

The geologically oldest specimen of *Pterodactylus*: a new exquisitely preserved skeleton from the Upper Jurassic (Kimmeridgian) Plattenkalk deposits of Painten (Bavaria, Germany)

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Abstract

Pterodactylus from the uppermost Jurassic of southern Germany represents one of the most iconic pterosaurs, due to its status of being the first member of the Pterosauria to have been described and named. During the early phase of pterosaur research, *Pterodactylus* was a wastebasket taxon containing dozens of sometimes distantly related assigned species. Decades later, a comprehensive revision of the genus significantly reduced the number of species. To date, only one species remains in the genus, *Pterodactylus antiquus*, although the referral of several specimens to this taxon and the taxonomic relationships of them is still debated. Thus far, the genus has been only reported from the Upper Jurassic Plattenkalk deposits of Bavaria, and all of these occurrences are Tithonian in age. Here we describe the first record of *Pterodactylus* from the Torleite Formation near Painten (Bavaria), which represents the first occurrence of the genus from the Kimmeridgian. The specimen is a complete, articulated and exquisitely preserved skeleton of a small-sized individual. Aside from its old geological age, it is a typical representative of the genus, greatly resembling other specimens from younger strata. Certain characters, such as the overall size, skull length, relative orbit size, and phalangeal formula indicate that the specimen from Painten represents a juvenile to young subadult individual, an ontogenetic stage rarely found among *Pterodactylus* specimens. The find significantly expands the temporal range of the taxon and represents one of the best-preserved specimens of the genus reported so far.

Key Words

Kimmeridgian, Pterodactyloidea, *Pterodactylus*, Pterosauria, Solnhofen Archipelago, Upper Jurassic

Introduction

The very first pterosaur that was scientifically described and named, and which thus led to the recognition of this extremely diverse group of flying reptiles that dominated the skies of the Mesozoic, was *Pterodactylus* from the famous Upper Jurassic Plattenkalk deposits of southern Germany, although the affinities of the first specimens have caused considerable debate (Collini 1784; Cuvier 1809; Wellnhofer 2008a). The earliest finds of *Pterodactylus* date back to the 18th century but the precise date of their discovery remains difficult to es-

tablish (Ösi et al. 2010; Tischlinger 2020). Usually, the holotype specimen of *Pterodactylus antiquus* or ‘Mannheim Exemplar’ (BSP AS.I.739), found between 1767 and 1784, is regarded as the first discovered pterosaur fossil (Wellnhofer 1970, 1978, 2008a), although the holotype of *Pterodactylus micronyx* or ‘Pester Exemplar’ (ELTE V 256) was found between 1757 and 1779 and thus might have been found earlier (Ösi et al. 2010). First described by Cosimo Alessandro Collini in 1784, the ‘Mannheim Exemplar’ was originally regarded as an aquatic vertebrate with uncertain relationships (Collini 1784), before the German naturalist Johann Hermann

identified the animal as a flying vertebrate, although he regarded it as a mammal (Taquet and Padian 2004). The French naturalist and founder of comparative anatomy, Georges Cuvier, finally recognized the reptilian affinities of the specimen and later coined the term ‘pterodactyle’ for it (Cuvier 1809), which was later latinized into *Pterodactylus*. In the following years, however, the specimen was still variably regarded as a mammal or bird by some researchers like the German naturalist Samuel Thomas von Soemmerring, who regarded it as a bat and erected the species ‘*Ornithocephalus antiquus*’ for it (Soemmerring 1812), the first binomial name for a pterosaur. Even more confusion was involved in the classification of the ‘Pester Exemplar’ that was initially identified as a crustacean by the Italian naturalist Ignazio Born (1779), and only over 70 years later its true affinities were recognized by Herrmann von Meyer, who used it as the holotype for the new species *Pterodactylus micronyx* (Meyer 1856).

After the initial discoveries of the Mannheim and Pester specimens, numerous additional specimens of *Pterodactylus* were discovered in the Solnhofen area from the beginning of the 19th century onward, including some with preserved soft tissues (Abel 1925), making ‘*Pterodactylus*’ one of the best-known pterosaur genera early on. Partly due to its iconic status of being the first known pterosaur genus, *Pterodactylus* became a wastebasket taxon, especially during the 19th century. Numerous, even rather distantly related taxa, have originally been placed in the genus *Pterodactylus*, many of them, however, representing nomina dubia and species assignable to other genera. In 1970, Wellnhofer in his monograph on the pterodactyloids from the Franconian laminated limestone, provided a taxonomic revision of the genus and listed a total of six valid species for *Pterodactylus* (Wellnhofer 1970). Of these, five species have subsequently been moved to other genera, including *P. suevicus* (*Cycnorhamphus suevicus*, Bennett 1996a), *P. elegans* (*Ctenochasma elegans*, Jouve 2004), *P. micronyx* (*Aurorazhdarcho micronyx*, Bennett 2013a), *P. longicollum* (*Ardeadactylus longicollum*, Bennett 2013a), and *P. kochi* (*Diopecephalus kochi*, Vidovic and Martill 2018). Recently, there has been substantial discussion about the taxonomic status and validity of *P. kochi* and it is now either regarded as a junior synonym of *P. antiquus* or as belonging to a separate genus (see below). Although ‘*Pterodactylus*’ has been reported also from France, England, Portugal and Tanzania, all of these finds were subsequently referred to other genera or to indeterminate pterodactyloids (see Barrett et al. 2008 and references therein). Therefore, *Pterodactylus* is currently known only from Bavaria and all of the reported finds are of Tithonian age (Barrett et al. 2008; Bennett 2013a). In this paper, we report the geologically oldest specimen of *Pterodactylus* from the Kimmeridgian and the first report of the genus from the Upper Jurassic Torleite Formation.

Institutional abbreviations

BMMS, Bürgermeister Müller Museum Solnhofen, Solnhofen, Germany; **BSPG**, Bayerische Staatssammlung für

Paläontologie und Geologie, Munich, Germany; **DMA**, Dinosaurier Museum Altmühltal, Denkendorf, Germany; **ELTE**, Eötvös Loránd University, Budapest, Hungary; **JME**, Jura Museum Eichstätt, Eichstätt, Germany; **RGM**, Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands; **SM**, Senckenberg Museum, Frankfurt, Germany; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TM**, Teyler Museum, Haarlem, Netherlands.

Geological setting

The specimen described herein was found near Painten, a small town situated in the southern part of the Franconian Alb in central Bavaria (Fig. 1). The Franconian Alb forms, together with the Swabian Alb (its western continuation in the state of Baden-Württemberg), a low mountain range in southern Germany that extends from the southwest to northeast and is composed of Lower to Upper Jurassic marine sedimentary rocks. A number of uppermost Jurassic localities on the Franconian and Swabian Alb have yielded abundant and exceptionally well-preserved fossils of plants, invertebrates and vertebrates. These sites are generally characterized by an extremely fine-grained, laminated and planar limestone usually lacking bioturbation. This laminated limestone is often called by its German name ‘Plattenkalk’ (Viohl 2015b). The most important fossil localities, which also yielded the majority of the historical finds including the first specimens of *Pterodactylus* mentioned above, are located in the southern part of the Franconian Alb near Solnhofen and Eichstätt. The fossil treasures of this area were recognized early on, when the fine-grained limestone was mined in numerous small and large quarries for building stones and later for lithographic plates. Aside from the region near Solnhofen and Eichstätt, several other localities of the southern Franconian Alb yielded a rich fossil assemblage with a similar preservation, including (from southwest to northeast) Daiting, Schamhaupten, Painten, Kelheim, Jachenhausen, Zandt and Brunn (Fig. 1). Together, the Plattenkalk deposits of the southern Franconian Alb form the ‘Solnhofen Archipelago’, also referred to as the ‘Solnhofen Limestone’. Two other important fossil sites preserving a similarly rich and well-preserved fauna are located on the northern Franconian Alb near Wattendorf, respectively on the southwestern part of the Swabian Alb near Nusplingen (Fig. 1).

Although these sites are overall similar, some significant differences are noteworthy with respect to lithology, age and fossil composition. As outlined above, the deposits are all composed of fine-grained limestones, the so-called Plattenkalk, yet the amount of silica and mud as well as the thickness of the limestone layers is highly variable, likely reflecting slightly distinct depositional environments (Viohl 2015b). Moreover, the different fossil sites of the Solnhofen Archipelago belong to at least four distinct formations – from oldest to youngest, the Torleite (Malm Epsilon), Geisental (Malm Zeta 1), Painten (Malm Zeta 1), Altmühltal (Malm Zeta 2) and Mörsenheim (Malm Zeta 3) formations – ranging in age from the upper Kimmeridgian to the lower Tithonian (Schweigert 2007, 2015;

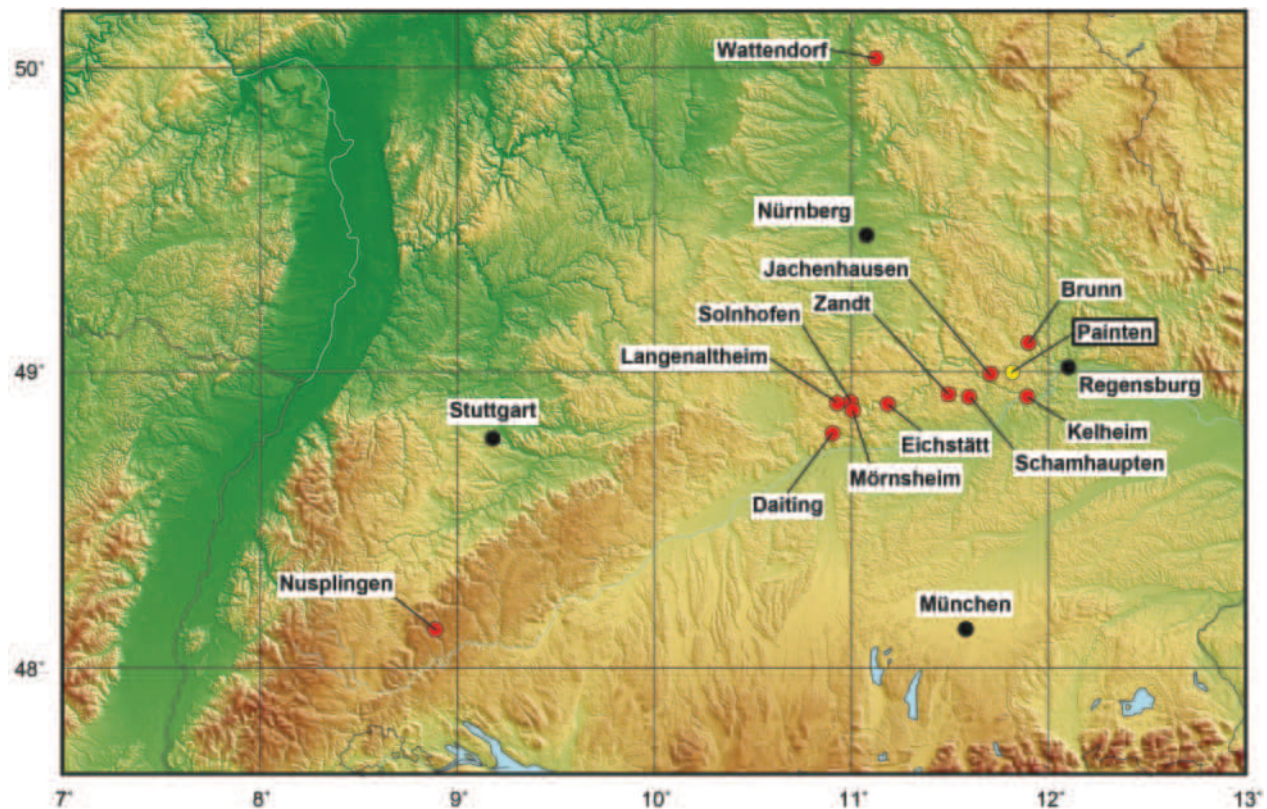


Figure 1. Map of southern Germany with the Franconian and Swabian Alb. The new specimen of *Pterodactylus antiquus* described in this study (DMA-JP-2014/004) was found 2 km northeast of Painten in the Rygol Quarry. The map was created with GMT6 (Wessel et al. 2013).

Niebuhr and Pürner 2014). During the time of deposition in the latest Jurassic, the area of today's southern Germany was situated in a shallow, tropical sea with small and larger islands. In this setting, the 'Plattenkalk' was likely deposited in locally restricted basins or 'Wannen' that were bordered by sponge bioherms and thus were separated from the open sea. The resulting stagnant water conditions in these lagoons coupled with the tropical climate caused the depletion of oxygen and hypersaline conditions near the ground, which, together with rapid sedimentation during periodic storm events, probably led to the exceptional preservation of the fossils (Viohl 2015a).

The faunal assemblage of the Solnhofen Archipelago comprises an extremely diverse array of invertebrates and vertebrates, often showing a spectacular preservation, which made these Upper Jurassic Plattenkalk deposits world famous (especially those of the southern Franconian Alb). Unsurprisingly, terrestrial and aerial vertebrates are more rarely found than marine ones but over the last centuries, numerous specimens have been discovered, including exquisitely preserved rhynchocephalians, squamates, atoposaurid crocodyliforms, theropod dinosaurs, early avialians, and pterosaurs (Wellnhofer 1970, 1975, 2008b; Ostrom 1978; Göhlich and Chiappe 2006; Rauhut et al. 2012, 2019; Frey and Tischlinger 2015; Tischlinger and Rauhut 2015). Among these, pterosaurs represent the most abundant reptile group and in total more than 500 pterosaur specimens are known (Tischlinger and Frey 2015). Interestingly, *Pterodactylus* has so far only been report-

ed from the Solnhofen Archipelago (i.e. sediments of the southern part of the Franconian Alb), and all occurrences are Tithonian in age, ranging from the Malm Zeta 2 to Malm Zeta 3 (Bennett 2013a; Vidovic and Martill 2018).

The new specimen of *Pterodactylus* described herein represents the first occurrence of the genus from the Torleite Formation (Malm Epsilon) and was found in the quarry of the Rygol Company near Painten. The quarry is situated in the northern part of the 'Paintener Wanne', a locally restricted basin covering an area of approximately 15 × 12 km (Albersdörfer and Häckel 2015). The *Pterodactylus* specimen was found at the bottom of the exposed section in the 'Kieselplattenkalk', a 5.9 m thick package of laminated, fine-grained, silicified limestone intercalated with graded turbidite horizons consisting of carbonate debris (Albersdörfer and Häckel 2015; Keupp et al. 2016). Stratigraphically, the 'Kieselplattenkalk' of Painten belongs to the Arnstorf member of the Torleite Formation, which has been assigned to the *Hybnoticeras beckeri* ammonite Zone and the *Lithacoceras ulmense* Subzone, corresponding to a latest Kimmeridgian age (Schweigert 2007; Niebuhr and Pürner 2014). The 'Kieselplattenkalk' of Painten is characterized by an unusually high amount of silica and, in this respect, resembles the roughly coeval 'Plattenkalk' deposits of Schamhaupten and Kelheim (Viohl 2015b).

Although the Rygol Quarry has been operated since the 1950s, fossils only came to light after 2001, when systematic excavations were conducted, first led by the shift worker Wolfgang Häckel and, later, by the private Albersdörfer

institute (Albersdörfer and Häckel 2015). Excavations conducted over the last 20 years yielded a rich and diverse fossil assemblage comprising abundant plant remains, invertebrates (including sponges, corals, crinoids, brachiopods, ammonites, coleoids, gastropods, crustaceans, echinoderms) and vertebrates (Albersdörfer and Häckel 2015; Keupp et al. 2016). Among the latter, fishes are by far the most common group being represented by actinopterygians, chondrichthyans, and coelacanth (Albersdörfer and Häckel 2015). Fossil reptiles are abundant compared to other quarries and include rhynchocephalians, ichthyosaurs, turtles, the thalattosuchians *Cricosaurus albersdoerferi* and *Dakosaurus* sp., atoposaurid neosuchians, pterosaurs and the theropod dinosaur *Sciurumimus albersdoerferi* (Rauhut et al. 2012; Tischlinger and Frey 2013; Albersdörfer and Häckel 2015; Spindler and Albersdörfer 2019; Sachs et al. 2021; Spindler et al. 2021), though it must be noted that most specimens have not been described in detail yet and thus several may represent new taxa. In general, the fossils from the Rygol Quarry are extremely well preserved and relatively abundant, especially those of terrestrial vertebrates. The abundance of plants and terrestrial vertebrates indicates that coastlines must have been located nearby, while the presence of coleoids demonstrates that the local basin ('Paintener Wanne') was connected to the open sea (Röper 2005).

Materials and methods

The specimen described in this paper was found during systematic excavations on the 2nd of June 2014 by Márton Vremir in the Rygol Quarry, approximately 2 km north-east of Painten (49°0'31"N, 11°49'35"E). The pterosaur

was meticulously prepared mechanically in more than 120 h by Wolfgang Haeckel under magnification of 26–20×, exclusively using pneumatic tools and needles. The specimen is permanently housed and accessible in the collection of the Dinosaurier Museum Altmühltal in Denkendorf, Bavaria, Germany (DMA) under the collection number DMA-JP-2014/004. In addition, it is guaranteed by contract that the privately owned specimen will always be available for science. The anatomical nomenclature mainly follows Wellnhofer (1985). Anatomical orientations in the wing bones are described according to a laterally extended wing, and therefore, we use the terms dorsal and ventral instead of lateral and medial.

Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Pterodactylidae Bonaparte, 1838

***Pterodactylus* Cuvier, 1809**

***Pterodactylus antiquus* Soemmerring, 1812**

Figs 2–5

Holotype. BSP AS.I.739, an almost complete skeleton including the skull.

Amended diagnosis. Modified after Bennett (2013a): Upper Jurassic pterodactyloid with a slender and elongated rostrum; the dorsal margin of the skull straight to only slightly concave upward; nasoantorbital fenestra length ~20–25% of skull length in large individuals; number of teeth proportional to skull length with up to ~25 teeth



Figure 2. *Pterodactylus antiquus*, DMA-JP-2014/004, from the Upper Jurassic (Kimmeridgian) Torleite Formation of Painten; overview photograph.

per jaw side in large individuals; teeth low conical; teeth largest anteriorly and decreasing in size posteriorly; tooth row length ~75% of jaw length; upper tooth row extending posterior to the anterior margin of the nasoantorbital fenestra; a low sagittal bony crest dorsal to the nasoantorbital fenestra and orbit in large individuals, which apparently lacks the striations seen in *Ctenochasma*, *Germanodactylus*, and *Gnathosaurus*; a soft tissue crest extending dorsally from the bony crest in large individuals; an occipital lappet of soft tissues extending posteriorly from the occipital region; cervical vertebrae 3–7 elongate and neck relatively longer than in *Cycnorhamphus*, *Ctenochasma*, and *Aurorazhdarcho* (shared with “*P.*” *longicollum*); in small specimens, WP2 is 93–96% of WP1 length, in large ones ~91%; in modified Nopcsa curves, WP1–4 lengths typically exhibit a convex upward curve (shared with *Germanodactylus*); in the pes, MtII is longer than MtI or equal to MtI in length; the proximal phalanges of digit I–III show progressive reduction in length whereas those of digits I and IV are subequal (shared with *Germanodactylus*).

Referred material. DMA-JP-2014/004, a nearly complete and articulated skeleton including the complete skull.

Locality. Rygol Quarry near Painten, Niederbayern, Bavaria, Germany.

Stratum. Torleite Formation, *Beckeri* zone, *Ulmense* subzone, upper Kimmeridgian, Upper Jurassic.

Taxonomic remarks. For many decades after its discovery, *Pterodactylus* has been essentially a wastebasket taxon and dozens of species have been assigned to the genus, many of which later turned out to represent rather distantly related taxa. In 1970, Wellnhofer, in his classic monograph on the pterodactyloids from the Solnhofen Limestones, provided a thorough revision of the genus and listed a total of six species: *P. antiquus*, *P. kochi*, *P. longicollum*, *P. suevicus*, *P. micronyx* and *P. elegans* (Wellnhofer 1970). Subsequently, four of these species have been assigned to their own genera, a decision followed by most researchers without much controversy, with *P. suevicus* having been assigned to *Cycnorhamphus* (= *Gallodactylus*) (e.g. Fabre 1976; Wellnhofer 1978; Bennett 1996a, 2013b; Unwin 2003), *P. elegans* to *Ctenochasma* (e.g. Bennett 1996b, 2007; Unwin 2003; Jouve 2004), *P. micronyx* to *Aurorazhdarcho* (Bennett 1996b, 2013a, Hone et al. 2013), and *P. longicollum* to *Ardeadactylus* (Bennett 2013a; Vidovic and Martill 2018). In contrast to this, the taxonomic status of *Pterodactylus kochi* has caused considerable debate recently and it is now usually regarded either as a junior synonym of *P. antiquus* or as belonging to a distinct genus. After the revision of the genus, Mateer (1976) was the first to suggest that *P. kochi* and *P. antiquus* are extremely similar and that the former therefore represents a junior synonym of the latter (although it should be noted that a synonymy of the two species has originally been proposed already by Zittel, 1883). Later, Bennett (1996b) conducted statistical analyses of *Pterodactylus* and other pterodactyloids from the Solnhofen Limestone, likewise concluding that the specimens assigned to *P. kochi* likely represent immature

individuals of *P. antiquus*. This view has been also expressed by several other subsequent studies (Jouve 2004; Bennett 2013b, 2018).

Despite the synonymization of *P. kochi* with *P. antiquus*, several later studies have treated the two species as separate taxa (e.g. Frey and Martill 1998; Kellner 2003; Unwin 2003). Recently, Vidovic and Martill (2014) found the holotype of *P. scolopaceps*, which has been synonymized with *P. kochi* by Zittel (1883) and was listed as such by Wellnhofer (1970), to differ considerably from other *Pterodactylus* specimens and thus assigned it to the new genus *Aerodactylus*. In addition, they assigned a number of other specimens to *Aerodactylus scolopaceps* that previously were referred to *P. kochi* (Vidovic and Martill 2014). Subsequently, Vidovic and Martill (2018) re-studied several specimens assigned to *Pterodactylus* and found the holotype of *P. kochi* and two referred specimens to differ in several respects from *P. antiquus*. Therefore, they proposed that *P. kochi* actually belongs to a separate genus, *Diopecephalus*, which was originally coined by Harry Govier Seeley in the second half of the 19th century (Vidovic and Martill 2014, 2018). Thus far, a consensus on this topic has not been reached. Regarding the taxonomy of *Pterodactylus*, we here tentatively follow Mateer (1976), Bennett (1996b, 2013b), and Jouve (2004) and consequently regard *P. kochi* as representing a junior synonym of *P. antiquus*, because we find it difficult to differentiate the two taxa based on the proposed diagnoses for the time being.

Comparative description

The specimen consists of a complete, articulated and extremely well-preserved skeleton lying on its right side (Fig. 2). Only a very small portion of the left mandible as well as of the left and right tibia is missing. Otherwise, the skeleton is nearly perfectly preserved with every bone present and in its roughly correct anatomical position. The mandible is slightly detached from the skull and is preserved in ventral view. The hyoid bones are present and, like the mandible, are slightly dislocated ventrally, being preserved between the left and right mandibular rami. The wings are folded with the right wing lying partly under the left one and partly under the body skeleton. The hind limbs extend laterally and both are visible in posterolateral view.

For the comparison below, we largely relied on the classical monograph of Wellnhofer (1970), in which he described every *Pterodactylus* specimen known at the time and additionally provided the most comprehensive overview of the genus including five specimens of *P. antiquus* and 23 specimens of *P. ‘kochi’*. Wellnhofer (1970) also provided detailed measurements for all of these *Pterodactylus* specimens, which formed the basis for the quantitative comparison presented below (for details, see Wellnhofer 1970: chapter 10). Note that we here use the corrected measurements for TM 10341 by Bennett (2013a)

that differ considerably from those listed by Wellnhofer (1970). In order to make the comparison as clear as possible, and because there has been considerable debate on the taxonomy of *Pterodactylus* (see above), we here refer to individual specimens instead of referring simply to *P. antiquus* or *P. kochi*. Moreover, we provide both the specimen number used in the Wellnhofer (1970) monograph (i.e. his ‘Exemplar Nr.’) and the official repository number. Notably, specimen JME 29.III.1950 (Exemplar Nr. 9), which was originally referred to *P. kochi* by Wellnhofer (1970), has been reassigned to *Germanodactylus cristatus* by Bennett (2006), and we herein follow this referral. When referring to *Pterodactylus* in the comparison below, we include both *P. antiquus* and *P. kochi*, as we tentatively accept the synonymy of the two as outlined above. For an overview of the measurements of the skeleton and individual bones as well as some selected dimensions, see Table 1.

Cranial skeleton

The skull of DMA-JP-2014/004 is complete and exposed in left lateral view (Fig. 3). It has a total length of approximately 48 mm, and thus lies within the lower range previously observed in *Pterodactylus* with reported skull lengths ranging between 23 mm in the smallest specimen (BSPG 1967 I 276, Exemplar Nr. 6) and 149 mm in the largest specimen preserving a complete skull (BMMS 7, without Exemplar Nr.) (Wellnhofer 1970; Bennett 2013a). Like in other specimens of *Pterodactylus*, the orbit is circular in outline and has a diameter of slightly more than 10 mm. The orbit is thus relatively large compared to overall skull length (ca. 20%), likely reflecting the young ontogenetic age of the specimen. Wellnhofer (1970) provided SOL-indices (=Schädel-Orbita-Längen-Index,

Table 1. Measurements (in mm) of the new *Pterodactylus* specimen from Painten (DMA-JP-2014/004).

skull	48
orbit	10
nasoantorbital fenestra	16
lower jaw	38
mandible symphysis	14
neck	28
Precaudal thoracic vertebral column (PCRW)	33
scapula	13
coracoid	11
humerus	18
radius	25
mc IV	16
wp 1	22.5
wp 2	21.5
wp 3	19.5
wp 4	17
femur	18.5
tibia	23.5

German for skull-orbit-length index) for the pterodactyloids from the Solnhofen Archipelago, which range from 30 in the smallest individual of *Pterodactylus* (BSPG 1967 I 276, Exemplar Nr. 6; skull length of 23 mm) to 15 in the largest (BSPG 1883 XVI 1, Exemplar Nr. 28; skull length of 113.5). With an SOL-index of 20 and a skull length of 48 mm, the new specimen from Painten matches the observed relationship between SOL-index and skull length for pterodactyloids very well (see Wellnhofer 1970: fig. 17) and falls within the range defined as the transitional ontogenetic stage (between juvenile and adult).

The sclerotic ring is preserved within the dorsal half of the orbit and even the individual sclerotic elements can be discerned, although an exact number of sclerotic elements



Figure 3. *Pterodactylus antiquus*, DMA-JP-2014/004, from the Upper Jurassic (Kimmeridgian) Torleite Formation of Painten; detail photograph of the skull.

cannot be provided due to the small size and imperfect preservation. The sclerotic ring is ellipsoidal in shape being slightly longer than high, although it seems to be diagenetically somewhat compressed dorsoventrally. Judging from other specimens preserving the sclerotic ring like BSPG 1968 I 95 (Exemplar Nr. 2) and SMNS 81775 (without Exemplar Nr.), the sclerotic ring normally has a circular outline and occupies almost the entire orbit (Wellnhofer 1970; Bennett 2006: fig. 6). The nasoantorbital fenestra has an anteroposterior length of 16 mm, occupying around one third of the skull length, which is similar to other *Pterodactylus* specimens including the holotype of *P. antiquus* (BSPG AS I 739, Exemplar Nr. 4) (Wellnhofer 1970). In very young individuals, the ratio between nasoantorbital length and skull length is slightly smaller, around one fifth to one fourth (e.g. BSPG 1967 I 276, Exemplar Nr. 6) (Wellnhofer 1970). The parietal region of the skull posterior to the orbit is rounded. The dorsal margin of the skull is relatively straight and slightly concave. The ventral margin of the skull and the palatal region are completely straight.

The mandible is complete and preserved in ventral view, although it is slightly distorted in a way that the left lateral aspect is partly visible. It has a total length of 38 mm, while the symphysis is 14 mm long, thus occupying slightly more than one third (approximately 37%) of the length of the mandible. In general, it seems as if the symphysis becomes proportionately slightly larger (relative to mandible length) during ontogeny, with the ratio ranging between 37% in small individuals (BSPG 1967 I 276, Exemplar Nr. 6; skull length of 23 mm) and 43% in large individuals (BSPG AS I 739, Exemplar Nr. 4; skull length of 108 mm) (Wellnhofer 1970). The distance between the left and right mandibular ramus at the level of the joint is 7 mm, although this value should be treated with caution due to the slight distortion of the lower jaw. The suture between the mandibular rami is well discernible, being completely straight and extending anteroposteriorly. The paired hyoid bones are located between the posterior parts of the lower jaw and have an elongated, slightly bowed morphology, and thus resemble those of the very small specimen BSPG 1967 I 276 (Exemplar Nr. 6) (Wellnhofer 1970: fig. 5).

The tooth crowns are overall low and conical, just as in all other specimens of *Pterodactylus*. There are 14 teeth preserved in the left upper jaw, extending from the jaw tip up until the anterior third of the nasoantorbital fenestra. The size of the teeth progressively decreases posteriorly – again a feature present in several other *Pterodactylus* specimens including the type specimens of both *P. antiquus* (BSPG AS I 739, Exemplar Nr. 4), and of *P. kochi* (BSPG AS XIX 3, Exemplar Nr. 23) (Wellnhofer 1970: fig. 3, pl. 1–2). In the left lower jaw, 14 teeth are present that gradually become smaller posteriorly and extend for 17 mm measured from the tip of the jaw (roughly 45% of the total mandible length). As was demonstrated by Wellnhofer (1970) as well as later by Jouve (2004) and Bennett (2013a), the tooth count in *Pterodactylus* changes in proportion with the length of the skull and thus the ontogenetic age of the specimen. The number of teeth in the

upper jaw ranges between 12 in small individuals (BSPG 1967 I 276, Exemplar Nr. 6; skull length of 23 mm) and 18 in large individuals (BSPG AS I 739, Exemplar Nr. 4; skull length of 108 mm) (Wellnhofer 1970).

Axial skeleton

The neck of DMA-JP-2014/004 (Fig. 4a) comprises seven cervical vertebrae (but see Bennett 2004, 2013a) and has a length of approximately 28 mm, which compares well with other *Pterodactylus* specimens of a similar size such as (the slightly smaller) TM 10341 (Exemplar Nr. 1) that has a neck length of 25.9 mm and a skull length of 44.5 mm (Bennett 2013a). The dorsal series comprises 15 vertebrae, while the number of sacral vertebrae is difficult to assess due to the slightly displaced ilium (Fig. 4a). The combined length of the dorsal and sacral region (= PCRW-length of Wellnhofer 1970 and Bennett 2013a) is 33 mm and thus similar in size but proportionately slightly smaller compared to that of the similarly-sized specimen TM 10341 (Exemplar Nr. 1), in which the dorsal and sacral vertebral column have a combined length of 33.3 mm (Bennett 2013a). The tail of the new specimen from Painten is partially covered by the ilium, and therefore its exact length and the number of caudal vertebrae cannot be reliably determined. The ribs are still attached to their respective vertebrae, are very thin and slightly curved. However, they are partly concealed by the overlying forelimb elements. The overlapping gastralia are present in the abdominal area of the specimen, anteroventrally of the pelvis.

Appendicular skeleton

The forelimbs are complete and mostly articulated, although the right wing is partly underlying the body skeleton (Fig. 4b). The measurements were thus taken from the left forelimb. The scapula and the coracoid are preserved next to each other, the former having a length of 13 mm and the latter of 11 mm, although the coracoid is not fully visible in the left or the right side. The left humerus, which is slightly dislocated from the glenoid, has a length of 18 mm. Radius and ulna are lying next to each other, being completely parallel and more or less equal in length. Both are considerably longer than the humerus with a length of 25 mm. As discussed by Wellnhofer (1970), the wrist of *Pterodactylus* consists of two proximal carpals and four distal carpals. In the new specimen from Painten, the two proximal carpals contact the distal joints of radius and ulna, while the four distal carpals are preserved as small, blocky elements between the proximal carpals and the metacarpals. The four metacarpals are subequal in length and preserved parallel to each other, but metacarpals I–III are much smaller and partly covered by metacarpal IV. The wing metacarpal (i.e. metacarpal IV) is similar in size to, albeit slightly shorter than, the humerus with a length of 16 mm. The pulley-like distal joint of the wing metacarpal is well visible in dorsal view. The phalanges of the wing finger are elongated and rod-like and decrease in



Figure 4. *Pterodactylus antiquus*, DMA-JP-2014/004, from the Upper Jurassic (Kimmeridgian) Torleite Formation of Painten; detail photograph of the axial skeleton (a), as well as the forelimbs (b).

size distally, with lengths of 22.5 mm (wing phalanx 1), 21.5 mm (wing phalanx 2), 19.5 mm (wing phalanx 3) and 17 mm (wing phalanx 4). The distal-most phalanx of the left wing finger is slightly dislocated from the third one. The right wing is completely articulated but largely hidden under the body skeleton. The other fingers are articulated with their respective metacarpals and are completely preserved. The phalangeal formula of the hand is 2-3-4-4-0, as is typical for pterosaurs. The proportions of the wing of the Painten specimen are very similar to those reported from other specimens of *Pterodactylus*, with the humerus being around a quarter to a third shorter than the radius, the wing metacarpal being similar in size to (albeit slightly smaller than) the humerus, and the wing phalanges becoming progressively but slowly shorter (for a comparison of the forelimb proportions in *Pterodactylus*, see also below).

The pelvis comprises the articulated ilium, which is firmly attached to the sacral vertebrae, the pubis and the ischium (Fig. 5). The hind limbs are both well visible, being stretched out laterally (Fig. 5). The femora are articulated with the pelvis, the slightly demarcated femoral head still being connected to the acetabulum. The femur has a length of 18.5 mm and thus is slightly shorter than the tibia, which has a length of 23.5 mm, a condition also

seen in all other *Pterodactylus* specimens (Wellnhofer 1970; Bennett 2013a). The fibula is very thin, tightly attached to the tibia, and only extending for the proximal half of the tibia. The tarsals are tightly interlocked and articulated in the right hind limb, whereas in the left hind limb, the tarsals are somewhat disarticulated. Of the five tarsals (two proximal and three distal ones) typically present in *Pterodactylus* (Wellnhofer 1970), at least four (two proximal and two distal ones) are visible in the specimen from Painten. The feet are again well preserved and articulated, comprising all five metacarpals and all five digits. Among the metatarsals, metatarsal II is the longest, metatarsal I and III are subequal in length and slightly shorter than metatarsal II. Metatarsal IV is shorter than metatarsal I and II, and metatarsal V is considerably shorter than the other metatarsals, being only a small splint-like bone. The first four digits bear small claws, whereas the fifth digit consists only of a single short phalanx. The phalangeal formula is 2-3-3-3-1. As demonstrated by Wellnhofer (1970), the phalangeal formula of *Pterodactylus* is dependent on the ontogenetic age of the animal, varying between 2-3-3-3-1 in juveniles and 2-3-4-4-1 in adults. Therefore, the phalangeal formula of the specimen from Painten again indicates an individual of juvenile to subadult age.

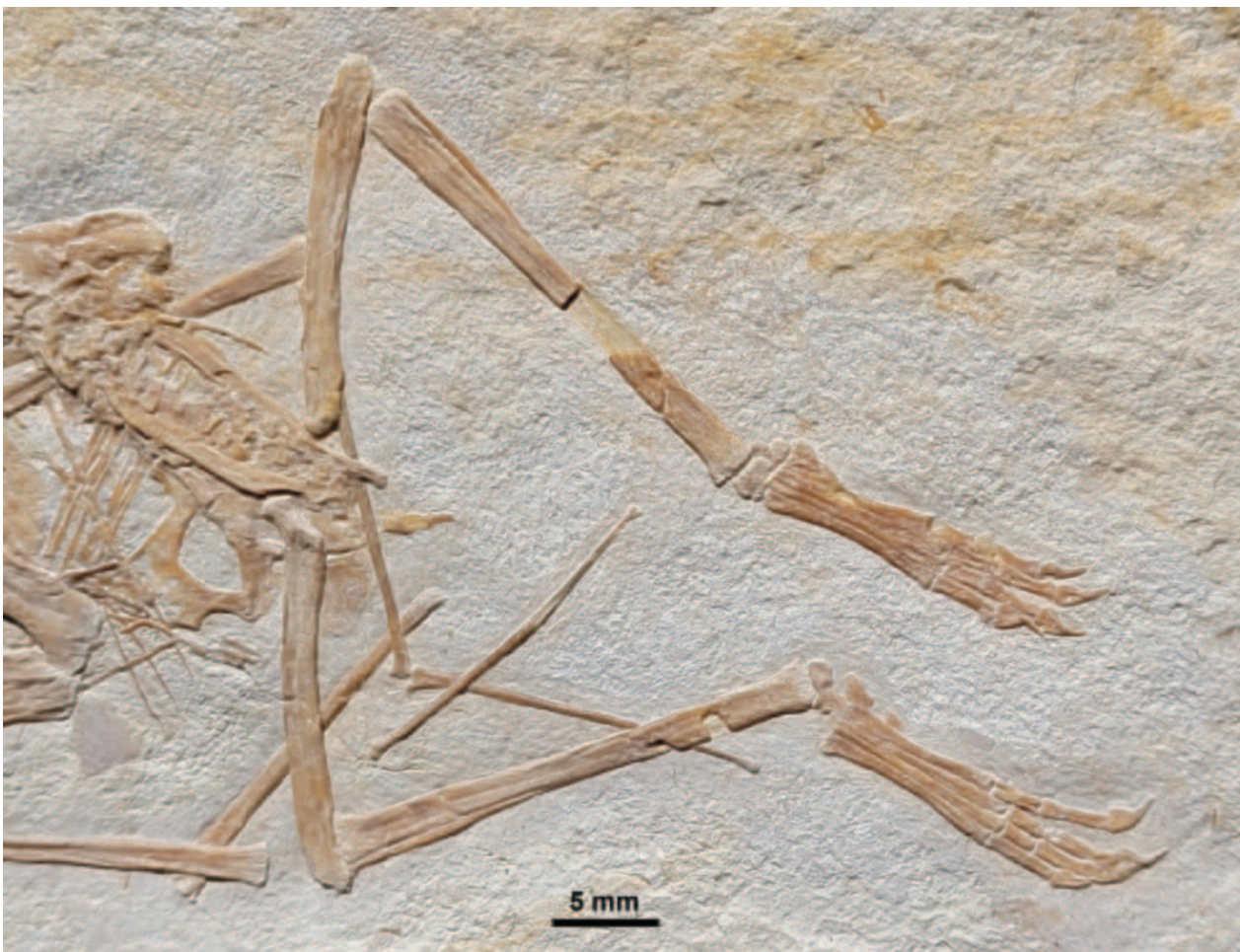


Figure 5. *Pterodactylus antiquus*, DMA-JP-2014/004, from the Upper Jurassic (Kimmeridgian) Torleite Formation of Painten; detail photograph of the hind limbs.

Skeletal proportions and Nopcsa curves

The length of the skull, neck, combined dorsal and sacral vertebral column (=PCRW-length of Wellnhofer 1970 and Bennett 2013a), humerus, radius, wing metacarpal, wing phalanx 1–4, femur and tibia were plotted in order to produce a modified Nopcsa curve (see Bennett 2013a). In this diagram, we also plotted the respective lengths of all other *Pterodactylus* specimens (measurements taken from Wellnhofer 1970 as well as Bennett 2013a for specimen TM 10341 and Frey and Tischlinger 2000 for an uncatalogued specimen stored in a private collection). The resulting Nopcsa diagram (Fig. 6) is essentially an updated version of the one figured by Bennett (2013a: fig. 9). In general, the specimen from Painten, DMA-JP-2014/004, is remarkably similar to the other *Pterodactylus* specimens regarding its skeletal proportions. The skull is the longest element in all specimens, while the neck is significantly shorter. In the large majority of specimens, including DMA-JP-2014/004, the combined length of the dorsal and sacral vertebral column (=PCRW-length) is greater than that of the neck, with some notable exceptions such as the holotype of *P. antiquus* (BSPG AS I 739, Exemplar Nr. 4), in which the PCRW-length is smaller than, or equal to, the length of the neck. Notably, all of these exceptions

are relatively large specimens with skull lengths of more than 80 mm. All specimens smaller than that (i.e. having skull lengths below 80 mm) have a neck shorter than their combined dorsal and sacral vertebral column.

In all specimens referred to *Pterodactylus*, the humerus is much shorter than the PCRW-length and the radius is longer than the humerus (Fig. 6). The metacarpal of the wing finger is again considerably shorter than the radius and has a similar size as the humerus in all specimens aside from SM R4074, in which the wing finger metacarpal is comparatively very long, having almost the same length as the radius. In all specimens except SM R4074 (which seems to have an unusually long fourth metacarpal), the first wing finger phalanx is much longer than the wing finger metacarpal. In all specimens of *Pterodactylus*, phalanges 1–4 of the wing finger are progressively shorter, which, in the diagram (Fig. 6), results in a slightly convex and gentle downward curve. The femur is significantly longer than the wing phalanx 4 but shorter than the tibia. In summary, the outline of the Nopcsa curve of the specimen from Painten is nearly identical to that of similarly sized *Pterodactylus* specimens, thus indicating remarkably similar skeletal proportions and placing DMA-JP-2014/004 unequivocally within the genus *Pterodactylus*.

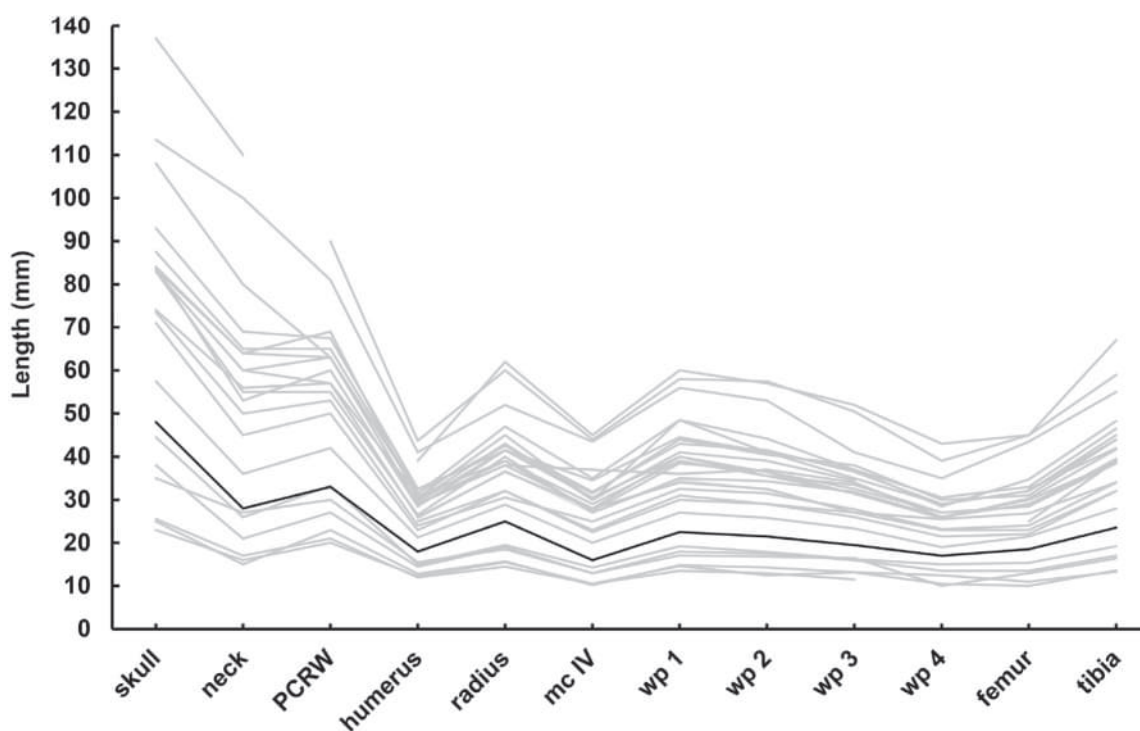


Figure 6. Modified Nopcsa curves of the skeletal proportions of *Pterodactylus antiquus* (including *P. kochi*). The measurements were taken from Wellnhofer (1970) as well as from Frey and Tischlinger (2000). Note that we used the corrected values of TM 10341 (Exemplar Nr. 1) provided by Bennett (2013a) that differ considerably from those listed by Wellnhofer (1970). Specimen JME 29.III.1950 (Exemplar Nr. 9) was excluded because it was shown by Bennett (2006) to belong to *Germanodactylus cristatus*. The heavy black line represents the curve for the new specimen from Painten described herein (DMA-JP-2014/004). The line with the third-largest skull represents the holotype of *P. antiquus* (BSPG AS I 739, Exemplar Nr. 4; skull length of 108 mm), and the line directly below that of the Painten specimen (DMA-JP-2014/004) represents TM 10341 (Exemplar Nr. 1; skull length of 44.5 mm). **Abbreviations:** mcIV, metacarpal IV (i.e. the wing finger metacarpal); PCRW, combined length of the dorsal and sacral vertebral column (=PCRW-length of Wellnhofer 1970 and Bennett 2013a; praecaudale Rumpfwirbelsäule); r, radius; s, skull; t, tibia; wp1–4, wing finger phalanx 1–4.

Discussion and conclusion

The new specimen from Painten is clearly referable to *Pterodactylus antiquus*, based on the diagnosis proposed by Bennett (2013a). More specifically, it has an elongate skull, a slender and elongated rostrum, a straight to only slightly concave dorsal skull margin, low and conical teeth that are large anteriorly and decrease in size posteriorly, an upper tooth row extending to the anterior margin of the nasoantorbital fenestra, wing phalanx 2 being 93–96% (exactly 95.6%) as long as wing phalanx 1, wing phalanges 1–4 exhibiting a convex upward curve in modified Nopcsa curves, and a longer metatarsal II than I (for the diagnosis of *P. antiquus* see also above). Only features listed by Bennett (2013a) as being characteristic of adult individuals and varying across ontogenetic stages (e.g. tooth count, length of nasoantorbital fenestra, presence of a sagittal bony crest), are absent in DMA-JP-2014/004. In addition, the Painten *Pterodactylus* is extremely similar to other specimens assigned to *P. antiquus* (including *P. kochi*), especially those of a similar size and thus ontogenetic stage, with respect to both gross morphology and skeletal proportions (see above). The Painten *Pterodactylus* most likely represents a juvenile to young subadult individual as shown by its overall size, absolute skull length, the size of the orbit (relative to skull length), and phalangeal formula of the pes. Based on the SOL-index of Wellnhofer (1970), the specimen is assignable to the transitional stage (‘Übergangsbereich’) between juvenile and adult individuals. Interestingly, the DMA-JP-2014/004 falls here into a size range that is relatively rare in the known sample of *Pterodactylus* specimens. So far, only four specimens with a skull length between 30 and 60 mm have been reported, and only one of these falls into the size range between 38 and 57.5 mm (TM 10341, Exemplar Nr. 1; skull length of 44.5 mm).

In general, small and immature individuals dominate the sample of *Pterodactylus* from Solnhofen, whereas large and adult individuals are comparatively rare (Bennett 1996b). The same pattern can also be observed in other pterodactyloids and *Rhamphorhynchus* from the Solnhofen Archipelago (Bennett 1995, 1996b). As observed by Bennett (1996b), the specimens are, however, not evenly distributed across the full size range but predominantly fall into distinct size-classes that are separated by marked gaps. For *Pterodactylus*, these size classes are characterized by a skull length of 15–45 mm and 55–95 mm for the small and large size-classes, respectively (Bennett 1996b). The gaps bounding these size-classes are between 38–57 mm and more than 93 mm skull length. The specimen from Painten (with a skull length of 48 mm) thus is a rare representative of the first gap between the small and large size-classes. Bennett (1996b) interpreted the distinct size-classes as year-classes, which consequently means that DMA-JP-2014/004 was of an intermediate (and rarely found) ontogenetic age at the time of its death, between two consecutive year-classes. In his statistical study on *Rhamphorhynchus* from the Solnhofen Limestone (a taxon showing similar size-classes), Bennett (1995) provided two explanations for the observed

size-pattern: either these pterosaurs suffered from seasonal mortalities, or the conditions allowing the preservation of the carcasses were present only seasonally. Seasonal mortality, in turn, could be explained by migratory behaviour of the animals (i.e. they were present in the region only seasonally) or it could mean that the animals died from environmental factors occurring seasonally, such as monsoons or toxic algal blooms (Bennett 1995). Seasonal preservation, on the other hand, would indicate seasonal changes in water quality (Bennett 1995) or seasonal changes of sedimentary influx into the basins (the ‘Wannen’). Therefore, both the seasonal mortality hypothesis and the seasonal preservation hypothesis could be explained by the reconstructed seasonal (perhaps monsoonal) climate prevailing at the time of deposition of the Solnhofen Limestone (see above). The dominance of small, immature individuals in the sample of *Pterodactylus* specimens probably reflects their higher vulnerability and/or their higher potential to be preserved in the shallow basins (Bennett 1995).

Interestingly, the tetrapod assemblage from the Plattenkalk deposits of the Painten area appears to be highly distinctive on an alpha-taxonomic level. Although closely related species are also known from other strata of the laminated limestone of the Franconian Alb, several taxa are so far unique to the Painten limestones, including new but so far undescribed turtles (Albersdörfer and Häckel 2015; Spindler and Albersdörfer 2019), a new species of *Cricosaurus* (Sachs et al. 2021), the theropod *Sciurumimus* (Rauhut et al. 2012), a so far undescribed new pro-pterodactyloid (Tischlinger and Frey 2013), and a so far undescribed *Cycnorhamphus*-like pterosaur (Bennett 2013b), among others. The specimen described in this paper represents an intriguing exception because it can be confidently assigned to *Pterodactylus antiquus*, a species otherwise well-known from much younger limestone deposits of the Solnhofen Archipelago referable to the Malm Zeta 2 to Malm Zeta 3 (Bennett 2013a; Vidovic and Martill 2018). The Plattenkalk deposits from Painten (Torleite Formation) have been assigned to the *Beckeri* ammonite zone, the *Ulmense* subzone and the *rebouletianum* ammonite horizon corresponding to the latest Kimmeridgian age. The youngest occurrence of *Pterodactylus antiquus* comes from the Mörsheim limestone deposits (Wellnhofer 1970), which have been assigned to the Malm Zeta 3, and more specifically, *Hybonotum* ammonite zone, *Moernsheimensis* subzone and *moernsheimensis* ammonite horizon (Schweigert 2015). Therefore, *Pterodactylus antiquus* spans at least six ammonite horizons, which are from oldest to youngest, the *rebouletianum*, *eigeltingense*, *riedlingensis*, *leisackerensis*, *rueppellianus*, and *moernsheimensis* (Schweigert 2007, 2015). Following the reasoning of Rauhut et al. (2018), it is possible to estimate the approximate duration of this timespan based on the assumption of Schweigert (2005), who calculated an average ammonite horizon duration of 165,000 years. This leads to a temporal range for *Pterodactylus antiquus* of roughly one million years. The unique taxonomic composition of the vertebrate fauna from Painten (at least on an alpha-taxonomic level) might be related

to the relatively old geological age of the deposits or, alternatively, to the particular palaeogeographic or palaeoecological characteristics of the Painten basin ('Paintener Wanne'). Ultimately, this could also explain the somewhat unusual ontogenetic age of the *Pterodactylus* specimen described here (see above). However, for the time being, the exact reasons for the distinctiveness of the vertebrate assemblage from Painten cannot be resolved conclusively, as much of the material from there still awaits detailed study. In general, this paper highlights the potential of the Plattenkalk deposits from Painten for yielding important new insights into the vertebrate fauna of the Solnhofen Archipelago but, at the same time, it also illustrates the importance of future work regarding the material.

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