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First record of a non-pterodactyloid pterosaur (Reptilia: Archosauria) from Switzerland

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Key words: Pterosauria, non-pterodactyloid, wing phalanx, Kimmeridgian, Jura, Switzerland

ABSTRACT

The remains of pterosaurs, the "flying reptiles" of the Mesozoic Era, are usually rare in vertebrate deposits, except in the few pterosaur Lagerstätten. The Upper Jurassic carbonate deposits of the Swiss Jura mountains well illustrate this rarity, with only one pterosaur remain reported until now, a wing phalanx (from the fourth digit, bearer of the flight membrane) from the Solothurn Turtle Limestone (upper Kimmeridgian, Canton Solothurn), assigned to a Pterodactyloidea. Here we report the second occurrence of a pterosaur from Switzerland, a shaft fragment of a wing phalanx from the upper Kimmeridgian of Porrentruy (Canton Jura). This bone is the first record of a Swiss non-pterodactyloid pterosaur. It is assigned to a large-sized Rhamphorhynchinae indet. (Rhamphorhynchidae). A comparison with tetrapod assemblages from other Late Jurassic coastal environments of western Europe underlines the peculiar aspect of this discovery.

RESUME

Les restes de ptérosaures, les «reptiles volants» de l'ère mésozoïque, sont généralement rares dans les dépôts à vertébrés, excepté dans les quelques Lagerstätten à ptérosaures. Les dépôts carbonatés du Jurassique supérieur de la chaîne du Jura suisse illustrent bien cette rareté, avec seulement un reste de ptérosaure mentionné jusqu'à présent, une phalange alaire (du doigt IV, porteur de la membrane alaire) des Calcaires à Tortues de Soleure (Kimméridgien supérieur, Canton de Soleure), attribuée à un Pterodactyloidea. Nous présentons ici la deuxième mention d'un ptérosaure en Suisse, un fragment de diaphyse d'une phalange alaire du Kimméridgien supérieur de Porrentruy (Canton du Jura). Cet os est le premier signalement d'un ptérosaure non-ptérodactyloïde en Suisse. Il est attribué à un Rhamphorhynchinae indet. (Rhamphorhynchidae) de grande taille. Une comparaison avec les assemblages de tétrapodes d'autres environnements littoraux du Jurassique supérieur d'Europe occidentale souligne l'aspect singulier de cette découverte.

1. Introduction

The pterosaur fossil record is relatively poor, despite the longevity of this Mesozoic archosaur group (Late Triassic-Late Cretaceous, ca. 160 million years), including about 50 genera and some 100 species (Wellnhofer 1991, Unwin 2003). Except pterosaur-bearing Lagerstätten (exceptional fossil deposits), such as the Upper Jurassic Solnhofen Beds (Tithonian, Germany) or the Lower Cretaceous Santana Formation (Aptian–Albian, Brazil) (Wellnhofer 1991, Kellner 1994, Buffetaut 1995), that have yielded a large amount of very well-preserved, more or less complete and articulated skeletons, pterosaur discoveries are usually limited to some disarticulated or isolated remains, generally crushed (Unwin 1987b, Wellnhofer 1991). The poorly preserved bones and rarity of these flying reptiles has been mainly interpreted as the result of both the fragility of their very thin walled hollow bones, the thinnest bone walls of any tetrapods (Ricqlès et al. 2000), and unsuitable settings for their fossilization in continental environments (Unwin 1987a, Wellnhofer 1991, Unwin 1999). According to the rarity of pterosaur fossils, each discovery of a pterosaur bone can provide important informations, for example in terms of biodiversity.

The purpose of this study is to describe a pterosaur bone fragment from the upper Kimmeridgian of Porrentruy (Canton Jura, northwestern Switzerland), discovered by the "Section d'archéologie et paléontologie" during systematic excavations along the future course of the "Transjurane" highway. Pterosaurs are very poorly known from Switzerland, including only one undoubtedly pterosaur bone, a pterodactyloid phalanx from the upper Kimmeridgian Solothurn Turtle Limestone (Meyer & Hunt 1999). Although fragmentary, the well-preserved (uncrushed and unworn) reported specimen gives

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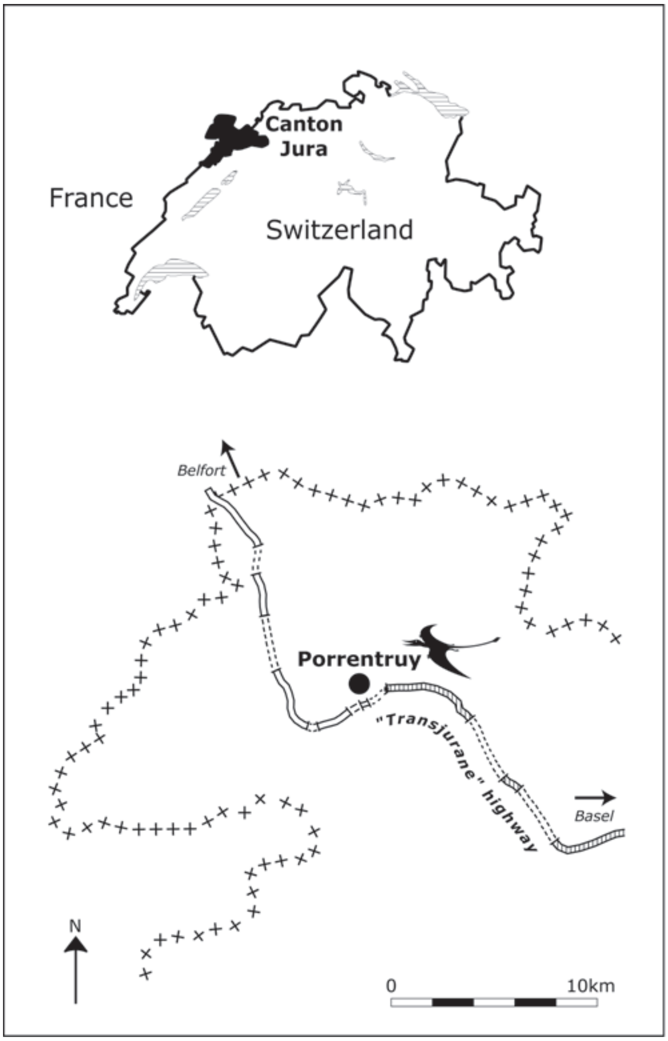

Fig. 1. Location of the town of Porrentruy (Jura, Switzerland), along the future course of the "Transjurane" highway (A16), where the pterosaur specimen (MJSN RDM000-7) was found.

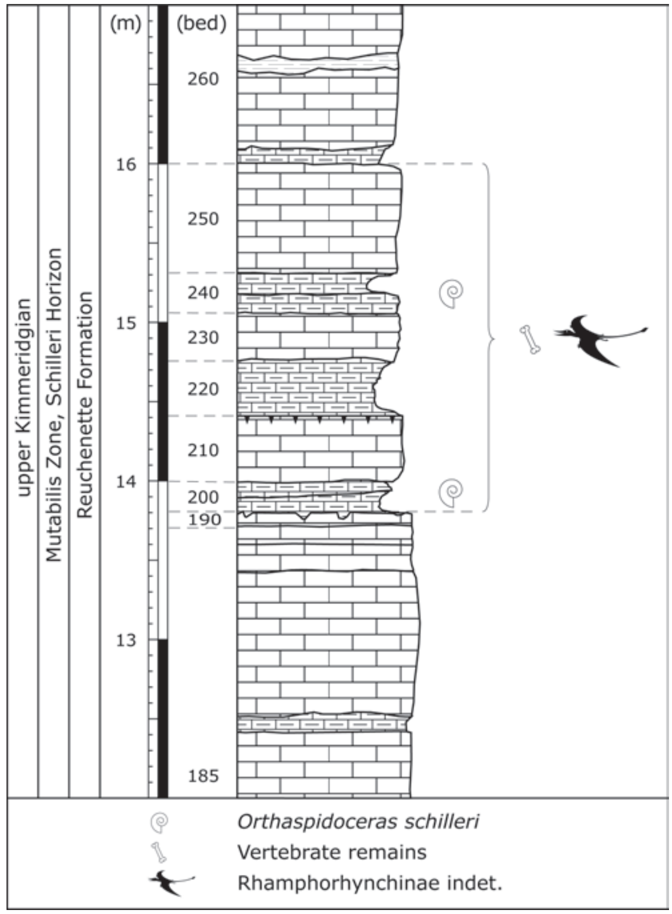

Fig. 2. Stratigraphic position of the pterosaur specimen (MJSN RDM000-7) within the simplified section of the "Roche de Mars" locality (Porrentruy; Swiss co-ordinates: 574300 / 252000). The bone has been found on the road cut during geological prospecting, the matrix surrounding the bone attributes it to the 200–250 bed interval (D. Marty, pers. comm.), dated by ammonites to the early late Kimmeridgian.

the opportunity to describe the second pterosaur bone from Switerzland and to reveal the first occurence of a Swiss non-pterodactyloid pterosaur.

Institutional abbreviations: BMNH, Natural History Museum, London (UK); MJSN, Musée Jurassien des Sciences Naturelles, Porrentury (Switzerland); NMS, Naturmuseum Solothurn, Solothurn (Switzerland); SMF, Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt (Germany).

2. Geological setting and taphonomy

The pterosaur specimen was found in 2000 east of the town of Porrentruy (Canton Jura, northwestern Switzerland) (Fig. 1), in a fossiliferous limestone marl at the "Roche de Mars" locality (Fig. 2). Vertebrate remains from this locality were mentioned by Thurmann & Etallon (1861–1864) as early as the nineteenth century. The depositional sequence is situated between the Banné Member and the Virgula Member of the Reuchenette Formation (Thalmann 1966, Gigy 2000). It is precisely dated to the early late Kimmeridgian (Mutabilis Zone, Schilleri Horizon) by ammonites *(Orthaspidoceras schilleri)*, following the zonation in Hantzpergue (1979) and Hantzpergue et al. (1997). It has been deposited in a coastal marine environment of a shallow carbonate platform (Marty et al. 2003). The bed that yielded the bone is a subtidal glauconite- or chamosite-bearing marly wacke- to packstone (D. Marty, pers. comm.). This depositional sequence is the object of systematic excavations at different localities in the vicinity of Porrentruy, revealing a rich and diverse coastal biota of invertebrates (annelida, bivalvia, gastropoda, cephalopoda, crustacea, echinoidea) and vertebrates (chondrichthyes, osteichthyes, chelo-

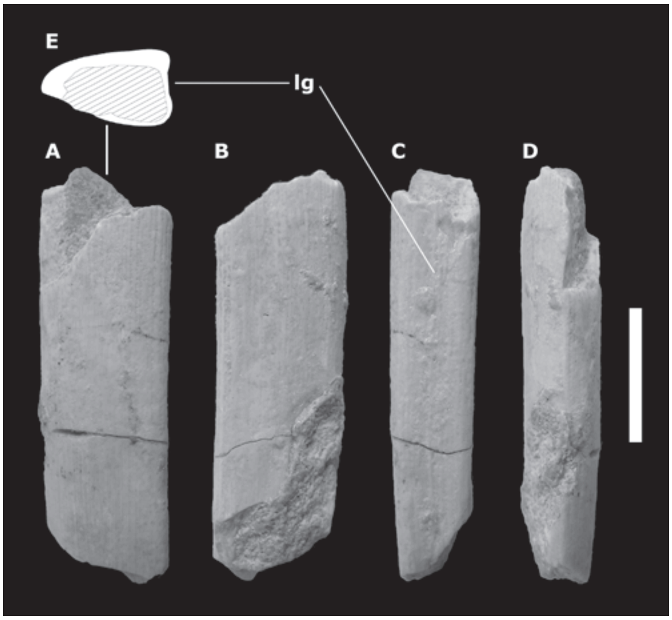

Fig. 3. Rhamphorhynchinae indet. MJSN RDM000-7 (Reuchenette Formation; upper Kimmeridgian, Porrentruy, Switzerland). Fragment of the shaft of a wing phalanx in dorsal (A), ventral (B), caudal (C), and cranial (D) views; sketch of the tranverse cross section (E). Scale bar: 1 cm. Abbreviation: lg, longitudinal groove.

nians, crocodilians). The most important discoveries are multiple surfaces with dinosaur tracks found in laminated limestones situated a few meters below the unit that yielded the pterosaur bone (Marty et al. 2003, Marty & Billon-Bruyat 2004).

The pterosaur bone (Fig. 3) shows the presence of the same sediment into the medullar cavity and surrounding the cortex of one of the broken extremities (see the lower part of Fig. 3B). This indicates that the bone was broken before the fossilisation and suggests that the pterosaur carcass was disarticulated (by decay or scavenging) before deposition. In addition, the bone is broken but unworn, excluding a long post-mortem transport.

3. Description

The reported specimen (MJSN RDM000-7) is stored in the palaeontological collection of the Musée Jurassien des Sciences Naturelles, at Porrentruy (Canton Jura, Switzerland). It corresponds to a section of a bone shaft (Fig. 3), 31.1 mm long and 9.8 mm wide. It is relatively narrow, subtriangular in tranverse cross section, flattened, hollow, thin-walled, slightly bent vertically and horizontally, and a longitudinal shallow groove extends along one side of the entire preserved part of the shaft (Fig. 3). These characters show that it pertains to a pterosaur wing phalanx (Kuhn 1967, Wellnhofer 1975a, 1978, 1991), that is one of the four long phalanges of the greatly elongated fourth digit (bearer of the flight membrane). The shaft of the reported phalanx is massive, is dorsoventrally flattened, has an almost right-angled triangle shape in tranverse cross section, and is slightly bent dorsoventrally and craniocaudally (Fig. 3). The longitudinal shallow groove is located on the caudal margin or flight membrane side (Fig. 3C, E), which is "doubly keeled", the dorsal ridge being slightly drawn further caudally than the ventral one (Fig. 3E). The leading edge is located cranially, and is relatively sharp (Fig. 3D, E). The diameter slightly decreases along the preserved short section of the shaft, both in width (9.8 to 9.0 mm) and in thickness (5.7 to 4.9 mm, measured on the caudal side), suggesting that it might belong to the middle part of the shaft.

4. Discussion

The pterosaurs are traditionally divided into the two suborders "Rhamphorhynchoidea" (long-tailed pterosaurs) and Pterodactyloidea (short-tailed pterosaurs), the "rhamphorhynchoids" or non-pterodactyloids being paraphyletic (Kellner 2003, Unwin 2003). The presence of a longitudinal groove on the caudal margin of all the flight digit phalanges was considered as a distinctive character of the non-pterodactyloids by Wellnhofer (1975a, 1978, 1991), but it has been restricted to the diagnosis of the Rhamphorhynchinae (Rhamphorhynchidae) by Unwin (2003). According to the known distribution of this groove within pterosaurs, the presence of this character on the reported specimen indicates that it can be assigned to a non-pterodactyloid, more precisely to an indeterminate Rhamphorhynchinae. This subfamily extends from the Toarcian to the Tithonian (Unwin 2003), with two genera in the Upper Jurassic, *Nesodactylus* from the Oxfordian of Cuba (Colbert 1969) and *Rhamphorhynchus* from the Tithonian of Germany (Wellnhofer 1975b). The discovery of a rhamphorhynchine from a coastal marine environment, without evidence for a long post-mortem transport (see Geological setting and taphonomy), is consistent with the hypothesis that these pterosaurs were mainly coastal inhabitants (e.g. Wellnhofer 1991, Unwin & Bakhurina 2000).

A pterosaur phalanx (NMS 20870) was reported from the upper Kimmeridgian (Reuchenette Formation) of the Solothurn Turtle Limestone (Canton Solothurn, northwestern Switzerland) by Meyer & Hunt (1999). This bone, previously interpreted as a coelurosaurian dinosaur fibula by Huene (1926) was identified by Meyer and Hunt (1999) as a second wing phalanx of a large pterodactyloid, the largest Jurassic pterosaur (wingspan between 3.5 and 5 metres). Other potential skeletal remains of pterosaurs have been mentioned from the same locality (Meyer & Hunt 1999) but are indeterminate. Furthermore, a short broken piece of a probable pterosaur phalanx has been discovered from the upper Oxfordian near Olten (Canton Solothurn), it is on display in the "Naturama Aarau" (C. Meyer, pers. comm.). Also, several pterosaur bones have been found from the upper Oxfordian around Biel (Canton Bern), they are stored in the collection of the "Fonda-

Table 1. Measurements (millimetres) and ratio for the first phalanx of digit IV in the two Late Jurassic genera of Rhamphorhynchinae *(Nesodactylus and Rhamphorhynchus)* and the reported Rhamphorhynchinae indet.*. Parentheses indicate estimated values.

	Total length (l)	Shaft width (w)	l/w	Specimen No.	Age; Country	Source of data
Nesodactylus hesperius	137.0	6.3	21.9	A.M.N.H. 2000	Oxfordian; Cuba	Colbert (1969)
Rhamphorhynchus muensteri (gemmingi)	114.5	5.3	21.8	SMF R4128	Tithonian; Germany	Colbert (1969) & Wellnhofer (1978)
Rhamphorhynchus "longiceps"	202.0	9.0	22.4	BMNH 37002	Tithonian; Germany	Wellnhofer (1975b) & Cavin (pers. comm.)
Rhamphorhynchinae indet.*	(215.6)	9.8	(22.0)	MJSN RDM000-7	Kimmeridgian; Switzerland	Present study

* According to the hypothesis that the reported shaft fragment belongs to the first phalanx (see Discussion).

tion paléontologique jurassienne" at Glovelier (Meyer & Thüring 2003, pers. obs.). However, these Oxfordian pterosaur remains from northwestern Switzerland have never been figured nor described. Thus, the reported bone is actually the only remain of a non-pterodactyloid in Switzerland. Moreover, it is the second locality for Kimmeridgian rhamphorhynchines, along with indeterminate rhamphorhynchine remains from Guimarota in Portugal (Wiechmann & Gloy 2000).

Even if the extremities of the reported bone are missing, it can be attempted to estimate its original length using the width of the shaft. Assuming that this preserved part of the mid-shaft belongs to the first phalanx, the longest phalanx of the digit IV in *Rhamphorhynchus* (Wellnhofer 1975b, Kellner 2003), permits to estimate the minimum wingspan. Based on the ratio of length to width for the first digit IV phalanx shaft in *Nesodactylus* and *Rhamphorhynchus* (despite possible allometric changes, see Bennett 1995 for *Rhamphorhynchus*), the original length has been estimated close to 22 cm (Table 1). Such an important length for the first digit IV phalanx is similar to that of the largest known specimen of Rhamphorhynchidae (BMNH 37002: 20 cm long; Table 1), a *Rhamphorhynchus* with an estimated wingspan of 1.80 metres (Wellnhofer 1975b). Among non-pterodactyloids, only *Campylognathoides zitelli* (Campylognathoididae) reached a similar wingspan (Wellnhofer 1991). Despite the uncertainty about the estimation of the phalanx length, the wingspan of the Swiss specimen is clearly among the largest known non-pterodactyloids. It is noteworthy that both the pterodactyloid specimen described by Meyer & Hunt (1999) and the non-pterodactyloid reported here belong to large Jurassic pterosaurs.

The rarity of pterosaurs among the late Kimmeridgian tetrapod assemblages of northwestern Switzerland, both at Porrentruy and Solothurn, strongly contrasts with the abundance of turtle and crocodilian skeletal remains, and dinosaur trackways (Meyer 1994, Meyer & Hunt 1999, Marty et al. 2003, Marty & Billon-Bruyat 2004). Among the coeval sites of western Europe deposited in coastal environments of shallow marine carbonate platforms, a similar rarity of pterosaur bones has been noted at Cerin (upper Kimmeridgian–lower Tithonian, Ain, France) (Buffetaut et al. 1990) and at Crayssac (lower Tithonian, Lot, France) (Mazin et al. 1997, Billon-Bruyat 2003). It contrasts with the numerous skeletons from the pterosaur-bearing Lagerstätte of Solnhofen (lower Tithonian, Bavaria, Germany) (Wellnhofer 1991, Kemp 2001), a skeleton at Canjuers (lower Tithonian, Var, France) (Fabre 1981) and many trackways at Crayssac (Mazin et al. 2003). It has been argued that the difference in pterosaur abundance and diversity between these sites could be partly due to different collecting histories and/or taphonomic biases (Buffetaut 1994, 1995, Kemp 2001, Billon-Bruyat 2003). Despite these potential biases, the low representation of pterosaurs within the coastal marine tetrapod assemblages from the Upper Jurassic of northwestern Switzerland suggests that their skeletal remains might remain rare in these facies.

5. Conclusion

With the reported bone fragment of a large-sized rhamphorhynchine (Rhamphorhynchidae), both non-pterodactyloid and pterodactyloid pterosaurs are now recorded from the Upper Jurassic of Switzerland. The comparison with tetrapod assemblages from other Upper Jurassic localities of western Europe suggests that pterosaur remains will be sporadic in coastal marine environments of northwestern Switzerland, leading to an underestimate of the pterosaur abundance and diversity. The Swiss pterosaur record is still very poor but the description of remains from the Oxfordian would improve that condition.

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