

A new Triassic pterosaur from Switzerland (Central Austroalpine, Grisons), *Raeticodactylus filisurensis* gen. et sp. nov.

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Key words: pterosaur, non-pterodactyloid, Upper Triassic, Ela nappe, Kössen Formation, Switzerland

ABSTRACT

A new basal non-pterodactyloid pterosaur, *Raeticodactylus filisurensis* gen. et sp. nov., is reported. It has been discovered in shallow marine sediments from the Upper Triassic of the lowest Kössen beds (late Norian/early Rhaetian boundary) in the central Austroalpine of Canton Grisons (Switzerland). The disarticulated specimen is comprised of an almost complete skull and a partial postcranial skeleton. A high and thin bony, sagittal cranial crest characterizes the anterodorsal region of the skull. The large mandible, with an additional keel-like expansion at the front, partly matches the enlarged sagittal cranial crest. A direct and close relationship to *Austriadactylus cristatus*, the only known Triassic pterosaur with a bony cranial crest so far, cannot be established. The teeth of the premaxilla are monocuspid and exhibit very strongly bowed enamel wrinkles on the lingual side whereas the enamel is smooth on the labial side. These monocuspid teeth are large and fang-like. The numerous smaller teeth of the maxilla show three, four and five cusps. These are very similar to the teeth of the Triassic pterosaur *Eudimorphodon ranzii*. The humerus shows a thinner construction than that seen in other Triassic pterosaurs. The femur is quite unusual with a caput femoris perpendicular to the shaft. The bones of the extremities are almost twice as long as the ones from the largest Triassic specimen *E. ranzii* (MCSNB 2888). The newly described pterosaur is an adult, with a wingspan of approximately 135 cm. A morpho-functional analysis suggests that *R. filisurensis* was a highly specialized piscivore and possibly a skim-feeder.

ZUSAMMENFASSUNG

Beschrieben wird ein früher langschwänziger Pterosaurier *Raeticodactylus filisurensis* gen. et sp. nov. Entdeckt wurde dieser in den Flachwasserkarbonatablagerungen aus der oberen Trias aus den untersten Kössener Schichten (Grenzbereich Norian/Rhaetian) des Zentralostalpins von Graubünden (Schweiz). Der disartikulierte Fund enthält den beinahe kompletten Schädel und Teile des postcranialen Skelettes. Der Schädel trägt auf der Schnauzenpartie einen hohen und dünnen Knochenkamm. Im Zusammenhang mit dem sagittalen Schädelkamm steht der hohe Unterkiefer mit einer im vorderen Unterkieferbereich zusätzlich auftretenden kielartigen Erhöhung. Eine direkte und enge verwandtschaftliche Beziehung zu *Austriadactylus cristatus*, welcher bisher der einzige bekannte Flugsaurier mit knöchernem Schädelkamm aus der Trias war, konnte nicht festgestellt werden. Die Zähne der Prämaxilla sind einspitzig und zeigen auf der lingualen Seite eine starke komplizierte, bogenartige Riefung, während sie lateral einen glatten Zahnschmelz aufweisen. Die einspitzigen Zähne haben eine fangähnliche Funktion. Die vielen, kleinen Maxillarzähne zeigen drei, vier und fünf Spitzen. Diese sind den Zähnen des triassischen Flugsauriers *Eudimorphodon ranzii* sehr ähnlich. Der Humerus zeigt im Vergleich zu andere triassischen Pterosaurier eine deutlich schlankere Bauweise. Das Femur ist ungewöhnlich, weil der Gelenkkopf rechtwinklig zum Knochenschaft steht. Die Extremitätenknochen sind fast doppelt so lang wie diejenigen des grössten Exemplares *E. ranzii* (MCSNB 2888). Der neubeschriebene Pterosaurier stammt von einem adulten Exemplar, welches eine Flügelspannweite von ungefähr 135 cm hatte. Die funktionsmorphologische Analyse zeigt, dass *R. filisurensis* gen. et sp. nov. ein hochspezialisierter Fischfresser und möglicherweise ein Skimmer war.

Institutional abbreviations

BNM, Bündner Naturmuseum, Chur (Switzerland); BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich (Germany); MCSNB, Museo Civico di Scienze Naturali, Bergamo (Italy); MFSN, Museo Friulano di Storia Naturale, Udine (Italy); MGUH, Geological Museum, University of Copenhagen, (Denmark); MNHNL, National Museum of Natural History, Luxemburg (Luxemburg); MPUM, Dipartimento de Scienze della Terra, Università di Milano

(Italy); PIMUZ, Paläontologisches Institut und Museum der Universität Zürich (Switzerland); SMNS, Staatliches Museum für Naturkunde, Stuttgart (Germany).

Introduction

Zambelli described the first known Triassic pterosaur, *Eudimorphodon ranzii*, in 1973. In the following 30 years new remains of Triassic pterosaurs were discovered, especially in northern Italy (Wild 1978, 1984, Dalla Vecchia 1995). Other specimens



Fig. 1. Map of Switzerland and the Canton Grisons indicating the locality of Tinzenhorn, where *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524) was found.

from the Triassic were reported from Austria (Dalla Vecchia et al. 2002, Wellnhofer 2003), France (Godefroit & Cuny 1997), Britain (Fraser & Unwin 1990), Luxembourg (Cuny et al. 1995), Greenland (Jenkins et al. 2001) and the USA (Murry 1986). Remains of Triassic pterosaurs are also known from Switzerland. Clemens (1980) noted that some mammal-like teeth from the Rhaetian of Hallau described by Peyer (1956) are potentially teeth of *Eudimorphodon*. More recently, Fröbisch & Fröbisch (2006) described an incomplete lower jaw from the Schesaplana (Northern Calcareous Alps) in Switzerland and established a new genus and species, *Caviramus schesaplanensis*. Other Swiss pterosaur finds are from the Upper Jurassic: a second wing phalanx of a pterodactyloid from the Solothurn Turtle Limestone (Canton Solothurn, Meyer & Hunt 1999), a wing phalanx fragment of a non-pterodactyloid from Porrentury (Canton Jura, Billon-Bruyat 2005) and unpublished bones from the areas of Biel (Canton Bern) and Olten (Canton Solothurn) (Billon-Bruyat 2005). Swiss pterosaur finds can therefore be considered rare and generally poorly preserved. This makes the pterosaur described in this paper the more complete skeleton from Switzerland known so far.

The aim of this study is to describe this new pterosaur and compare it to other Triassic pterosaurs. Currently, five genera and seven species of Triassic pterosaurs are known: *Austriadactylus cristatus* DALLA VECCHIA, WILD, HOPF & REITNER 2002 (Holotype: SMNS 56342, a poorly preserved specimen with a bony crest on the skull; Seefeld Schichten, Austria); *Caviramus schesaplanensis* FRÖBISCH & FRÖBISCH 2006 (Holotype: PIMUZ A/III 1225, a right mandible that is overall poorly preserved; Kössen Formation, Alplihorn Member, Schesaplana, Northern Calcareous Alps, Switzerland); *Eudimorphodon cromptonellus*



Fig. 2. Photograph of *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524, Upper Triassic, Tinzenhorn, Filisur, Switzerland), after preparation. The scale bar is in centimetres.

JENKINS, SHUBIN, GATESY & PADIAN 2001 (Holotype: MGUH VP 3393, a disarticulated skeleton; Fleming Fjord Formation, Orsted Dal Member, Greenland); *Eudimorphodon ranzii* ZAMBELLI 1973 (Holotype: MCSNB 2888, a nearly complete skeleton; Calcare di Zorzino, Cene, Bergamo, Italy); *Eudimorphodon rosenfeldi* DALLA VECCHIA 1995 (Holotype: MFSN 1797, a nearly complete skeleton with partially preserved skull; Dolomia di Forno Formation, Enemonzo, Udine, Italy); *Petinosaurus zambellii* WILD 1978 (Holotype: MCSNB 2886, a complete skeleton; Calcare di Zorzino, Cene, Bergamo, Italy); and *Preondactylus buffarinii* WILD 1984 (Holotype: MFSN 1770, a nearly complete postcranial skeleton without skull; Dolomia di Forno Formation, Friuli, Udine, Italy).

Geology and depositional environment

The new pterosaur was found at the Tinzenhorn (Corn da Tinizong, Canton Grisons), located in the Bergüner Stöcken (Piz Ela, Tinzenhorn, Piz Michel), Mittelbünden, eastern Switzerland (Fig. 1). Tectonically, the Tinzenhorn belongs to the Ela Nappe (Furrer 1993), and consists of Triassic and Jurassic marine sediments. The top of the Tinzenhorn is a lying anticline and at its northern part the layers are vertical and show impressively the transition from the Norian, Rhaetian to the Jurassic sediments. The first detailed stratigraphical and tectonical descriptions of this region were from Frei (1925) and Frei & Ott (1926). Frei (1925) mentioned that the best locality for fossils is the small valley next to the Fil da Stidier. It is noteworthy that he only mentioned fossils of invertebrates, although those of vertebrates are mostly black in colour and then very noticeable. Almost 50 years later, Furrer (1974) described vertebrates from the Kössen Formation found at the Piz Mitgel. Rohrbach (1977) also found vertebrate remains at the Tinzenhorn including teeth of hybodont sharks, teeth and scales of actinopterygians. Studies by Duffin & Furrer (1981), Bürgin & Furrer (1992, 1993) and Furrer (1993) uncovered yet more vertebrates (mainly tooth plates and fin spines of myriacanthoid holoccephalans). They also mentioned remains of hybodont sharks, actinopterygians, placodonts, ichthyosaurs and phytosaurs. The vertebrates were usually found in bonebeds, on layer surfaces and on hardgrounds.

In August 2005, the author discovered some long, thin, blackish, fossil bones on a massive (12 cm thick) limestone slab (40 cm by 40 cm), in the basal part of the Kössen Formation (Fig. 2). Only the posterior part of the skull was visible. Some bones were corroded by the weather and others had been destroyed. The limestone slab was lying directly under vertical beds from the Kössen Formation. It can be confidently assigned to the Alplihorn Member of the Kössen Formation (Central Austroalpine) (Figs. 3a, b). The Alplihorn Member, the most basal Member of the Kössen Formation, is very rich in invertebrate and vertebrate fossils, however the vertebrates are mostly highly disarticulated and fragmented. At the Fil da Stidier, the Alplihorn Member can reach about 58 m in thickness. It originates from a short transition zone from the basal Uglig-Plat-

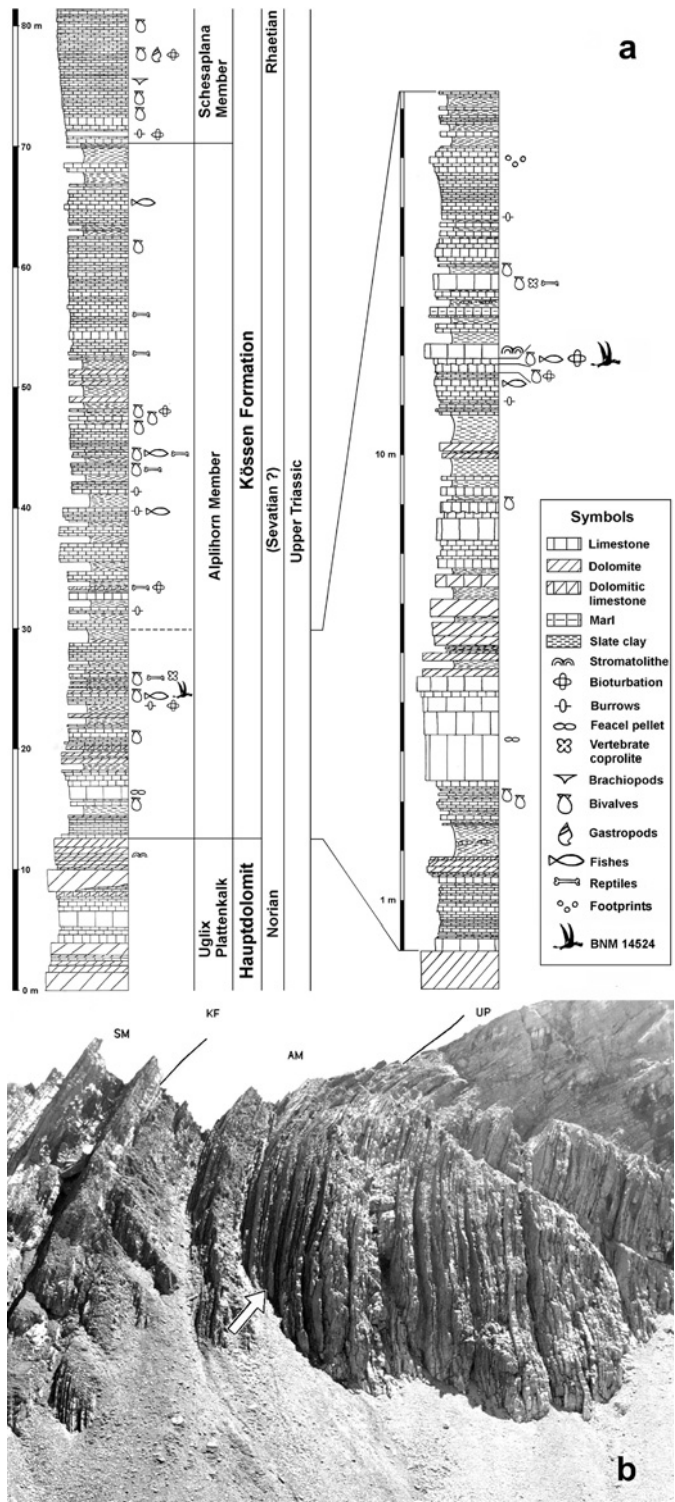


Fig. 3. a) Stratigraphy of the Alplihorn Member (Kössen Formation, Upper Triassic) at the Fil da Stidier (Canton Grisons). b) View of Fil da Stidier as seen from the Val Gravaratschas. The arrow shows the location where BNM 14524 was found. Abbreviations: AM, Alplihorn Member; KF, Kössen Formation; SM, Schesaplana Member of KF; UP, Uglig-Plattenkalk.

tenkalk (Hauptdolomit-Gruppe). It consists of interbedded strata of black, brown, yellow weathered clayey shales, dark-grey micritic limestones and olive calcareous dolomite, often laminated micrites and marly intercalations. This sequence was interpreted as a wide, flat lagoon or shallow basin on the extensive carbonate platform of the western margin of the Tethys Ocean in the Late Triassic (Furrer 1993).

Under the pterosaur-bearing layer, a blue-grey weathered, massive limestone occurs. Immediately below the specimen, the sediment shows conspicuous bioturbation. The sediment encasing the pterosaur is a dark grey limestone. The sedimentary unit (12 cm thick) including the fossil can be divided into three main parts (Fig. 4): 1) Basal most part (3 cm thick): a micritic limestone with less fossil shells than seen elsewhere; the base is erosional with scour-and-fill-structures; 2) Middle part (5 cm): the matrix is micritic and contains many ooids, and shells (mostly convex side up) and shell fragments; lamellibranchs with both shells preserved are rare; the ooids often have fragments of bivalves and gastropods as nuclei; towards the upper part the ooids show a decrease in grain size, indicating a small scale fining upward sequence; 3) Upper part (4 cm): this micritic part is the matrix of the pterosaur, it shows marly laminated intercalations; the ooid content decreases gradually, they are missing in the uppermost part; the last part of the slab is built up by laminated, yellow, calcareous marl; the latter yields thin shell fragments and rare ganoid scales.

The layer above the specimen is of a 1 cm thick grey clay followed by a 28 cm thick finely laminated grey limestone. The presence of ooids indicates shallow turbulent water in a subtidal environment (Furrer 1993). The ooids from the middle part come from such an environment but were transported and redeposited by a storm. The normal graded bedding, the convex up/down position of the shells and the frequent telescoping position support this. The layer including the pterosaur is interpreted as a storm deposit, a tempestite that was subsequently bioturbated (presence of *Thalassinoides*). The increased marl content, the complete absence of ooids in the uppermost part and the clay layer indicate laminar, non-turbulent lower energy conditions. The thin layer of grey clay can be interpreted as a fine deposition during a quiet sedimentation period. The finely laminated, yellow, limestone is interpreted as cyanobacterial mats developed in the intertidal zone.

It is suggested that the pterosaur body sank shortly after the storm to the bottom of the shallow marine environment and was rapidly buried (excluding a long post-mortem transport), leading to the excellent preservation of the specimen.

Material and methods

The reported specimen (BNM 14524) consists of a disarticulated skeleton, two isolated teeth, an isolated rib fragment and an isolated hyoid fragment. One of the isolated teeth lay 6 cm from the skull, completely embedded in the limestone; it was fully separated from the slab for further examination. The second isolated tooth was still in the mouth but not attached to

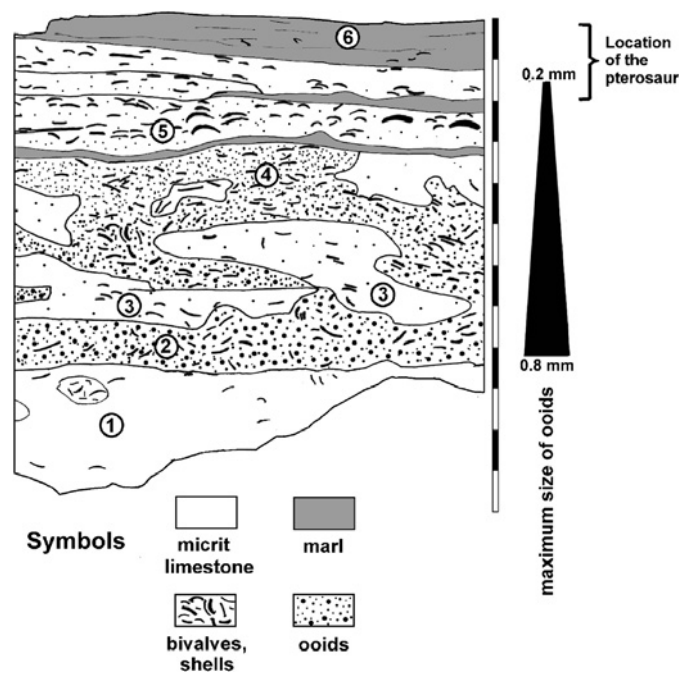


Fig. 4. Sedimentological section through the layer where the reported pterosaur was found. 1) Micrit limestone with only few shells. 2) Micrit, limy matrix with many ooids (the largest are 0.8 mm in diameter) and shells (mostly convexly adjusted). 3) Micrit, limy matrix with only few ooids. Bioturbation. 4) Micrit, limy matrix with little ooids (the largest are 0.2 mm in diameter) and broken shells which are convexly adjusted. 5) Micrit, limy matrix with rare ooids but many shells. 6) Laminated calcareous marl with few shells but without any ooids. The scale bar is in centimetres.

the jaws, it was also removed. The rib fragment was a rib stem lying on the lower jaw, covering several teeth. To allow further examination of these teeth, it was necessary to separate a part of this bone from the main slab.

The preparation was challenging because of the very fragile skull. The bones were embedded in a very hard and massive limestone. The preparation was first carried out using a weak formic acid; this allowed the extraction of the black bones from the light-grey weathered limestone. Bones were protected from acid by using a high quality acrylic resin ("OSTEO-FIX"). The upper part of the limestone slab is a finely laminated calcareous marl, making impossible a preparation with acid alone; an abrasive fibreglass eraser ("ECOBRA") was used. The final conservation of the fossil was completed with "OSTEO-FIX".

Systematic palaeontology

Class Reptilia LAURENTI 1768

Subclass Archosauria COPE 1869

Order Pterosauria KAUP 1834

Although the tail is not preserved, BNM 14524 can be assigned with confidence to a non-pterodactyloid ("short-tailed") pterosaur according to the following features (Wellnhofer 1993, Un-

win 2003a): The narial and antorbital fenestrae are separated by a bony strip; the occipital condyle is arranged backwards; the wing phalanges have a furrow on the posterior side; a long 5th toe is present.

Genus *Raeticodactylus* gen. nov.

Etymology. – Raetia (Latin): old name of the Swiss Canton Grisons, where the pterosaur was found; dactylus (Greek): for the long fourth wing finger.

Diagnosis. – As for the type species.

Species *Raeticodactylus filisurensis* sp. nov.

(Figs. 2, 5–11)

Etymology. – Filisur (Romansch): name of the village where the pterosaur was found; ensis (Latin): for “from”.

Holotype. – The holotype is housed in the Bündner Naturmuseum (BNM) of Chur (Grisons, Switzerland), with the collection number BNM 14524 (Fig. 2).

Material. – A disarticulated skeleton including a nearly complete skull, a mandible, two isolated teeth and a postcranial skeleton (right humerus, right ulna, right metacarpals I–III, right and left wing phalanges 1–4, right femur, right tibia, part of the right fibula, part of the right pes, several cervical, dorsal and several ribs).

Locus typicus. – 1.25 km northeastern of the Tinzenhorn at the Fil da Stidier. The Tinzenhorn (Corn da Tinizong) is a mountain of the Bergüner Stöcke in Mittelbünden, commune Filisur, Canton Grisons, Switzerland (Fig. 1). The exact geographical coordinates are deposited in the BNM.

Stratum typicum. – The layer in which BNM 14524 was found is located in the lower part of the Alplihorn Member of the Kössen Formation. Characteristics for the Alplihorn Member are the interbedded strata of black, brown, yellow weathered shale

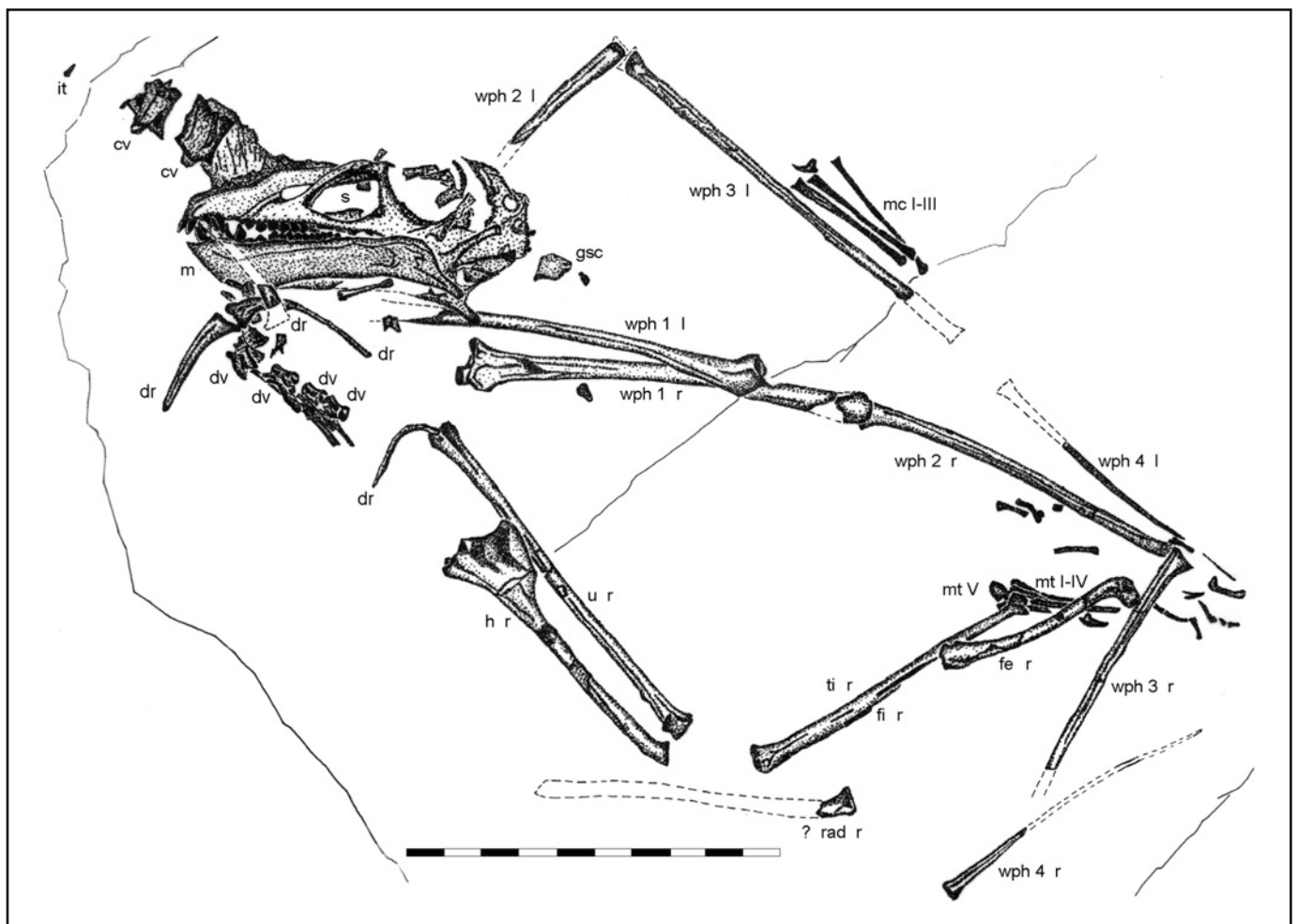


Fig. 5. Drawing of *Raeticodactylus filisurensis* gen. et sp. nov. (BNM 14524). Abbreviations: cv, cervical vertebra(e); dr, dorsal rib(s); dv, dorsal vertebra(e); fe, femur; fi, fibula; gsc, ganoid fish scale; h, humerus; it, isolated tooth; l, left; m, mandible; mc I–III, metacarpals I–III; mt I–V, metatarsals I–V; rad, radius; r, right; s, skull; ti, tibia; tv, thoracic vertebra(e); u, ulna; wph 1–4, wing phalanges 1–4. The scale bar is in centimetres.

clay, dark-grey micritic limestones and the olive calcareous-dolomite, often laminated micrites and marl layers (Figs. 3a, b).

Age. – Late Triassic: late Norian (Sevastian) or Rhaetian. Furrer (1993) states that the age from the Alplihorn Member is not exactly known, most probably it is Sevastian (late Norian) in age.

Diagnosis. – The holotype specimen of the monospecific genus *Raeticodactylus* presents the following diagnostic features: Bony, anterior cranial crest formed from the premaxilla; keel like extension of the anterior part of the mandible; heterodont dentition with large monocuspid teeth in the anterior part and multicuspid (tricuspid, quadricuspid, quinticuspid) teeth in the posterior part of the dentition; diastema in the upper jaw between the premaxilla and maxilla; lingual side of the anterior teeth with heavy and conspicuous bowed enamel wrinkles; multicuspid teeth of the upper jaw more bulbous than the teeth of the lower jaw; multicuspid teeth of the upper jaw aligned in one row and show distinct gaps between the teeth; multicuspid teeth of the lower jaw packed close together causing the orientation of the teeth to slope and laterally overlap; very long, slender (length to diameter shaft ratio: 18.2) and straight humerus, with a subrectangular deltopectoral crest.

Description. – The holotype (BNM 14524) is mainly a disarticulated skeleton. Nevertheless, some parts are in natural association, especially the skull and the mandible, the wing phalanges and elements of the right pes (Fig. 5). The pectoral girdle, the pelvis, the majority of the ribs and vertebrae, particularly all caudal vertebrae and some bones of extremities are missing. The ossification of the epiphysis, the complete and fine porous surface of the bones (possibly) and the relatively small orbit (see below the comparisons of the skull-orbit length index) suggest that BNM 14524 was fully grown.

Skull and mandible (Figs. 6a–c). The skull is well preserved. Only some teeth are broken or lost and the posterior part of the skull was distorted by diagenesis. The skull lies on its right, lateral side. The mandible is still articulated with the skull. The skull has a low and long form; it measures 95 mm from the tip of the snout to the occipital condyle. At its highest point (above the orbit) the skull is 19 mm high. The largest opening of the skull is the orbit with a diameter of 20 mm. The antorbital fenestra is oval and longer than high (19 mm and 11 mm respectively). The naris lies in a posterior position on the snout. It has an unusual “tear-drop” shape with the rounded part located rostrally. The naris is 14 mm long and 4.5 mm high.

The outstanding anatomical feature of the skull is the anterior, large, sagittal bony crest, extending from the premaxilla and lying over the naris. It ascends from the tip of the snout directly to a height of about 21 mm and descends with a slight concave curve smoothly to end above the middle part of the antorbital fenestra. The anterior part of the bony crest is about 1 mm thick; the posterior part is only a fraction of a millimetre. The bony crest surface shows strong radial ridges, as does the anterior part of the skull. It is supposed that the bony crest but also the tip of the snout were covered by a keratinized sheath (a rhamphothecae). A conspicuous suture like structure, visible

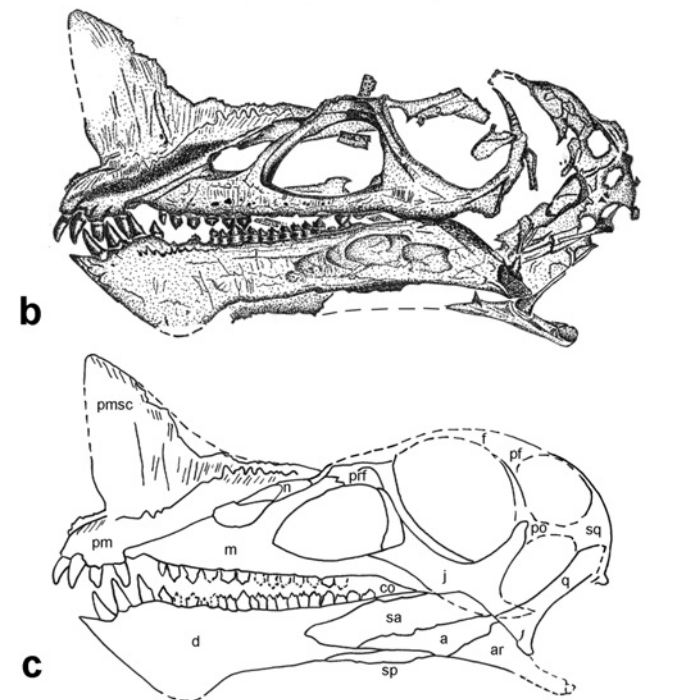
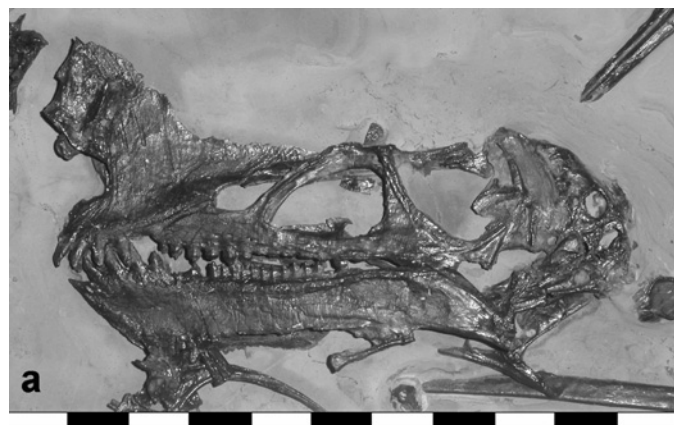


Fig. 6. Skull of *Raeticodactylus filisurensis* gen. et sp. nov. (BNM 14524) in left lateral view. Photograph (a), drawing (b) and reconstruction (c). Abbreviations: a, angular; ar, articular; co, coronoid; d, dentary; f, frontal; j, jugal; m, maxilla; n, nasal; pf, postfrontal; pm, premaxilla; pmsc, premaxillar sagittal crest; po, postorbital; prf, prefrontal; q, quadrate; sa, surangular; sp, splenial; sq, squamosal. The scale bar is in centimetres.

between the bony crest and the premaxilla, may have separated the soft tissue part from the rest of the skull.

The very thin mandible is 84 mm long and 9.5 mm height. The right and left lower jaws meet in an extremely thin, common keel. Its anterior end descends to form a keel-like expansion measuring 14 mm at its deepest point. The tip of the mandible is toothless, pointed and directed dorsally. The surface of the tip of the mandible reveals similar ridges than on the premaxilla and on the bony crest; the anterior part of the mandible was probably covered by a keratinous rhamphothecae. Numer-

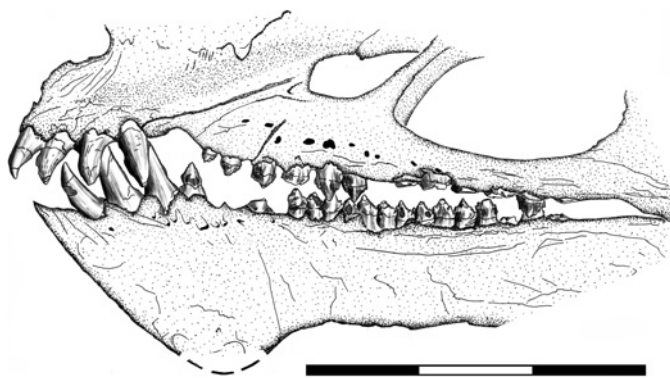


Fig. 7. Detailed drawing of the upper and lower jaws of *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524). The scale bar is in centimetres.

ous foramina are found on both the maxilla and mandible. The maxilla exhibits 13 irregularly spaced, backwards facing foramina. Seven pocket-shaped foramina are present in the anterior part of the mandible.

Dentition (Figs. 7–9). Some teeth were broken before the death of the pterosaur, or were lost post mortem, but before fossilisation. The teeth have a single root in both the upper and lower jaws. Based on the teeth and alveoli, it is possible to state the original number of teeth of the specimen: the left upper jaw and mandible have 17 and 22 teeth respectively, that is a total of 78 teeth. In the left upper jaw, the 11th–15th and 17th teeth are broken. The 7th, 8th and 16th teeth show strong wear facets. In the left mandible, the 5th and 6th teeth were lost before the pterosaur was preserved. The 8th, 20th and 22th teeth are broken. The 7th tooth shows also important wear facets, so much so that is impossible to reconstruct its original form. In the premaxilla are four monocuspid, fang-like teeth. Distally the 4th tooth has a conspicuous bulge. The first three teeth are slightly recurved. Between the teeth of the premaxilla and the maxilla a 5 mm

long diastema is apparent. The thirteen teeth of the maxilla are tricuspid to quinticuspid. The first quinticuspid tooth in the upper jaw is the 9th.

In the anterior part of the mandible, three large monocuspid, fang-like teeth are visible. Another monocuspid tooth and some tri-, four-, and quinticuspid teeth succeed these three teeth. The first quinticuspid tooth of the mandible is the 10th.

The monocuspid teeth in the anterior dentition are large and have a crown up to 4 mm in length. On the labial side there is – to a greater or lesser extent – smooth enamel with hardly any enamel wrinkles. In contrast, on the lingual side strong and conspicuous enamel wrinkles are apparent. The narrow standing enamel wrinkles are partially bifurcated and have a bowed form along the crown (Fig. 8).

The multicuspoid teeth in the posterior part have generally a conical, flat form and show no or one to two small accessory cusps mesially and/or distally to the main cusp. The cutting distal and mesial edges have a convex form. Some of the most anterior multicuspoid teeth exhibit thickened bulges along the cutting edges. The multicuspoid teeth of the maxilla are slightly more bulbous, as the conical teeth of the mandible, and have larger gaps between them. The multicuspoid teeth of the mandible are very close together, in a sloping position and mutually overlap. The five supplementary teeth of the mandible are within the same distance, therefore the upper/lower teeth ratio is 0.78.

Some teeth of the upper jaw and mandible mainly show two types of strong wear facets, at the top of the crown (horizontal wear) and on the labial side of mandible teeth. This can be traced back to contact of the teeth of the upper jaw. No wear facets are present on the labial side of teeth of the upper jaw. The horizontal heavy wear facet of the main cusp suggests a durophagous diet.

Examining the mutual position of the skull to the mandible, this latter seems slightly displaced forwards. Moving the mandible backwards would enable its 3rd tooth to fit exactly in the diastema of the upper jaw. However, this would result in a shorter

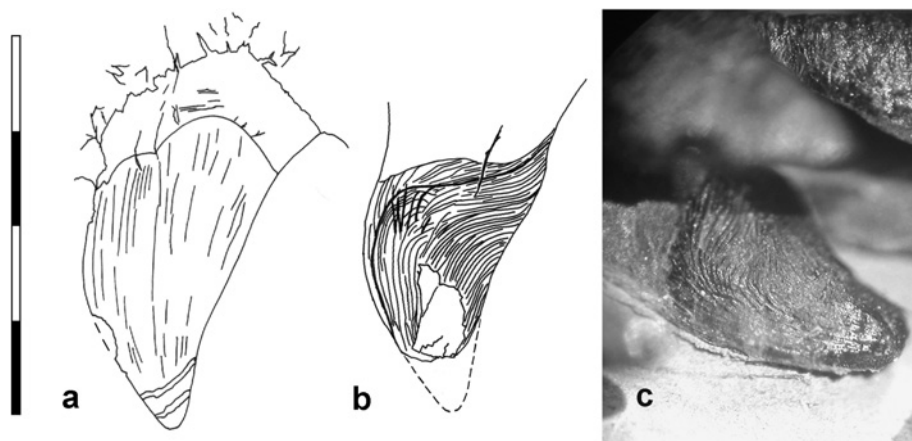


Fig. 8. Detailed drawings and photograph of fang-like teeth of *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524). a) Labial view of the 2nd tooth of the left upper jaw. b) Lingual view of the 2nd tooth of the right upper jaw. c) Photograph of the 2nd tooth (~ lingual view) of the right upper jaw. The scale bar is in millimetres.

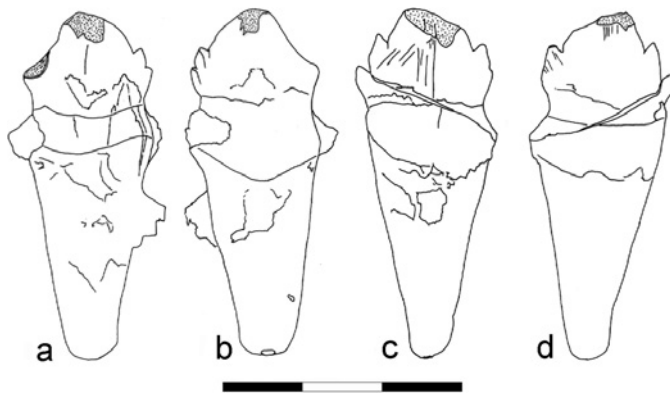


Fig. 9. Drawing of two isolated multicuspoid teeth of *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524). a, b) Labial (a) and lingual (b) views of an originally isolated tooth. c, d) A second isolated tooth (that initially lay in the mouth of the specimen) in labial (c) and lingual (d) views. Stippling represents where the teeth are broken. The scale bar is in millimetres.

mandible compared with the upper jaw. A keratinized beak, at the tip of the mandible, could have completed this missing length.

The two isolated teeth are very thin and show two small accessory cusps mesially and/or distally of the main cusp (Fig. 9). The size and shape of the two teeth suggest that both are from the mandible.

Vertebrae and ribs. Eight vertebrae are preserved, including two cervicals and six dorsals. The cervical vertebrae look very large and massive. They are up to 20 mm long and 14 mm wide. They are very weak, pneumatized and show very thin bony walls. The six dorsal vertebrae lie on their lateral faces, nearly in articulation. These vertebrae are smaller (7 mm in length) and more pneumatized. No caudal vertebrae are preserved. Six ribs are preserved. The length of three dorsal ribs ranges between 30 and 35 mm. The ribs are two headed and then taper distally to a point. Some vertebrae cover two further ribs. The 6th rib is preserved in abutted position at the humerus; it has only one head, is very thin with a strongly evolved arch in the proximal part and is straight in the distal part.

Forelimb (Fig. 10). The right humerus lies parallel next to the right ulna with adjacent articular ends. The humerus lies on its lateral face. The shaft of the humerus is partly broken and shows that it is hollow with a large pneumatic cavity. The humerus has a length of 82 mm, the diameter of the shaft is 4.5 mm and at its widest it is 22 mm across. It has a straight and slender form with a subrectangular, wide and well-developed deltopectoral crest.

The right ulna is long, slender with well-developed articular ends. It is 106 mm long and pneumatized. Only a few centimetres from the distal end of the humerus and of the proximal end of the ulna, a fragment of another bone with parts of an articular end is present; it was not possible to identify it.

The metacarpals I–III of either the right or the left side are preserved in association. These slender bones have approximately

similar lengths (metacarpal I: 40 mm; II: 41 mm; III: 42 mm). The distal ends of the metacarpals are slightly wider than the proximal ends. A well preserved manual claw lies close to these metacarpals. The wing metacarpal (IV) is not preserved.

The wing phalanges of BNM 14524 are nearly complete from both left and right wings and are mostly articulated. All wing phalanges of the right wing are preserved, at least partially. Of the 1st wing phalanx, the dorsal side is visible. It is 113 mm long and the most robust of the wing phalanges. The 2nd wing phalanx is 109 mm long. Only the proximal articular ends of the 3rd and 4th wing phalanx are preserved, the distal ends were destroyed during weathering. The 1st and 2nd wing phalanges of the left wing are most likely complete. However, they lie underneath the skull and therefore make impossible the determination of the length of these two bones. The 1st wing phalanx shows its ventral side. The proximal end of the 3rd wing phalanx is preserved, however the distal end is missing. By contrary, only the distal end of the 4th wing phalanx is preserved, it ends in a very fragile, flattened point. Two vague impressions, from these missing articular ends are present on the slab; the length of the 3rd and 4th wing phalanx are roughly estimated to 117 mm and 83 mm, respectively. The pteroid was not found.

Hindlimb and pes (Fig. 11). Only the right femur is preserved, it is 56 mm long and shorter than the tibia. The shaft of the femur is slender and slightly bowed, and circular in cross-

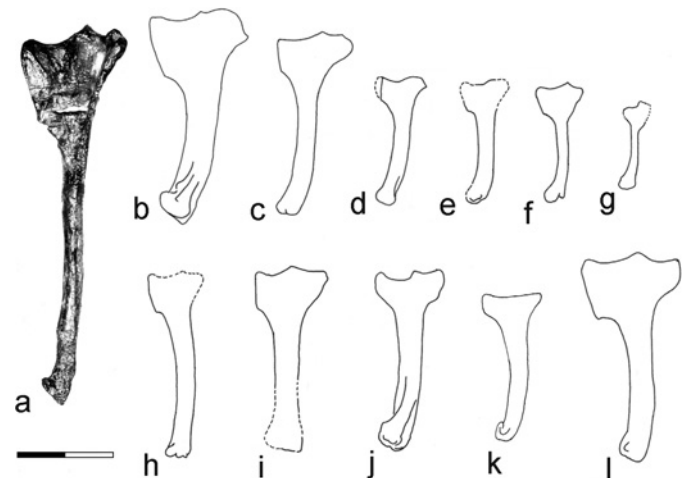


Fig. 10. Left humeri of various Triassic pterosaurs and the Liassic *Campylognathoides liasicus* (QUENDSTEDT), in anconal view. a) *Raeticodactylus filisurenensis* gen. et sp. nov. (BNM 14524), right humerus is mirrored. b) *Eudimorphodon ranzii*, Holotype (MCSNB 2888), after Wild (1978). c) *Eudimorphodon* cf. *ranzii* (BSP 1994 I 51), after Wellnhofer (2003). d) *Eudimorphodon* sp., Milano specimen (MPUM 6009), after Wild (1978). e) *Eudimorphodon* cf. *ranzii* (MCSNB 2887), after Wild (1978). f) *Eudimorphodon* sp. (MCSNB 8950), after Wild (1994). g) *Eudimorphodon cromptonellus*, Holotype (MGUH VP 3393), right humerus is mirrored, after Jenkins et al. (2001). h) *Eudimorphodon rosenfeldi*, Holotype (MFSN 1797), after Dalla Vecchia (2004). i) *Eudimorphodon* sp. (MFSN 1922), after Dalla Vecchia (2004). j) *Peteinosaurus zambellii* (MCSNB 3359), after Wild (1978). k) *Preondactylus buffarinii*, Holotype (MFSN 1770), after Wild (1984). l) *Campylognathoides liasicus* (CM 11424) after Wellnhofer (1974). The scale bar is in centimetres.

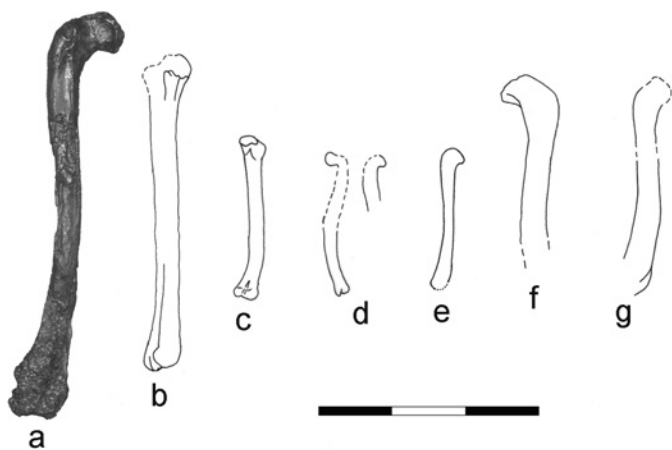


Fig. 11. Femora of various Triassic pterosaurs, in lateral view. a) *Raeticodactylus filisurensis* gen. et sp. nov. (BNM 14524), right femur. b) *Eudimorphodon ranzii*, Holotype (MCSNB 2888), left femur, after Wild (1978). c) *Eudimorphodon* cf. *ranzii* (MCSNB 2887), right femur, after Wild (1978). d) *Eudimorphodon* sp. (MCSNB 8950), left and right femur, after Dalla Vecchia (2002). e) *Eudimorphodon cromptonellus*, Holotype (MGUH VP 3393), right femur, after Jenkins et al. (2001). f) *Pteinosaurus zambellii* (MCSNB 3496), left femur, after Dalla Vecchia (2003b). g) *Preondactylus buffarini*, Holotype (MFSN 1770), after Wild (1984). The scale bar is in centimetres.

section. The caput femoris has a stout neck. The head is perpendicular to the shaft. The shaft of the femur was weathered along the shaft; it shows that the femur is pneumatized and hollow. The pneumatic space has been filled with an orange-red stone matrix. The tibia is very thin, straight, hollow, and 83 mm in length. It is adjacent to the relic of the 1.5 mm wide fibula. The right tarsus is partially articulated and connected to the tibia. In addition, the calcaneus, the tarsalia and the four metatarsals are articulated. The metatarsals are about 32 mm long. The phalanges are disarticulated. Next to the pes is a toe, which seems less robust and less strongly bowed. Bones from the elongate 5th toe, typical of non-pterodactyloid pterosaurs, are also preserved.

Comparisons. – Comparison with *Caviramus* (Fig. 12). Fröbisch & Fröbisch (2006) recently described a new Triassic pterosaur from Switzerland, *Caviramus schesaplanensis*, based on a poorly preserved mandible (PIMUZ A/III 1225). It consists of three bone fragments with two teeth. According to Fröbisch & Fröbisch (2006), the teeth of *Caviramus* show many similarities with those of *Eudimorphodon*. It is noteworthy that this mandible was found in the Alplihorn Member (Kössen Formation) of the Schesaplana (Northern Calcareous Alps, Canton Grisons). In other words, *Caviramus* was found in the same stratigraphical unit than *Raeticodactylus*, but in another tectonic nappe. Unfortunately, the exact stratigraphical and geographical data where PIMUZ A/III 1225 was found are not mentioned.

The following differences have been established thanks to a personal examination of *Caviramus*: PIMUZ A/III 1225 does not present any quinticuspid tooth; BNM 14524 presents only

seven cup-shaped structures (which might be part of the attachment for the rhamphothecae) on the anterior part of the mandible, which are hardly visible and smaller; the lower edge of the mandible of PIMUZ A/III 1225 is convex instead of concave in BNM 14524; parallel to the tooth row, PIMUZ A/III 1225 has large, oval foramens, located every 2nd tooth, BNM 14524 has also such foramen but every 3rd tooth. The following features are common in *Raeticodactylus* and *Caviramus*: a relatively tall mandible; multicuspid teeth; retroarticular process angled at about 30–35 degrees. Elsewhere, Fröbisch & Fröbisch (2006) suppose that the dentition of *Caviramus* is isodont and that the anterior end of the mandible reveals its original form but this seems weakly supported. Although *Raeticodactylus* could be interpreted as relatively similar to *Caviramus* at first glance, the above differences are well supported. In conclusion, *Raeticodactylus* and *Caviramus* are defined as two different genera. Their precise relationship cannot be established, *Caviramus* being too incomplete.

Comparison with other Triassic pterosaurs (Tables 1–3). Kellner (1996, 2003) and Unwin (2003a) separately investigated the phylogeny and the evolutionary history of pterosaurs. Using cladistic analyses they both concluded that Triassic pterosaurs are not related as previously thought. Unwin (2003a) defined that all *Eudimorphodon* species belong to a single family, the Campylognathoididae (including also *Campylognathoides* and *Austriadactylus*). Kellner (1996, 2003) showed that *E. ranzii* and *Campylognathoides liasicus* (QUENSTEDT) are sister taxa belonging to the Campylognathoididae; however, he also suggested that '*E. rosenfeldi* and *Pteinosaurus zambellii* are in a different clade, in other words that *Eudimorphodon* species do not necessarily belong to a single genus or family. It is not the purpose of this paper to revise *Eudimorphodon* but the variations observed within this genus are considered. The following anatomical sections will detail the cranial and postcranial differences and similarities between *Raeticodactylus* and other Triassic pterosaurs. A

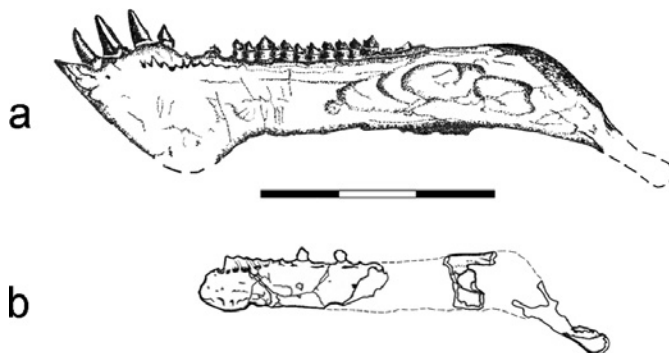


Fig. 12. Lower jaws of the two Triassic pterosaurs from Switzerland. a) Drawing of the lower jaw of *Raeticodactylus filisurensis* gen. et sp. nov. (BNM 14524). b) Drawing of the mirrored lower jaw of *Caviramus schesaplanensis* (PIMUZ A/III 1225), modified after Fröbisch & Fröbisch (2006). The scale bar is in centimetres.

Table 1. General data of *Raeticodactylus filisurenensis* gen. et sp. nov. and various holotypes of Triassic pterosaurs having multicuspid teeth.

	<i>Austriadactylus cristatus</i> (Holotype, SMNS 56342)	<i>Caviramus schesaplanensis</i> (Holotype, PIMUZ A/III 1225)	<i>Eudimorphodon cromptonellus</i> (Holotype, MGUH VP 3393)	<i>Eudimorphodon ranzii</i> (Holotype, MCSNB 2888)	<i>Eudimorphodon rosenfeldi</i> (Holotype, MFSN 1797)	<i>Raeticodactylus filisurenensis</i> gen. et sp. nov. (Holotype, BNM 14524)
Formation	Seefeld Schichten	Kössen Formation / Alplihorn-Member of the Lechtal nappe	Fleming Fjord Formation / Orsted Dal Member	Zorzino-Calcarei	basic part of the Dolomia di Forno Formation	Kössen Formation / Alplihorn-Member of the Ela nappe
Age	late Norian (late Alaunian–early Sevatian)	late Norian–early Rhaetian	Norian–Rhaetian	middle Norian, late Alaunian	middle Norian (Alaunian 2–3)	late Norian (Sevatian) or early Rhaetian
Bony crest	20 mm high; long crest	–	no	no	–	21 mm high; crest on the premaxilla and naris
Largest skull opening	narial fenestra	–	–	orbit	orbit	orbit
Skull-orbit length index	20.8%	–	–	24.5%	–	21.4%
Mandible length / height ratio	–	7.4–8.7	–	14.6	more than 13.8	8.8
Shape of the anterior end of the mandible...	–	... forms a rounded edge	–	... is curved ventrally	–	... is keel-shaped and ends in a dorsally deflected tip
Dentition and teeth	heterodont: monocuspid and triangular formed multicuspid (up to 12 denticles on each cutting edge) teeth	isodont: at least tri- and four-cuspid teeth in the lower jaw	heterodont: mono-, tri-, four- and five-cuspid teeth	heterodont: mono-, tri-, five-cuspid teeth	heterodont: at least mono- and five-cuspid teeth	heterodont: mono-, tri-, four- and five-cuspid teeth
Comparison of teeth size between upper and lower jaws	teeth of the upper jaw are larger	–	teeth of the lower jaw are partially smaller	same size	–	teeth of the upper jaw are larger
Teeth of the upper jaw...	... have small gaps between them	–	... have wide gaps between them	... have no gaps between them	... have small gaps between them	... have small gaps between them
Teeth of the lower jaw...	... are aligned in one row and have small gaps between them	–	... are aligned in one row and have wide gaps between them	... are standing very close together in one row, but do not overlap	... are aligned in one row and have small gaps between them	... are standing very close together and overlap partially
Number of teeth in the upper jaw	17–25	–	12 or more	29	–	17
Number of teeth in the lower jaw	–	at least 12, maximum 17	12 (?)	28	–	22

comparison with the holotypes of Triassic pterosaurs having multicuspid teeth is summarized in Table 1.

Skull and mandible. The overall skull morphology of *Raeticodactylus* is different from that of *Eudimorphodon* (MCSNB 2888) and *Austriadactylus* (SMNS 56342) (Fig. 13). The size – i.e. the wingspan – in comparison to the skull length makes it clear that *Raeticodactylus* has a relatively small skull compare to other Triassic pterosaurs (BNM 14524: 14.2; *E. sp.*, MPUM 6009: 11.3; *E. ranzii*, MCSNB 2888: 8.3–11.1; *A. cristatus*, SMNS 56342: 10.9). The length/height ratio of the skull of *Raeticodactylus* (without the sagittal crest) is relatively high with a value of 3.84 (*E. ranzii*, MCSNB 2888: 2.84; *E. sp.*, MPUM 6009: 2.41; *A. cristatus*, SMNS 56342: 3.0).

The comparison of the skull-orbit length index shows that the orbit of *Raeticodactylus* is relatively small, only *Austriadactylus* has maybe a smaller orbit (BNM 14524: 21.4%; *E. ranzii*, MCSNB 2888: 24.5%; *E. sp.*, MPUM 6009: 28.5%; *A. cristatus*, SMNS 56342: 20.8%). The relatively small orbit also suggests that *Raeticodactylus* was fully grown (Wild 1978). While the narial fenestra of *Eudimorphodon* (MCSNB 2888) and *Raeticodactylus* show certain similarities, the antorbital fenestra of BNM 14524 is larger and with a different shape (Fig. 13). Only *Raeticodactylus* and *Austriadactylus* have a bony, sagittal crest on the skull. Comparing the mandibles of Triassic pterosaurs, *Raeticodactylus* mandible is taller than that of *E. ranzii*; this is obvious using the length to height ratio (BNM 14524: 8.8;

Table 1.

	<i>Austriadactylus cristatus</i> (Holotype, SMNS 56342)	<i>Caviramus schesaplanensis</i> (Holotype, PIMUZ A/III 1225)	<i>Eudimorphodon cromptonellus</i> (Holotype, MGUH VP 3393)	<i>Eudimorphodon ranzii</i> (Holotype, MCSNB 2888)	<i>Eudimorphodon rosenfeldi</i> (Holotype, MFSN 1797)	<i>Raeticodactylus filisurenensis</i> gen. et sp. nov. (Holotype, BNM 14524)
Monocuspid teeth with fang-like function in the upper jaw	5	–	1 or 2	4 (3rd tooth is tricuspid)	–	4
Monocuspid teeth with fang-like function in the lower jaw	–	0	1	2	–	3
Number of pseudo-unicuspid teeth under the processus ascendens	1 or 2	–	0	2	–	0
First five cusped tooth in the upper jaw	–	–	5 th place	17 th place (left), 18 th place (right)	–	9 th place
First five cusped tooth in the lower jaw	–	–	10 th place (left), 8 th place (right)	6 th place (left), 8 th place (right)	–	10 th place
Diastema	–	–	between the 3 rd and 4 th tooth in the upper jaw and between the 9 th and 10 th tooth in the lower jaw	no	–	large between the 4 th and 5 th tooth in the upper jaw
Shape of the humerus	slightly bowed with a wide deltopectoral crest	–	slightly bowed with subtriangular deltopectoral crest	bowed and robust with rectangular deltopectoral crest	slightly bowed and slender with a small, perpendicular deltopectoral crest	straight, slender, relatively long, with a well-developed subrectangular and wide deltopectoral crest
Humerus length / shaft diameter ratio	–	–	13	7.4	10.4	18.2
Humerus length / width ratio	–	–	3.5	2.2	3.0	3.7
(humerus + ulna) / (femur + tibia) ratio	–	–	0.95	1.23	1.05	1.34
(Σ humerus + ulna + metacarpal IV / Σ femur + tibia + average of metatarsals) \times 100	–	–	90.0%	–	103.8%	at least 134.3%
Data from	Dalla Vecchia et al. (2002)	Fröbisch & Fröbisch (2006)	Jenkins et al. (2001)	Zambelli (1973), Wild (1978)	Dalla Vecchia (1995)	This study

E. ranzii, MCSNB 2888: 14.6; *E. sp.*, MPUM 6009: 13.1). A further difference is the anterior tip of the mandible, the anterior end of *Eudimorphodon* (MCSNB 2888) is curved ventrally, whereas that of *Raeticodactylus* is keel-shape and ends in a dorsally deflected tip.

Dentition. Like all other *Eudimorphodon* specimens and *Austriadactylus*, *Raeticodactylus* has a heterodont dentition. The anterior teeth are monocuspids whereas the posterior ones are multicuspid. *Raeticodactylus* has the largest difference in the number of teeth between the upper and lower jaws compared to *Eudimorphodon* (MCSNB 2888, MPUM 6009). The mandible of *Raeticodactylus* has five supplementary teeth than the upper jaw; in contrast, the upper jaw of *Eudimorph-*

odon has a supplementary tooth. In the posterior part of the upper and lower jaws, *E. ranzii* has equally sized multicuspid teeth (Wild 1978). In comparison, *Raeticodactylus* has slightly bulbous teeth in the upper jaw and slightly shorter teeth in the mandible. The maxillary teeth of *Raeticodactylus* are aligned in one row and have small gaps between them; the mandible exhibits very narrowly standing teeth that partially overlap. These characteristics are only present on BSP 1994 I 51 (*E. cf. ranzii*) and to a certain degree on MPUM 6009 (*E. sp.*). *Raeticodactylus* has no enlarged pseudo-unicuspid teeth under the processus ascendens, like in *Eudimorphodon* (MCSNB 2888). At this position, *Raeticodactylus* has multicuspid teeth, which are slightly larger and of similar form than the surrounding

teeth. The mandible of *Raeticodactylus* has teeth along 55.4% of its length. In comparison with other Triassic pterosaurs this is relatively low, e.g. in *Eudimorphodon* (MCSNB 2888: 66.2%; MPUM 6009: 75.8%).

The rough-textured and rippled surface at the ends of the jaws of *Raeticodactylus* indicates a keratinized, beak-like edge on the jaws (see above), as Wild (1978) also suggested for *Eudimorphodon* (MCSNB 2888, MPUM 6009).

Humerus (Fig. 10). In contrast to *Eudimorphodon* (MCSNB 2888) and other humeri of Triassic pterosaurs, *Raeticodactylus* has a very straight and remarkably slender humerus. Its length to the shaft diameter ratio is 18.2. This ratio is clearly higher than from other Triassic pterosaurs (*E. ranzii*, MCSNB 2888: 7.8; *E. rosenfeldi*, MFSN 1797: 10.4; *E. cromptonellus*, MGUH VP 3393: 13). The length to width ratio of the BNM 14524 humerus is 3.7 and higher than other Triassic pterosaurs (*E. ranzii*, MCSNB: 2.2; *E. rosenfeldi*, MFSN 1797: 3.0). Only *E. cromptonellus* shows a similar value of 3.5. The humerus has a wide subrectangular deltopectoral crest, similar to that of *E. rosenfeldi*. The proximal articular end of the humerus exhibits two concave saddles. This is an apomorphic feature (Unwin 2003a) known in Juras-

sic non-pterodactyloid pterosaurs (*Campylognathoides*, *Rhamphorhynchus*). By contrary, *E. ranzii* (MCSNB 2888) shows the plesiomorphic state with a single concave saddle.

Femur (Fig. 11). BNM 14524 has a caput femoris that lies perpendicular to the shaft. Wellnhofer (1993) stated that all Triassic pterosaurs have a caput femoris that faces diagonally upwards, which is also a feature of Jurassic and Cretaceous pterosaurs. However, it is noteworthy that the specimens MCSNB 8950 (identified as *Eudimorphodon* sp., Wild 1994), MGUH VP 3393 (*E. cromptonellus*, holotype) and MCSNB 3496 (*Peteinosaurus zambellii*) also show a distinct perpendicular caput femoris. Interestingly, this is a very common feature in dinosaurs (O. Rauhut, pers. comm. 2007), it is now identified in some Triassic pterosaurs.

Comparison of skeletal lengths (Tables 1–3; Fig. 14). The skull length of *Raeticodactylus* is only slightly longer than in the adult specimen of *Eudimorphodon ranzii* (MCSNB 2888), their postcranial skeletons, however, clearly differ in size (Table 2). *Raeticodactylus* was considerably larger than MCSNB 2888; with longer and relatively thinner bones, *Raeticodactylus* was more gracile.

Table 2. Overview of skeletal lengths (mm) and wingspan (cm) in *Raeticodactylus filisurensis* gen. et sp. nov. and various Triassic pterosaurs.

	s	m	h	u	mcIV	fe	ti	wph1	wph2	wph3	wph4	Wing-span
<i>Preondactylus buffarinii</i> (Holotype, MFSN 1770) ^{2,4,7}	56*	54	32	42	19	34	49.5	30.8	39	39	28*	45–50
? <i>Peteinosaurus zambellii</i> (MCSNB 3359) ⁵	–	–	38.5	48	17	37	49	43	43	46.5	34.8	60
<i>Austriadactylus cristatus</i> (Holotype, SMNS 56342) ⁸	110	–	83	–	–	–	–	–	101	103.5	85.5*	120
<i>Eudimorphodon ranzii</i> (Holotype, MCSNB 2888) ^{1,3}	90*	74.5	47	65	29	41	50*	80*	–	–	–	75–100
<i>Eudimorphodon</i> cf. <i>ranzii</i> (MCSNB 2887) ^{1,9}	–	–	28	38	14*	21.2	28.5	39.5	36.5*	–	–	–
<i>Eudimorphodon</i> sp. (MPUM 6009) ^{1,3,9}	40	34	26	36	10.5	18.5	25*	38.5	33*	36.2	34*	45
<i>Eudimorphodon</i> cf. <i>ranzii</i> (BSP 1994 I 51) ⁵	–	–	40	–	–	–	57.7	52.9	–	–	–	70–80
<i>Eudimorphodon</i> sp. (MCSNB 8950) ^{3,5,9}	–	–	26	33.5	9.3	19.6	25.5	33	35.2	36.2	32	45
<i>Eudimorphodon rosenfeldi</i> (Holotype, MFSN 1797) ⁶	–	–	40.5	55	21	37	54.2	64	58.2	63.2	51.5	65–70
<i>Eudimorphodon cromptonellus</i> (Holotype, MGUH VP 3393) ¹⁰	–	–	18.15	20.15	8.4	19.7	20.5*	18*	20.5	20.5*	–	24
<i>Raeticodactylus filisurensis</i> gen. et sp. nov. (Holotype, BNM 14524)	95	84	82	106	–	56	84	113	109	117*	83*	135

* estimated

Abbreviations: fe, femur; h, humerus; m, mandible; mcIV, wing metacarpal (IV); s, skull; ti, tibia; u, ulna; wph1–4, wing phalanges 1–4.

Data sources: ¹ Wild (1978); ² Wild (1984); ³ Wild (1994); ⁴ Wellnhofer (1993); ⁵ Wellnhofer (2003); ⁶ Dalla Vecchia (1995); ⁷ Dalla Vecchia (1998); ⁸ Dalla Vecchia et al. (2002); ⁹ Dalla Vecchia (2003a); ¹⁰ Jenkins et al. (2001).

There are many differences between the bone length ratios (Table 3) of *Raeticodactylus*, *E. ranzii* (MCSNB 2888), *E. rosenfeldi* (MFSN 1797) and *E. cromptonellus* (MGUH VP 3393). *Raeticodactylus* shows close similarities with MCSNB 2887, (*E. cf. ranzii*), a highly disarticulated specimen, only partially preserved and lacking skull. *Raeticodactylus* is approximately three times larger in size than MCSNB 2887. Two main conclusions from the comparison of *Raeticodactylus* with *Eudimorphodon*, *Peteinosaurus* and *Preondactylus* are drawn: *Raeticodactylus* exhibits the shortest femur compared to the tibia, and also the longest humerus compared to the femur.

The forelimb (humerus + ulna) to hindlimb (femur + tibia) ratio (Table 1) is very high in *Raeticodactylus* with 1.34 (*E. ranzii*, MCSNB 2888: 1.23; *E. rosenfeldi*, MFSN 1797: 1.05; *E. cromptonellus*, MGUH VP 3393: 0.95). It is similar to that of *E. cf. ranzii* (MCSNB 2887) and *E. sp.* (MCSNB 8950) with a value of 1.32; only the ratio of *E. sp.* (MPUM 6009) is higher with a value of 1.43. Jenkins et al. (2001) also compared the dimensions of the forelimbs and hindlimbs in various pterosaurs, using the length of the metacarpal IV and the average length of metatarsals. The ratio was as follows: $(\sum \text{humerus} + \text{ulna} + \text{metacarpal IV} / \sum \text{femur} + \text{tibia} + \text{average of metatarsals}) \times 100$. Jenkins et al. (2001) determined it in the following Triassic pterosaurs: *E. cromptonellus* (90%), *Preondactylus buffarini* (95%), *Peteinosaurus zambellii* (100%) and *E. sp.* (MCSNB 8950) (130%). These values could be completed with *E. rosenfeldi* (103.8%). The ratio for the specimens MCSNB 2888 (*E. ranzii*) and SMNS 56342 (*A. cristatus*) cannot be determined. The metacarpal IV of BNM 14524 is not preserved, however, as this metacarpal is never shorter but rather longer than the metacarpal III in other Triassic pterosaurs, the length of the metacarpal III can be used as a proxy. The resulting ratio is of at least 134.3%, *Raeticodactylus* reveals the highest value of this comparison.

With a wingspan of 135 cm (Table 2), *Raeticodactylus* is one of the largest Triassic pterosaur known so far. Only two other Triassic specimens suggest the existence of even larger pterosaurs during the early history of this group: three wing phalanges from an Italian specimen, MCSNB 4562 (Pterosaur indet.), indicate a wingspan of 150–160 cm (Padian 1980); an isolated 4th wing phalanx from an Italian specimen, MFSN 19836 (Pterosaur indet.), indicates a wingspan of approximately 175 cm (Unwin 2003b).

An overall graphic comparison of skeletal lengths is presented in Figure 14. It well summarizes that even though *Raeticodactylus* has some similarities with some Triassic specimens (e.g. MCSNB 2887, *Eudimorphodon cf. ranzii*), this new genus is clearly distinct from other Triassic pterosaurs.

Functional morphology and palaeoecology

Bony, sagittal cranial crest

Bony cranial crests are known from many pterosaurs. According to Wellnhofer (1993), there are three groups of

crests: short or long crests on the posterior part of the skull (e.g. *Pteranodon*, *Dsungaripterus*); long and low crests on the middle part of the skull (e.g. *Germanodactylus*, *Gnathosaurus*, *Ctenochasma* and *Dsungaripterus*); high crests on the anterior part of the snout, which look like an inverse keel (e.g. *Ornithocheirus*).

Bony sagittal crests are only known from Triassic pterosaurs in *Austriadactylus cristatus* and now in *Raeticodactylus filisurenensis*. Both specimens have the crest on the premaxilla, but that of *A. cristatus* elongates all along the skull. One could hypothesize that the bony crests moved to a more posterior position during the Jurassic and Cretaceous, although preorbital sagittal crests are very common in the Cretaceous (e.g. *Ornithocheirus*). From this point of view the crests do not reflect an evolutionary trend in pterosaur evolution, the premaxillary bony crests could rather indicate a functional adaptation to a particular lifestyle. Until now, the function of these crests is not fully understood, different explanations are found in the literature: a structure linked to the sexual dimorphism (this has been argued for *Pteranodon*) (Bennett 1992); a display structure (Kellner 2002); imprints of bloodstreams on the bony crests show that they were strongly supplied with blood, they could have regulated the body temperature (e.g. in *Thalassodromeus*) (Campos & Kellner 1996, Kellner 2002); an aerodynamic function (Kellner 2002); an hydrodynamic role to feed by skimming, notably by analogy with the jaw anatomy of the modern skimming bird *Rhynchops* (Wellnhofer 1993).

It could be argued that *Raeticodactylus* caught fishes by skimming, as suggested by Wild (1978) for *Eudimorphodon ranzii*. Beyond the presence of premaxillary and mandibular crests, the following features (Kellner 2002) also suggest that *R. filisurenensis* could be a skimming pterosaur: laterally compressed upper and lower jaws with a bladelike horny covering (rhamphothecae); large cervical vertebrae for an important neck musculature; large adductor mandible complex musculature; several foramina on the tip of the premaxilla and of the mandible indicate that this region was well irrigated by blood vessels and likely well supplied by nerves; due to the possibility that the snout was dived into the water at least for a short time, the posterior position of the narial fenestra of BNM 14524 in relation to the skull could have been advantageous. A recent study by Humphries et al. (2007), however, strongly challenged the hypothesis of skimming pterosaurs, even in smaller forms.

Specialized dentition

Dalla Vecchia (2003a) mentioned that most Triassic pterosaurs have multicuspid or serrated teeth. Wellnhofer (1993) stated that multicuspid teeth do not reflect a primitive feature of reptiles, but rather a specialization to its environment and therefore to prey (e.g. *Eudimorphodon* as a piscivore). Multicuspid teeth are surely useful to penetrate and cut hard food (e.g. ganoid fishes, crustaceans, large insects or other animals with a robust exoskeleton) into small pieces (Dalla Vecchia 2003a).

Table 3. Bone length ratios of *Raeticodactylus filisurensis* gen. et sp. nov. and various Triassic pterosaurs. The ratios were calculated with the measurements of Table 2.

	u/h	h/mcIV	u/mcIV	h/fe	h/ti	u/fe	u/ti	ti/fe	fe/mcIV	ti/mcIV	wph1/h	wph1/u	mclV	wph1/fe	wph1/ti	wph2/wph1	wph3/wph2	wph3/wph4	wph3/wph1
<i>Preondactylus buf-farinii</i> (Holotype; MFSN 1770)	1.31	1.68	2.21	0.94	0.65	1.24	0.85	1.46	1.79	2.61	0.96	0.73	1.62	0.91	0.62	1.27	1	1.39*	1.27
? <i>Petinosaurus zam-bellii</i> (MCSNB 3359)	1.25	2.26	2.82	1.04	0.79	1.3	0.98	1.32	2.18	2.88	1.12	0.9	2.53	1.16	0.88	1	1.08	1.34	1.08
<i>Austriadactylus cristatus</i> (Holotype; SMNS 56342)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.02	–	–
<i>Eudimorphodon ranzii</i> (Holotype; MCSNB 2888)	1.38	1.62	2.24	1.14	0.94*	1.58	1.3	1.22*	1.41	1.72*	1.7*	1.23*	2.75*	1.95*	1.6*	–	–	–	–
<i>Eudimorphodon cf. ranzii</i> (MCSNB 2887)	1.36	2	2.27	1.32	0.98	1.79	1.33	1.34	1.57	2.03	1.43*	1.05*	2.82	1.89*	1.39*	0.91*	–	–	–
<i>Eudimorphodon</i> sp. (MPUM 6009)	1.37	2.5	3.43	1.42	1.05*	1.95	1.44*	1.35*	1.76	2.38*	1.48	1.04	3.57	2.03	1.5*	0.88	1.1*	1.06	0.96*
<i>Eudimorphodon cf. ranzii</i> (BSP 1994 I 51)	–	–	–	–	0.69	–	–	–	–	–	1.32	–	–	–	0.92	–	–	–	–
<i>Eudimorphodon</i> sp. (MCSNB 8950)	1.29	2.89	3.72	1.33	1.02	1.71	1.34	1.27	2.18	2.78	1.27	1.01	3.78	1.73	1.29	1.04	1.02	1.12	1.06
<i>Eudimorphodon rosenfeldi</i> (Holotype, MFSN 1797)	1.31	1.93	2.62	1.13	0.75	1.49	1.02	1.46	1.76	2.58	1.58	1.16	3.05	1.73	1.18	0.91	1.09	1.23	0.99
<i>Eudimorphodon cromptonellus</i> (Holotype, MGUH VP 3393)	1.11	2.16	2.39	0.92	0.89*	1.02	0.98*	1.04*	2.34	2.44*	0.99*	0.9*	2.14*	0.91*	0.88*	1.14*	1*	–	1.14*
<i>Raeticodactylus filisurensis</i> gen. et sp. nov. (Holotype; BNM 14524)	1.29	–	–	1.46	0.98	1.89	1.26	1.5	–	–	1.38	1.07	–	2.02	1.35	0.96	1.07*	1.41*	1.04*

* estimated

Abbreviations: fe, femur; h, humerus; mclV, wing metacarpal (IV); ti, tibia; u, ulna; wph1–4, wing phalanges 1–4.

Fastnacht (2005) noted that *Eudimorphodon*, with its small multicuspid teeth, could better hold very small food items, in contrast to *Preondactylus*.

Raeticodactylus filisurensis also has a heterodont dentition. In the anterior part are the long, monocuspid and fang-like teeth. On the labial side the enamel is more or less smooth, but has very strong wrinkles on the lingual side. The wrinkles are aligned very close to each other and show bowed ridges, which are partially bifurcated. The function of these enamel wrinkles can be interpreted as follows: better catching and holding (fixation through the enamel wrinkles) of slick nutrition (fish); increased stability of the tooth by construction ridges (less wide ridges or many fine ridges) like in *R. filisurensis* with its fine teeth.

One isolated fang tooth of *E. cf. ranzii* (BSP 1994 I 51) also reveals bowed enamel wrinkles on its lingual side. It is similar to BNM 14524, however, not so strongly developed as for *R. filisurensis*. The multicuspid teeth are equal in size in the upper and lower jaws. The wear facets on the labial side of the mandible teeth indicate a displaced contact between the upper and lower jaws. When the snout was closed, the upper multicuspid teeth were located on the outside whereas those of the mandible were inside. The cutting edges of some teeth of the upper jaw, distally and mesially in convex form, show a thickened bulge. These features indicate a cutter-like function of the dentition. Wellnhofer (1993) pointed out that in addition to the teeth, some pterosaurs (e.g. *Rhamphorhynchus*) had keratinized, beak-like edges on the tips of the jaws that were useful for fishing. Based on the structure of the bones, it is very likely that *Raeticodactylus* had such a soft tissue structure on the anterior part of its snout. These keratinized edges would have helped in cutting prey. The diastema between the monocuspid and multicuspid teeth in the upper jaw shows an analogous feature to other animals. Some theropod dinosaurs (e.g. *Baryonyx*, *Irritator*) and recent crocodiles reveal such diastema at similar position. This could indicate that *Raeticodactylus* also had a grasping and hunting style.

Conclusions

Raeticodactylus filisurensis gen. et sp. nov. is so far the best preserved pterosaur from Switzerland. This basal non-pterodactyloid pterosaur is very likely late Norian in age. Comparisons with other Triassic pterosaurs show clearly that it is a distinct genus.

Raeticodactylus filisurensis has a dentition that characterizes a grasping and holding preying style. In the anterior part of the dentition are monocuspid teeth (with strong enamel wrinkles on the lingual side) with a fang like function. In the posterior part of the dentition are tricuspoid, quadricuspoid and quinticuspid teeth with a crack or cutting-like function. The bony cranial crest of *R. filisurensis* is different from that in *Austriadactylus cristatus*. It is linked to the keel-like increase of the mandible and interpreted as a skim-feeder adaptation. With the discovery of *R. filisurensis*, two Triassic pterosaurs

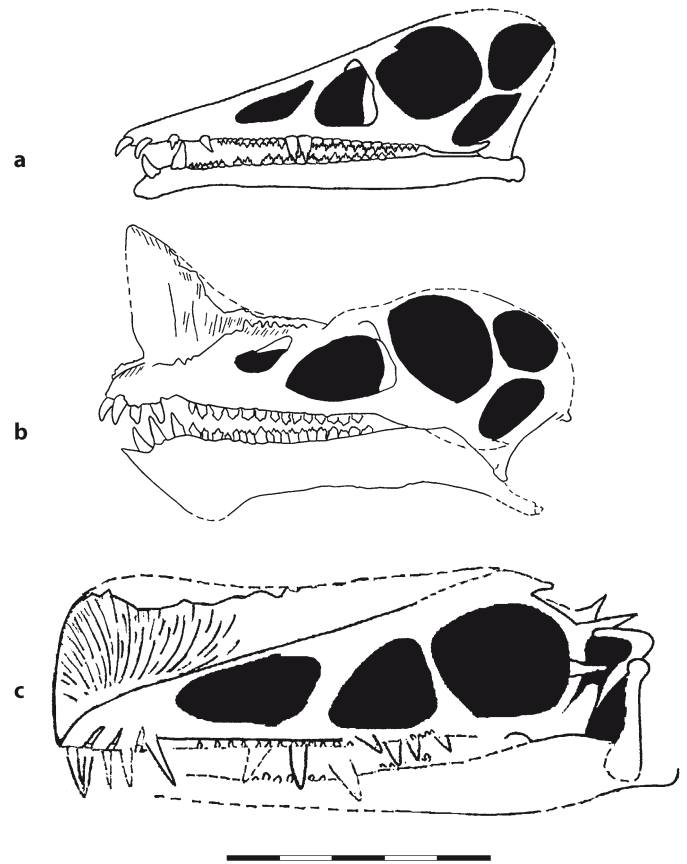


Fig. 13. Comparison of Triassic pterosaur skulls. a) *Eudimorphodon ranzii* (MCSNB 2888), after Wild (1978). b) *Raeticodactylus filisurensis* gen. et sp. nov. (BNM 14524). c) *Austriadactylus cristatus* (SMNS 56342), after Dalla Vecchia et al. (2002). The scale bar is in centimetres.

are known with bony sagittal cranial crests, suggesting that such crests were more common during the Late Triassic than previously thought. The femur of *R. filisurensis* is quite unusual with a caput femoris perpendicular to the shaft. Comparisons of skeletal measurements show that *R. filisurensis* was a gracile flyer with an important wingspan (at least 135 cm) for the Late Triassic.

Finally, *R. filisurensis* confirms that pterosaurs were diverse and highly specialized flying reptiles since the beginning of their long history. It gives additional evidence to the hypothesis of Unwin (2003a) suggesting that there was a significant radiation of basal pterosaurs during the Late Triassic.

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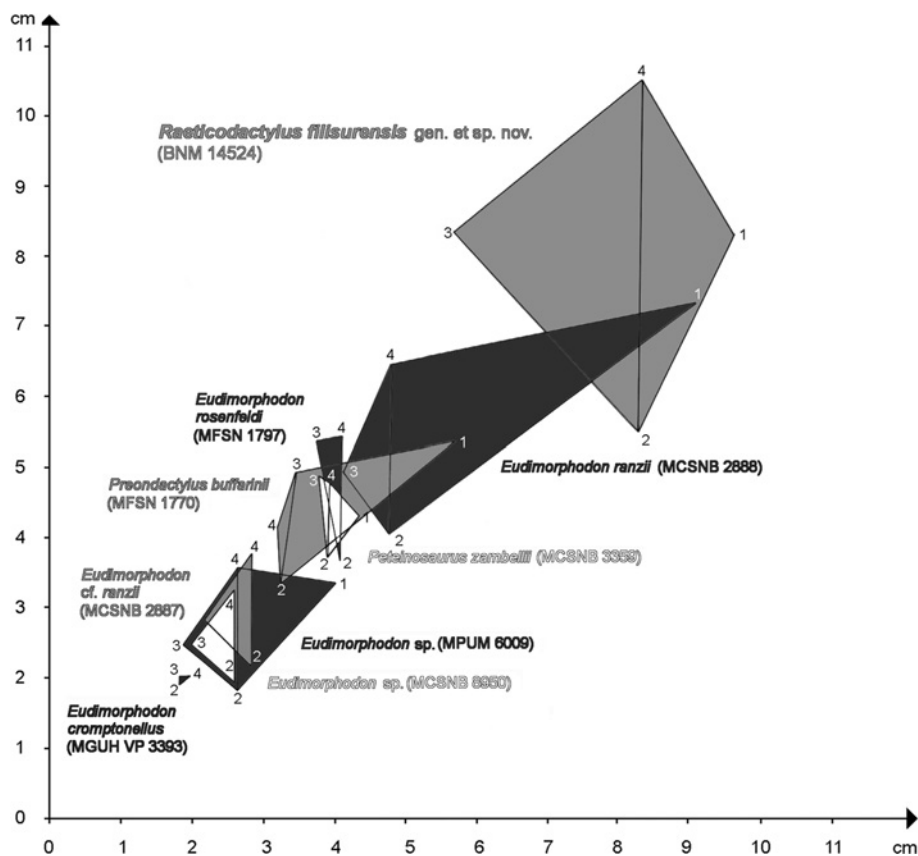


Fig. 14. Overall scatter diagram of skeletal lengths in *Raeticodactylus filisurenensis* gen. et sp. nov. and various Triassic pterosaurs (data from Wild, 1978, 1994; Dalla Vecchia 1995, 2003a; Wellnhofer 2003; this study: Table 2). Connecting the data determined for each specimen results in the presented quadrangles or triangles (e.g. a missing skull results in a triangle). The form and size of quadrangles or triangles give information about similarities and differences between the specimens. Length comparisons: 1, skull (x-axis) vs. mandible (y-axis); 2, humerus (x-axis) vs. femur (y-axis); 3, femur (x-axis) vs. tibia (y-axis); 4, humerus (x-axis) vs. ulna (y-axis).

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