAN & WILD 1992; PADIAN 2008b).

### 5.5.2 Vertebrae

The procoelous type of vertebrae typically occurs in the cervical spine or as one of the front thoracic vertebrae of pterosaurs (HAECKEL 1895). The thoracic vertebrae are getting smaller from the anterior to the posterior positions (PLIENINGER 1894).

Compared to the measurements of WIMAN 1923, the vertebral body SNHM-2833-R with a length of 7.6 mm is rather small to be a cervical vertebra of *Dorygnathus*, whose cervical vertebrae are between 15 and 20 mm long. As the middle thoracic vertebrae of *Dorygnathus*, exhibiting lengths between 8 and 10 mm, are smaller than the cervical vertebrae (cf. WIMAN 1923), it could be one of them, because the back thoracic vertebrae are no more procoelous and the front thoracic vertebrae are bigger than the ones in more posteriorly situated positions. It also could be a juvenile cervical vertebra. The thoracic vertebrae of *Campylognathoides* are 0.7 to 0.9 cm long, the caudal vertebrae between 0.7 and 3.5 cm (PLIENINGER 1894). As the caudal vertebrae are no more procoelous (HAECKEL 1895), it could be a middle thoracic vertebra, presumably of *Campylognathoides* (cf. PLIENINGER 1894), because it is smaller than those of *Dorygnathus* in the record (cf. WIMAN 1923), or of a smaller or juvenile individual of *Dorygnathus*. The missing diaphyses (Processus transversus) and postzygapophyses (Processus articulares caudalis) might be broken off.

### 5.5.3 Ribs

As the ribs strongly differ in length in one individual (ARTHABER 1921), it is not possible to assign it to a genus, on the basis of one isolated rib.

### 5.5.4 Humerus:

The humerus of *Dorygnathus* has a sharper separated Processus deltoideus than the humerus of *Campylognathoides* (WIMAN 1923; PLIENINGER 1894, 1907). Moreover, the Processus deltoideus is rounder than the more angular one of *Campylognathoides* (PLIENINGER 1894). In *Dorygnathus*, it extends to one fifth of the length of the humerus and in *Campylognathoides* even to one third (PLIENINGER 1907). Furthermore, because of its longer shaft and the less prominent deltopectoral crest, the humerus of *Dorygnathus* in general appears more gracile (PLIENINGER 1907).

*Campylognathoides* as well as *Dorygnathus* have a scapulocoracoid as their scapula and coracoid are fused together (PLIENINGER 1894). At the suture between the scapula and the coracoid, both genera have a rounded process that is more prominent in *Dorygnathus* than in *Campylognathoides* (PLIENINGER 1894).

The characteristics concerning the gracile proportions, the deltopectoral crest not extending up to one third of the bone, being sharply separated from the shaft and being relatively rounded, are characteristic of the features found in the genus *Dorygnathus*. Also, the length conforms to the length of a humerus of *Dorygnathus* of 57.5 mm to 62 mm (cf. WIMAN 1923).

### 5.5.5 Lower leg

As the fibula is fused to the tibia at the distal part (fig. 17), it cannot belong to *Campylognathoides*, which differ from most other Liassic pterosaur genera by having a separated fibula and tibia (PADIAN 2008a). So, it most likely belongs to *Dorygnathus*, but is comparatively small for this genus (cf. BUFFETAUT et al. 2010). That means that it could have belonged to a smaller individual of *Dorygnathus*, possibly because of sexual dimorphism, or it constitutes a bone of a juvenile individual. Both are just conjectures, as there is no evidence of a sexual dimorphism, and minor ossification of juveniles is only known from the phalanges of the toes and the shouldergirdle (WELLNHOFER 1991).



Fig. 17: High-resolution photograph of the lower leg SNHM-2972-R.

### 5.5.6 Phalanges

Both the phalanges in *Dorygnathus* and in *Campylognathoides* are thin and hollow (PLIENINGER 1907; PLIENINGER 1894). But all flight finger phalanges of *Dorygnathus* are more gracile than those of *Campylognathoides* (PLIENINGER 1894).

The longest flight finger phalanx of *Campylognathoides* is the second one (PLIENINGER 1894). They become shorter from the second to the fourth one, whilst the length of the first flight finger phalanx is more than two times the length of the forearm (PLIENINGER 1894). The first flight finger phalanx (and also the fourth) of *Dorygnathus*, by contrast, is shorter than the forearm (PLIENINGER 1907). We cannot systematically identify the phalanges using length ratios, because there are no articulated bones. Compared to lengths in the literature, the phalanges are too short to belong to *Dorygnathus* or *Campylognathoides liasicus* (WIMAN 1923) and too long to belong to *Campylognathoides zitteli* (PLIENINGER 1894). This could mean that it is a smaller or juvenile individual of *Dorygnathus banthensis* or *Campylognathoides liasicus* or a large *Campylognathoides zitteli*.

### 5.5.7 Fragmentary bones

The bone fragments have been hollow, as they either are flattened (PLIENINGER 1894; cf. BUFFETAUT et al. 2010) or still round and hollow in cross section. That means they must represent segments of longbones (WELLNHOFER 1991), but no systematical classification is possible.

## 6 Conclusions

Isolated bones of pterosaurs from the Posidonia Shale of the Lower Jurassic of Schan-delah were sketched, photographed and 3D-scanned to be accurately analyzed and compared to the literature to allocate them systematically.

The straight, right ramus of the lower jaw, with four enlarged front alveoles and a broadening in this area, as well as its gracile proportions (PLIENINGER 1894; PADIAN & WILD 1992; PADIAN 2008b), suggest its affiliation to the genus *Dorygnathus*. Because of its size (PLIENINGER 1894; cf. WIMAN 1923) and its procoelous character (HAECKEL 1895), the vertebra represents one of the middle thoracic vertebrae, but is not clearly assigned to a genus. Equally, the ribs show no features that are characteristic for a certain genus. However, the humerus features the length and proportions of the genus *Dorygnathus*. Also, the lower leg, showing tibia and fibula, that are fused together, can be classified as *Dorygnathus*, even though it is relatively small (cf. BUFFETAUT et al. 2010). The phalanges are not referable to a genus, because they show no characteristic features and are shorter than those of *Dorygnathus banthensis* and *Campylognathoides liasicus* and longer than those of *Campylognathoides zitteli* in the record. Equally, the fragmentary bones cannot be classified systematically, but only referred to any long bones. Basically, the findings either show characteristics of *Dorygnathus banthensis* or could belong either to *Dorygnathus banthensis* or to *Campylognathoides*.

But in many cases, the bones are smaller, compared to the measurements of *Dorygnathus banthensis* found in the literature. It is not possible to evaluate if they represent bones of juvenile or just smaller individuals, possibly due to a sexual dimorphism, because those bones that show a minor ossification in juveniles, are the phalanges of the toes and the shoudergirdle only (WELLNHOFER 1991), which are not at hand. The available bones have no characteristic features of juvenile individuals. The morphology of the humerus allows conclusions on the musculature that made flight possible, and, embryonic teeth left in some alveoles of the lower jaw provide indications for an ongoing cycle of tooth replacement.

The 3D scans that have been made, preserve the information for the future and enable international scientific cooperation. In the case of ongoing research, potential indications for a sexual dimorphism in *Dorygnathus banthensis* or characters of juvenile individuals may be found and possibly also fitted to the pieces described in this work.

## 7 Zusammenfassung

Der Posidonienschiefer aus dem unteren Toarcium innerhalb des oberen Lias ist bekannt für seine fossilen Wirbeltierreste. Seit dem Beginn der wissenschaftlichen Grabungen des Staatlichen Naturhistorischen Museums im Jahr 2014 wurden einige isolierte Flugsaurierknochen geborgen und vorläufig *Dorygnathus banthensis* (THEODORI 1830) zugeordnet. Die Entdeckung dieser Flugsaurierfossilien in Norddeutschland gilt als Besonderheit, da sie ansonsten eher von den berühmten Fundorten in Süddeutschland bekannt sind. Jeder Fund wurde individuell untersucht, mit 3D-Scans, zeichnerisch und mit hochaufgelösten Fotografien dokumentiert und mit der Literatur abgeglichen. Die meisten Knochen gehören wohl zu kleinen, möglicherweise juvenilen Exemplaren von *Dorygnathus banthensis*. Hierfür sprechen die Bezahnung, die Größe und Proportionen des Unterkiefers und des Humerus, die Länge der Phalangen der Flugfinger und die Länge der Unterschenkelknochen Tibia und Fibula. Am Oberarmknochen und an den Phalangen der Flugfinger wurden Anpassungen an die Flugfähigkeit nachgewiesen. Das Flugvermögen ist einer der Hinweise darauf, dass diese Tiere gleichwarm waren. Die embryonalen Zähne im Unterkiefer liefern Informationen über den Zyklus des Zahnwechsels.

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