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COMMENTS ON TRIASSIC PTEROSAURS WITH A COMMENTARY ON THE "ONTOGENETIC STAGES" OF KELLNER (2015) AND THE VALIDITY OF *BERGAMODACTYLUS WILDI*

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Abstract. Six stages (OS1-6) were identified by Kellner (2015) to establish the ontogeny of a given pterosaur fossil. These were used to support the erection of several new Triassic taxa including *Bergamodactylus wildi*, which is based on a single specimen (MPUM 6009) from the Norian of Lombardy, Italy. However, those ontogenetic stages are not valid because different pterosaur taxa had different tempos of skeletal development. Purported diagnostic characters of *Bergamodactylus wildi* are not autapomorphic or were incorrectly identified. Although minor differences do exist between MPUM 6009 and the holotype of *Carniadactylus rosenfeldi*, these do not warrant generic differentiation. Thus, MPUM 6009 is here retained within the taxon *Carniadactylus rosenfeldi* as proposed by Dalla Vecchia (2009a).

INTRODUCTION

The pterosaur specimen MPUM 6009 was discovered in 1971 or 1972 in the Norian (Upper Triassic) Calcare di Zorzino Formation at the Cene Quarry (Cene, Bergamo Province, Northwestern Italy) (Dalla Vecchia 2014). It was first identified as an immature individual of *Eudimorphodon ranzii* Zambelli, 1973 by Wild (1979; it is reported as "Exemplar Milano") and later retained as such in many following papers (e.g., Wild 1994; Dalla Vecchia 1998, 2003; Jenkins et al. 2001; Wellnhofer 2003). However, Kellner (1996, 2003), advanced doubts about the conspecificity of MPUM 6009 and the holotype of *E. ranzii* (MCSNB 2888). Dalla Vecchia (2009a) demonstrated that MPUM 6009 differs from the holotype of *Eudimorphodon ranzii* and that differences cannot be considered as ontogenetic features as claimed by Wild (1979). Dalla Vecchia (2009a) listed several features that are uniquely shared by MPUM 6009 and the holotype of *Eudimorphodon rosenfeldi* Dalla Vecchia, 1995 (specimen MFSN 1797). Dalla Vecchia (2009a) considered MPUM 6009 and MFSN 1797 to be conspecific and erected the new genus *Carniadactylus* (monospecific, *C. rosenfeldi*) for them. Dalla Vecchia (2009a) also highlighted several differences between the two specimens, suggesting that they might alternatively belong to different (although closely related) species, but considered it more parsimonious to regard them as conspecific. Dalla Vecchia (2013, 2014) retained MPUM 6009 in *Carniadactylus rosenfeldi* and stated that MGUH VP 3393 (holotype and unique specimen of *Eudimorphodon cromptonellus* Jenkins, Shubin, Gatesy & Padian, 2001) should be referred to a distinct genus and that BSP 1994 I 51 (first referred to as *Eudimorphodon* cf. *ranzii* by Wellnhofer 2003) belongs to a new genus and species. Dalla Vecchia (2014) provided an emended diagnosis for '*Eudimorphodon*' *cromptonellus*, but did not rename it; a list of potentially diagnostic features of BSP 1994 I 51 (reported as "Genus and species to be named"; Dalla Vecchia 2014: 82) was also published, but the formal naming of the new taxon was postponed to a later paper.

Kellner (2015) revised the taxonomy of MPUM 6009, MGUH VP 3393 and BSP 1994 I 51, erecting the new taxa *Bergamodactylus wildi*, *Arcticodactylus cromptonellus* and *Austriadraco dallavecchiai*, respectively. Kellner's (2015) taxonomic statements on Triassic pterosaurs are substantially based on his hypothesis of the existence of "six ontogene-

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tic states (OS)" (*sic*, p. 684) during pterosaur life history.

Here, the validity of Kellner's six ontogenetic stages (OS) and of *Bergamodactylus wildi* are discussed. The referral of MPUM 6009 to the genus *Carniadactylus* and provisionally to the species *C. rosenfeldi*, as proposed by Dalla Vecchia (2009a), is defended. The features characterizing each of the six ontogenetic stages is discussed and their presence in Triassic pterosaurs examined in order to confirm or deny their purported order of appearance during pterosaur ontogeny. Specimen MPUM 6009 is described, with particular focus on the features used by Kellner (2015) to establish its ontogenetic stage and the erection of *Bergamodactylus wildi*. Finally, the characters supporting the validity of *Bergamodactylus wildi* are analyzed and critiqued.

Material, methods and terminology

The object of this work is pterosaur specimen MPUM 6009, a partially articulated skeleton from the uppermost part of the Calcare di Zorzino Formation of Lombardy, Italy. The specimen was studied in detail using a Wild M3 binocular microscope with particular focus on those features used by Kellner (2015) to establish its ontogenetic stage and support for the erection of *Bergamodactylus wildi*.

The term "adult" is not considered here in the sense of sexual maturity, but of somatic maturity of an individual as it can be hypothesized through its osteological maturity. The degree of skeletal maturity is estimated by size-independent criteria such as the degree of ossification of the diaphyses and epiphyses of the long bones and the fusion or non-fusion of bones that normally fuse in the taxon of interest (Bennett 1993). The degree of skeletal maturity is also estimated by the histology of bone, which relates to bone growth rate and supposedly changes during ontogeny (e.g., de Ricqlès et al. 2000; Padian et al. 2004; Chinsamy et al. 2008). Macroscopic and histological features are interelated: the immature grain of the shaft surface due to the emergence of vascular canals is related to the relatively high degree of vascularization of the fast growing cortical bone and disappeared when the External Fundamental System (observable in histological thin sections of fossil bone) formed. However, although both macroscopic and histological observations provide information on skeletal maturity, they can lead to different interpretations of the ontogenetic stage of a same specimen because of differing definitions of adultness (based on complete fusion of the composite skeletal elements and on the histological features suggesting a marked slowdown in growth, respectively; Bennett 2017). For example, Prondvai et al. (2012) observed that three specimens of the Late Jurassic non-pterodactyloid *Rhamphorhynchus muensteri* belonging to the medium size-class of Bennett (1995) show different degrees of histological maturity and that one of these specimens was as mature histologically as the large size-class specimens. The medium size-class specimens were characterized by a fused scapula and coracoid, fused ischium and pubis, but the ilium is unfused to the puboischiadic plate and the proximal tarsals may not be fused to the tibia, whereas all composite bones are fused in specimens belonging to the large size-class (Bennett 1995). Apparently, Prondvai et al. (2012) suggested that an individual of *Rhamphorhynchus muensteri* with a fused scapula and coracoid, fused ischium and pubis, but with the ilium that is unfused to the puboischiadic plate and the proximal tarsals that may not be fused to the tibia, could be as histologically mature as one with all fused bones. Therefore, osteological maturity based on the fusion of the composite bones (i.e., the macroscopic criteria used by Kellner 2015) cannot be directly compared with histological maturity as defined by Prondvai et al. (2012).

The osteological structure termed as "surangular dorsal process" by Kellner (2015) has been reported previously as "coronoid process" (i.e., Wellnhofer 2003: 10). Recognizing that it is part of the surangular, Dalla Vecchia (2009a, 2013, and 2014) reported it as 'coronoid' process to avoid misunderstandings in the comparisons within older literature. In general, the term epiphysis is used to indicate the terminal portion of a long bone, which is composed also by the diaphysis (the shaft) and the metaphysis (the portion between the shaft and the epiphysis). Kellner (2015) used the term "epiphysis" to indicate the bones that are separated from the long bone extremity by a cartilaginous zone in immature individuals of species with determinate growth and fuse to it when an individual stops growing (Romer 1956). The cartilaginous zone is named "growth plate" or "epiphyseal plate"; the latter term was used improperly as a synonym of epiphysis by Kellner (2015: 684-685). The term "secondary center of ossification" is used here instead of the "epiphysis" as employed by Kellner (2015). The orientation (anterior, posterior, dorsal, ventral etc) of forelimb elements is that of the flying animal with the forelimb extended laterally. Measurements and long bones ratios of Triassic pterosaurs are from Dalla Vecchia (2014). *Raeticodactylus filisurensis* is probably congeneric with *Caviramus schesaplanensis* (see Dalla Vecchia 2009a), but the two taxa are here kept distinct, following Dalla Vecchia (2014), and pending a formal revision based on new specimens, and '*Raeticodactylus*' is cited in quotes.

Institutional abbreviations

BNM, Bündner Naturmuseum, Chur, Switzerland; **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich (Germany); **CM**, Carnegie Museum of Natural History, Pittsburgh (USA); **GSM**, British Geological Survey, Keyworth (UK); **MCSNB**, Museo Civico di Scienze Naturali di Bergamo "E. Caffi", Bergamo (Italy); **MFSN**, Museo Friulano di Storia Naturale, Udine (Italy); **MGC**, Museo Geologico della Carnia, Ampezzo (Italy); **MGUH**, Geologisk Museum - Statens Naturhistoriske Museum, Københavns Universitet, Copenhagen (Denmark); **MH**, Museum Hauff, Holzmaden (Germany); **MNHU**, Museum für Naturkunde Berlin, (former Humboldt Museum für Naturkunde), Berlin (Germany); **MPUM**, Museo Paleontologico del Dipartimento di Scienze della Terra, Università di Milano (Italy); **MT**, Geologisch-paläontologisches Institut und Museum der Universität Tübingen (Germany); **NHMUK**, Natural History Museum, London (UK); **NHMW**, Naturhistorisches Museum Wien, Vienna (Austria); **NSM-PV**, National Science Museum, Tokyo (Japan); **SMNS**, Staatliches Museum für Naturkunde Stuttgart (Germany); **ULowen** = University of Leuven, Leuven/Louvain (Belgium); **UUPM**, Palaeontological Museum, University of Uppsala (Sweden); **UZurich**, Palaeontological Institute and Museum of the University, Zurich (Switzerland).

PTEROSAUR ONTOGENY

The ontogeny of Triassic pterosaur specimens was discussed by Wild (1979, 1994) and Dalla Vecchia (2003, 2009a, 2013 and 2014). The osteological features of immaturity in other basal pterosaurs have been analyzed in detail by Wellnhofer (1975a-c) and Bennett (1993, 1995, 1996), while those in pterodactyloids were reported by Wellnhofer (1970), Bennett (1993, 1996, 2017), Kellner & Tomida (2000) and Codorniù & Chiappe (2004). Here only the six ontogenetic stages of Kellner (2015) are examined with arguments against their universality presented.

The six ontogenetic stages of Kellner (2015)

Kellner (2015: 684-685) identified six ontogenetic stages for pterosaurs based on the progressive ossification of the skeleton, the fusion of composite elements (i.e., sacrum, scapulocoracoid, carpus, and pelvis) and the fusion of secondary centers of ossification to forelimb bones. The stages OS1 to OS6 are numbered in order of increasing maturity and are listed below. The diagnostic characters of each stage are numbered in order to score them for Triassic pterosaur specimens in Table 1 and are listed and discussed below.

OS1: "All bones or complex [*sic*] of bones are unfused" (character OS1-1); "ossification of some elements like the sternum" (character OS1-2) and "the articulations [*sic*] of some long bones (ulna, radius, wing phalanges, tibia) present, but not fully developed" (character OS1-3). This is considered to be the condition of hatchlings.

OS2: "All bones [are] ossified although the degree of ossification might vary" (character OS2-1); "all long bones have their articular ends molded [*sic*]" (character OS2-2). "The texture of the external bone surface is immature, showing pits and small struts of bones" (character OS2-3). This is considered to be the condition of juveniles. According to Kellner (2015), MGUH VP 3393, the small holotype of *Arcticodactylus cromptonellus*, belongs to stage OS2.

OS3: Sacral vertebrae are fused (character OS3-1), "followed by fusion of the carpal elements" (character OS3-2), "with the distal carpal elements fusing earlier than the ones of the proximal series" (character OS3-3). Characters OS3-2 and OS3-3 have been rephrased as fusion of the distal carpals (OS3-2) and fusion of the proximal carpals (OS3-3) in the scoring of the Table 1.

OS4: "Scapula and coracoid are fused" (character OS4-1), "followed by the pubis and ischium that form a puboischiadic plate" (character OS4-2). "The ilium, however, is not fused with the remaining elements of the pelvic girdle" (character OS4-3).

OS5: "The ilium [is] fused with the puboischiadic plate" (character OS5-1) and "the extensor tendon process [is] fused with the wing phalanx

1" (character OS5-2). According to Kellner (2015: 685), the holotypes of *Austriadraco dallavecchiai* and *Bergamodactylus wildi* "have... reached at least OS5". As the holotype of *Austriadraco dallavecchiai* is reported as "adult" on Kellner (2015: 677), it is deduced that individuals at OS5 are considered as adults by Kellner (2015).

OS6: "All bones or complex [*sic*] of bones are fused" (character OS6-1). "The epiphyses [= secondary centers of ossification] of the humerus are among the last bones to fuse, with the larger distal epiphysis fusing before the smaller ventrodistal epiphysis" (character OS6-2). Also "the epiphyseal plate [= secondary center of ossification] of the proximal articulation of the ulna is among the last bones to fuse" (character OS6-3). OS6 represents the ontogenetic maturity and specimens can be considered full adults at this stage. Kellner (2015) considered the holotype of *E. ranzii* (MCSNB 2888) to belong to this stage.

Discussion

Characters OS1-1 to 3 are usually impossible to be fully checked on fossils because pterosaur specimens are in most cases incompletely preserved. However, character OS1-1 can be scored as "absent" when at least the elements of one composite bone are fused. The only specimen that is ambiguous in this sense is the holotype of *Arcticodactylus cromptonellus*, because it does not preserve or expose all composite bones, but all the bones that are visible are unfused.

As for "ossification of ...the sternum ...present but not fully developed" (character OS1-2; p. 64), it can be supposed that Kellner meant that some parts of the sternum are not yet ossified, because a somewhat incomplete ossification of the whole sternal plate occurs also in large Triassic individuals that are usually considered as adults (e.g., MCSNB 2888, holotype of *E. ranzii*; see below). The small specimen MCSNB 8950 (its humerus is only 26 mm long) is the only Triassic specimen showing some unossified portions of the sternum (Wild 1994). Other features of immaturity found in MCSNB 8950 are the absence of ossified sternal ribs; unfused sacral vertebrae; sacral ribs separated from their centra by visible sutures and unfused to the ilia; left scapula unfused to the coracoid (but the right scapula and coracoid could be fused); possible presence of secondary centers of ossification at the end of humerus and/or the proximal extremity of ulna (reported as sesamoids by Wild 1994); proximal carpals probably unfused in a syncarpus; pubis and the ilium separated by a suture; unfused tibia and fibula; and proximal tarsals unfused to tibia (Wild 1994). However, the phalanges of the pes are all ossified with well-formed ginglymi; the articular extremities of the long bones are well-ossified and have their final shape (which is plausibly the meaning of Kellner's "articular ends molded" mentioned above); the distal end of humerus is well-ossified; the process for M. triceps brachii on the ulna is well-formed and is not located on a secondary center of ossification; there is a distinct crista metacarpi of the metacarpal IV; the sesamoids between the penultimate manual phalanx and the ungual are ossified; and the extensor tendon process of the wing phalanx 1 is fused with the phalanx (which is character OS5-2 and should occur much later in ontogeny) (Wild 1994). Thus, this immature specimen has one feature of Kellner's earliest ontogenetic stage (OS1), but it also possesses features of later ontogenetic stages, up to the penultimate stage (OS5).

Character OS1-3 can be scored as "absent" when the condylar end of at least one ulna, radius, wing phalanges and tibia are fully developed, but note that this feature is often difficult to recognize in small and crushed specimens (i.e., a majority of Triassic pterosaurs). In Triassic and at least in some Jurassic pterosaurs, the tibia fused with the proximal tarsals to form a distal condylar end of the tibiotarsus only later in ontogeny. Proximal tarsals are still unfused to the tibia in individuals having fused scapulocoracoids with obliterated suture (e.g. MCSNB 3359; Dalla Vecchia 2003). Thus, the tibia should be excluded from the bones characterizing Kellner's stage OS1. In all Triassic pterosaurs, including the holotype of *Arcticodactylus cromptonellus*, the distal end of at least one long bone appears to be fully developed. In the holotype of *Preondactylus buffarinii*, this is established on the basis of the shape of the impressions of the bones.

The character "some bones are not ossified" should have been added to this first ontogenetic stage to account for specimens with totally unossified skeletal elements as in, for example, specimens considered to belong to *Pterodactylus* where small phalanges of pedal digits III and IV are missing because they were composed of cartilage when the pterosaurs died (Wellnhofer 1970, 1991). All phalanges of pedal digits III and IV are ossified in early juvenile individuals of the pterodactyloid *Pterodaustro guinazui* (see Codorniù & Chiappe 2004).

The character OS2-1 is highly ambiguous. The degree of ossification clearly varies within skeletal elements of specimens like MCSNB 2888 (see below), which Kellner (2015) refers to stage OS6. Furthermore, no Triassic pterosaur preserves all skeletal elements, thus this character has no practical use. Note that MCSNB 8950 is scored 'no' in Table 1, because some portions of the sternum are not ossified at all, while the rest of the skeleton is fully ossified. Only nearly complete skeletons with preserved pedes (MCSNB 3359 and MFSN 1797) are scored 'yes' in Table 1, although all bones were ossified in all other specimens and with variable degrees of ossification.

Character OS2-2 could be the most useful feature to distinguish between individuals belonging to the stages OS1 (hatchlings) and OS2 (juveniles) as defined by Kellner (2015), if all long bones were preserved, which unfortunately is rarely the case for Triassic pterosaurs. In all specimens, except possibly the holotype of *Arcticodactylus cromptonellus* (MGUH VP 3393), the articular ends of the preserved long bones are well-ossified and have their final shape. MGUH VP 3393 has well-ossified articular ends of the long bones, but the distal articular end of the wing metacarpal has a shape unlike that of the same region in the wing metacarpals of other pterosaurs (Jenkins et al. 2001; Dalla Vecchia & Cau 2015). This could be a case of an articular end without its final (adult) shape (not molded, according Kellner's terminology). As noted above, according to Kellner (2015) MGUH VP 3393 belongs to stage OS2 and is a juvenile. Jenkins et al. (2001) and Padian et al. (2004) had considered it a juvenile based on non-fusion of skeletal elements and also on histological analysis.

It is often impossible to assess the surface texture of the bones (character OS2-3) in the usually small-sized and crushed individuals of Triassic and Jurassic pterosaurs that are preserved in dolostone, recrystalized limestone and sandstone. In no Triassic specimens does the external surface of all skeletal elements show "pits and small struts of bone". Such a texture is not reported even for the holotype of *Arcticodactylus cromptonellus* (see Jenkins et al. 2001). The bone surfaces of MPUM 6009 are pitted, consequently Wild (1979) considered the pitting as evidence of immaturity. However, that pitting was caused by the diagenetic growth of a thin crust of small crystals over the bones (Dalla Vecchia 2009a; see below). Conversely, the grainy or 'orange-peel-like' appearance of the bone suggests the presence of local incomplete ossification in many specimens, including the large MCSNB 2888 (holotype of *E. ranzii*). I consider this feature as 'inapplicable' to Triassic pterosaurs.

According to Kellner (2015), fusion of the sacral vertebrae (character OS3-1) occurs before fusion of the scapula and coracoid (character OS4-1) and the ischium and pubis in a puboischiadic plate (character OS4-2). This is not the case for specimens MCSNB 3359 and MCSNB 3496 of *Peteinosaurus zambellii* (see Dalla Vecchia 2003, 2014). The scapulocoracoid is fused without suture and there is a puboischiadic plate in MCSNB 3359, but the sacral vertebrae remain unfused. MCSNB 3496 has puboischiadic plates, but the sacral vertebrae are unfused and a suture exists between the proximal tarsals and tibia. The sutures between the first three sacral vertebrae are not obliterated even in the large MCSNB 2888 and the last sacral vertebra is unfused (Wild 1979; Dalla Vecchia 2014: fig. 4.1.87). However, fusion of sacral vertebrae very early in ontogeny is known for some pterosaur taxa. Two early juvenile specimens of the pterodactyloid *Pterodaustro guinazui* have fused sacral vertebrae, although their transverse processes and neural arches remain unfused (Codorniù & Chiappe 2004). These *P. guinazui* specimens are quite immature having barely ossified condylar ends of long bones, cortical bone of long bones with a porous appearance, unfused neural arches in at least the proximal dorsals, unfused scapula and coracoid, only two poorly ossified elements in the carpus, unfused extensor tendon process of wing phalanx 1 and proximal tarsals not fused to the tibia (Codorniù & Chiappe 2004).

According to Kellner (2015), fusion of the sacral vertebrae occurs just before fusion of the carpal elements. This is based on the condition observed in the holotype of the pterodactyloid *Anhanguera santanae* (see Kellner & Tomida 2000: 84). However, this is not the case for the holotype of *A. piscator*, in which the carpals are partially fused while the sacral vertebrae are not (Kellner & Tomida 2000: 34 and 84).

Kellner (2015) is incorrect in considering the

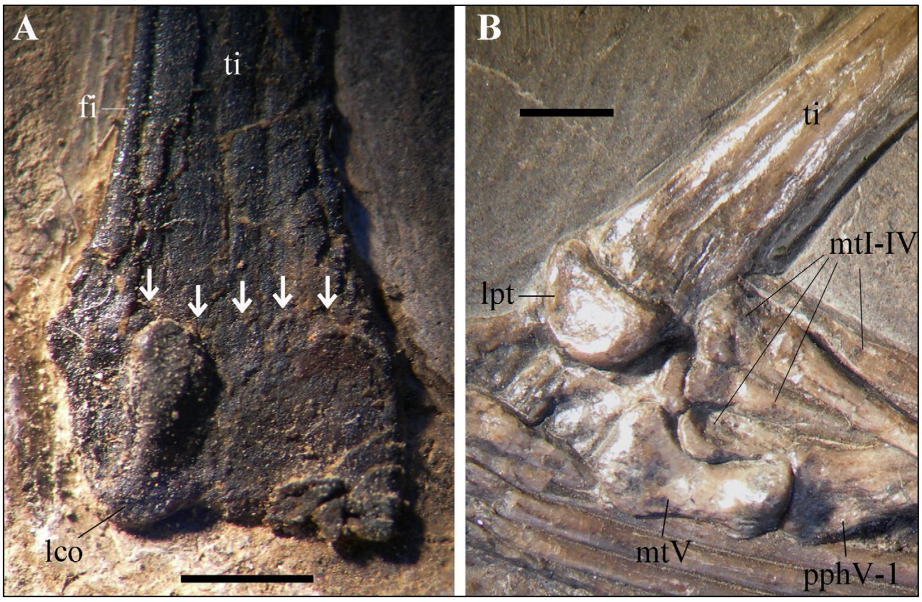

Fig. 1 - Non-fusion of the distal tarsals with the tibia. A) Right tibiotarsus of the holotype of *Austriadraco dallavecchiai* (BSP 1994 I 51) with the still visible suture; B) Right tibia, tarsus and proximal part of the pes of BSP 1938 I 49, *Dorygnathus banthensis*, with completely unfused proximal tarsals and tibia. Abbreviations: fi, fibula; lco, lateral condyle; lpt, lateral proximal tarsal (calcaneum); mtI-V, metatarsals I-V; pphV-1, pedal phalanx V-1; ti, tibia. The arrows in A point to the suture line between the tibia and proximal tarsals. The scale bars equal 2 mm.

order of fusion of the carpals (first the distal, then the proximal carpals; characters OS3-2 and 3) as universal among pterosaurs. His statement is based only on the Cretaceous pterodactyloids *Anhanguera piscator* and *A. santanae* (see Kellner & Tomida 2000: 84). In some non-pterodactyloid pterosaurs, the proximal carpals are clearly fused into a syncarpal, while the distal carpals comprise a large element corresponding with the wing metacarpal and one or more, much smaller elements articulating with metacarpals I-III (e.g., Salée 1928, fig. 5; Wild 1975: figs 1 and 3-4; 1979: 209, pl. 2 and fig. 17; Wellnhofer 1975a: fig. 12a-b; Padian 2008a: figs. 3; Dalla Vecchia 1998: fig. 2; 2009a: fig. 5; 2009b: fig. 4). In the small MCSNB 8950, Wild (1994: 105) mentions a large proximal carpal and two distal carpals, but he does not figure them. In the holotype of *P. buffarinii* (MFSN 1770), MGC 332466 (*Austriadactylus cristatus*) and the holotypes of *C. rosenfeldi* and *E. ranzii*, the pattern is that described above. In MCSNB 3359, the structure of the carpus is unclear, but there is a single large carpal articulating with the ulna, thus the proximal carpals could be unfused (Wild 1979: pl. 14; Dalla Vecchia 2014: fig. 4.1.65). The condition in MPUM 6009 is described below. The carpus of specimen CM 11424 of *Campylognathoides liasicus* (see Wellnhofer 1974) suggests that proximal carpals could remain unfused later in ontogeny: in CM 11424 they are still unfused, whereas the sacral vertebrae are fused (character OS3-1), the scapulae and coracoids are fused with obliterated sutures (character OS4-1), there is a puboischiadic plate (character OS4-2) that is fused with the ilium with an obliterated suture (character OS5-1), the ilium is fused to the sacral ribs and the extensor tendon process is fused to wing phalanx I (character OS5-2).

Definitive evidence for a single distal syncarpal in non-pterodactyloid pterosaurs (characters OS3-3) remains to be reported in literature; probably, a single distal syncarpal never formed (Dalla Vecchia 2009a). Even the large MCSNB 2888 (holotype of *E. ranzii*) has two small distal carpals (Wild 1979: 209, pl. 2 and fig. 17). The fusion of the distal carpals into a syncarpal is probably a pterodactyloid feature or perhaps even of a part of the pterodactyloids only.

Fusion of the scapula and coracoid (character OS4-1) is seen in all Triassic pterosaurs were those bones are preserved and visible, excluding only the holotype of *Arcticodactylus cromptonellus* (see Jenkins et al. 2001) and possibly MCSNB 8950. The state in the holotype of *Preondactylus buffarinii* is uncertain (Dalla Vecchia 2014). Specimen MCSNB 3359 (*Peteinosaurus zambellii*) has a fused scapula and coracoid, fused ischium and pubis (character OS4-2) and the ilium is unfused to the ischiopubic plate (character OS4-3), but the sacral vertebrae are unfused (character OS3-1), proximal tarsals are unfused to tibia and the proximal carpals are possibly unfused, too (character OS3-3). The scapula and coracoid and all the three pelvic bones are fused (characters OS4-2 and OS5-1, respectively) in the holotype of *Austriadraco dallavecchiai*, but the suture between the tibia and distal tarsals can still be seen (Fig. 1A). In one of the smaller *Dorygnathus banthensis* specimens (BSP 1938 I 49; see Tab. 1 and Padian 2008a), the scapulae and coracoids are co-ossified and all the pelvic bones are fused into a single plate, but the proximal tarsals are not fused to the tibia (Fig. 1B). The formation of the tibiotarsus seems to occur relatively late in ontogeny in non-pterodactyloid pterosaurs. It is an important ontogenetic feature that is not considered in the "six ontogenetic stages" of Kellner (2015). Note that fusion of scapula and coracoid also appears to occur relatively early in ontogeny in the pterodactyloid *Pteranodon* (Bennett 1993).

In MCSNB 2886 and MCSNB 3359, the ilia are unfused with the puboischiadic plates (character OS4-3), but the extensor tendon processes are clearly fused with the wing phalanges (character OS5-2). In MCSNB 2886, the extensor tendon processes has a slightly different texture in the suture zone (Dalla Vecchia 2014: fig. 4.1.56), but the suture is obliterated. The extensor tendon process is fused with wing phalanx 1 in all Triassic pterosaurs with the possible exclusion of the holotype of *Arcticodactylus cromptonellus* (however, Jenkins et al. 2001 did not report this non-fusion in their list of evidence of immaturity occurring in the specimen). In MCSNB 8950, the extensor tendon process is fused with the wing phalanx and the ilium is fused with a visible suture to the pubis (Wild 1994), but the specimen shows many features of osteological immaturity, which are listed above, and is probably a juvenile. The extensor tendon process also seems to be fused with wing phalanx 1 in some very small and immature *Rhamphorhynchus* specimens (Wellnhofer 1975b considered these to belong to *'R. longicaudus'*), like that figured in Wellnhofer (1975a: fig. 12a, exemplar 15; its skull is only 34 mm long) and BSP 1938 I 503 (Wellnhofer 1975b: fig. 22; skull 41 mm long). The process is fused to the phalanx in the *Dorygnathus banthensis* specimen BSP 1938 I 49, where all the pelvic bones are fused into a single plate, but the plate is not fused to the sacrum and the proximal tarsals are not fused to tibia. Thus, the fusion of the extensor tendon process occurred relatively early in the ontogeny of non-pterodactyloid pterosaurs, although total obliteration of the suture occurred somewhat later. However, the process appears to be unfused until late in ontogeny in the pterodactyloid *Pteranodon* (Bennett 1993). Thus, the late ontogenetic fusion of the extensor tendon process is probably a feature of the pterodactyloids or only of some of them. All of Kellner's hypotheses on the ontogenetic stage of the Triassic pterosaurs based on the fusion of the extensor tendon process are biased by this incorrect assumption.

Character OS6-1 (all bones or complex of bones are fused) is usually impossible to be fully established, because pterosaur specimens are in most cases incompletely preserved, thus the state cannot be known for all of the bones. Kellner (2015: 685) noted that the dentaries are not fused in MCSNB 2888 (holotype of *E. ranzii*), despite it being considered an adult individual. However, Kellner viewed that non-fusion as a "phylogenetic signal", meaning that non-fusion can be a phylogenetic feature in "some non-pterodactyloids", not an ontogenetic feature. Actually, the mandibular rami are also unfused at the symphysis in the holotypes of *Preondactylus buffarinii* (MFSN 1770; see Dalla Vecchia 2014: fig. 4.1.3A-B), *Austriadraco dallavecchiai*, *Arcticodactylus cromptonellus*, *Peteinosaurus zambellii*, *Carniadactylus rosenfeldi*, *Caviramus schesaplanensis* and *'Raeticodactylus' filisurensis*, specimens MPUM 6009 and MFSN 1922 of *Carniadactylus rosenfeldi*, specimen MFSN 21545 (Dalla Vecchia, 2014: fig. 4.1.164), and in a large and still unnamed pterosaur from the Triassic of the USA (Britt et al. 2015; pers. obs). All Triassic specimens where the relative displacement of the two rami can be checked show that the rami were unfused. This is also the case for specimens NHMUK R 1035 and NHMUK 43486 of the Early Jurassic *Dimorphodon macronyx* (see Sangster 2003). Thus, lack of fusion of the mandibular rami at the symphysis is typical within earliest pterosaurs. In contrast, mandibular rami fused very early during the ontogeny of the pterodactyloids (Kellner & Tomida 2000).

Kellner (2015) apparently thought that full skeletal maturity was reached in pterosaurs when the humeral (character OS6-2) and ulnar (character OS6-3) secondary centers of ossification fused to their respective bones. This is based on his observations on the large pterodactyloids from the Lower Cretaceous of Brazil (see Kellner & Tomida 2000: 84). Actually, those secondary centers of ossification are generally not reported in non-pterodactyloid pterosaurs (e.g., Wellnhofer 1975a-b; Wild 1979; Padian 2008a, b; Dalla Vecchia 2014), possibly because they are difficult to identify due to their small size or cannot be correctly identified in disarticulated skeletons, or because they fused very early during ontogeny, or because non-pterodactyloid pterosaurs did not have them. Possible secondary centers of ossification are reported only in the immature specimen MCSNB 8950 between the left humerus and ulna-radius and were identified as "sesamoids" by Wild (1994: 106). Note that the fusion of secondary centers of ossification in the humerus appear to occur relatively early in the pterodactyloid *Pteranodon* (Bennett 1993).

Adult specimens of *Pteranodon* have a low process for the insertion of M. triceps brachii on the ulna (e.g., Bennett 2000: fig. 74). That process is located on a large and unfused proximal secondary center of ossification in the immature holotype of *Anhanguera piscator* (see Kellner & Tomida 2000: figs. 33-34). The proximal extremity of the ulna presents a comparatively well-developed process for the insertion of M. triceps brachii in Triassic pterosaurs; this process is never located on an unfused secondary center of ossification and no suture separates it from the ulna. This situation is also see in immature individuals including MCSNB 3359 (Dalla Vecchia 2014: fig. 4.1.64), MCSNB 3496 (Dalla Vecchia 2014: fig. 4.1.70) and MCSNB 8950 (Wild 1994: fig. 2).

The holotype of *E. ranzii* (MCSNB 2888) and the holotype of *Austriadraco dallavecchiai* (BSP 1994 I 51) are supposed to have reached ontogenetic stages OS6 and "at least O5" (Kellner, 2015: 685), respectively. However, this is unsupported following the 'six ontogenetic stages': secondary centers of ossification are unreported in both specimens and both specimens are incompletely preserved, thus the complete fusion of all composite elements cannot be checked. Furthermore, the fusion of the ilium with the puboischiadic plate (character OS5-1) cannot be confirmed in MCSNB 2888 and the fusion of the extensor tendon process (character OS5-2, occurring in both specimens) is present also in some juveniles and subadults too, as shown above.

Specimen MCSMB 2888 shows other evidence of non-fusion and incomplete ossification of skeletal elements, most of which was previously listed by Dalla Vecchia (2014): the nasals are unfused to the premaxillae, maxillae and frontals; the postorbital and supraorbital are unfused to adjacent elements; a suture is visible between the maxilla and the premaxilla and the maxilla and jugal (the maxilla and premaxilla are rostrally fused very early in the ontogeny of pterodactyloids; Kellner & Tomida 2000); the last sacral vertebra is unfused to the penultimate sacral vertebra; the sutures between the other sacral vertebrae remain visible; the neurocentral sutures in the last dorsal vertebrae seem to be present; prepubes are not fused at the symphysis; tibia and fibula are not completely fused proximally (a groove separates them); the sternal plate, sternal ribs and prepubic blade are very thin and with a grainy, unfinished surface; and the sacral ribs also show a grainy, unfinished surface. The degree of fusion of the proximal tarsals to the tibia cannot be evaluated as the distal portion of both tibiae are missing.

The holotype of *Austriadraco dallavecchiai* also shows evidence of osteological immaturity (Dalla Vecchia 2014): the jugal is not fused with maxilla and the postorbital is unfused with adjacent elements; sutures between mandibular elements are still visible; the ilium is unfused with the sacrum; fibula is probably unfused proximally with tibia; the suture between the proximal tarsals and the tibia is still visible (Fig. 1A); and some bones (e.g. scapula and ischium) have a grainy bone surface suggesting incomplete ossification (Dalla Vecchia 2014: figs 4.1.40 and 4.1.44).

In the large holotype of *Anhanguera piscator* (NSM-PV 19862), which has a 617 mm-long skull and an estimated wing span of about 5000 mm (Kellner & Tomida 2000), most of the skeletal elements (including many skull bones, atlas-axis complex, neural arches of dorsals and some cervicals, the notarium, the sacral vertebrae, scapula and coracoid, proximal and distal carpals, epiphyses of humerus and ulna, the extensor tendon process of the wing phalanx 1, pelvic elements, proximal tarsals and tibia) are unfused. According to the ontogenetic stages of Kellner (2015), this large pterosaur was in a pre-OS3 when it died, thus it would have been an old juvenile at best. The histological features of this specimen should be investigated to test this conclusion.

The smallest *Pteranodon* specimen (1760 mm estimated wing span), which is considered a juvenile by Bennett (2017), shows the same evidence of osteological immaturity in the distal radius and ulna, carpus, pteroid, wing metacarpal and wing phalanx 1 as the subadult *Pteranodon* individuals with wingspans over twice its size.

In Triassic pterosaurs, two options are possible: 1) no fully mature individuals have ever been found, or 2) the full osteological maturity (fusion and complete ossification) of all skeletal elements

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
OS1														
1	?	no	no	no	no	no	no	no	no	no	no	no	no	no
2	?	yes	?*	no	?	?	?	?	?	no†	?*	no	no	?
3	yes	no*	no	no	no	?	no	no	?	no	no	no	no	no
OS2														
1	?	no	yes	?	?	?	yes	yes	?	?	yes	yes	?	?
2	?	yes*	yes	yes	yes	?	yes	yes	?	yes	yes	yes	yes	yes
3	?	?	?*	?	?	?	?	?	?	?	?	?	?	?
OS3														
1	?	no	?	no	?	?	?	no	no	?	?	no††	?	?
2	?	no+	no	?	no	no	?	?	?	?	no	no	?	?
3	?	yes+	no	?	yes	yes	?	?	?	?	yes	yes	?	?
OS4														
1	no	no*	yes	yes	?	yes	?	yes	?	yes	yes	yes	yes	?
2	?	?	?	?	?	?	yes	yes	yes	yes	yes	?	?	?
3	?	yes#	?	?	yes	?	yes	yes	yes	no	?	?	?	?
OS5														
1	?	no#	?	?	no	?	no	no	no	yes	?	?	?	?
2	?*	yes	yes	?	yes	yes	yes	yes	?	yes	yes	yes	?	yes
OS6														
1	no	no	no	no	no	?	no	no	no	no	?	no	?	?
2	?	no*	?	?	?	?	?	?	?	?	?	?	?	?
3	?	yes§	yes§	yes§	yes§	yes§	?	yes§	yes§	?	yes§	yes§	?	?

Tab. 1 - The presence or absence of the features characterizing the six ontogenetic stages (OS1-6) of Kellner (2015) in the Triassic pterosaur specimens listed in order of increasing body size. See text for the description of the features. Legend: 1 = *Arcticodactylus cromptonellus*, holotype (MGUH VP 3393); 2 = MCSNB 8950; 3 = MPUM 6009; 4 = MCSNB 2887; 5 = *Preondactylus buffarinii*, holotype (MFSN 1770); 6 = *Austriadactylus cristatus* (MGC 332466); 7 = *Peteinosaurus zambellii*, holotype (MCSNB 2886); 8 = *Peteinosaurus zambellii* (MCSNB 3359); 9 = *Peteinosaurus zambellii*, (MCSNB 3496); 10 = *Austriadraco dallavecchiai*, holotype (BSP 1994 I 51); 11 = *Carniadactylus rosenfeldi*, holotype (MFSN 1797); 12 = *Eudimorphodon ranzii*, holotype (MCSNB 2888); 13 = *Austriadactylus cristatus*, holotype (SMNS 56342); 14 = '*Raeticodactylus*' *filisurensis*, holotype (BNM 14524); no = absent; yes = present (it fits the character state); ? = unknown because missing, uncertain or impossible to establish. * = Alternative interpretation is discussed in the text; + = *fide* Wild (1994); # = a suture is visible between bones; § = if the process for M. triceps brachii of ulna is considered to have been on a secondary center of ossification in immature individuals; † = I provisionally assume that the bone identified as the sternum by Wellnhofer (2003) is the sternum, not the fused frontals as done by Kellner (2015, text; however, it is reported as a sternum in fig. 2e); †† sutures are visible (see text).

was never reached during their life history (i.e., their growth was indeterminate and they grew throughout life, albeit at a slower rate in later years.

The order of fusion of skull elements could be species specific or even individually variable in early pterosaurs. For example, the suture between maxilla and jugal is still visible in the largest individual of *Dimorphodon macronyx* (see Sangster 2003), while it is obliterated in a close and still unnamed taxon (Britt et al. 2015) that is about 20% smaller in linear size and shows other evidence of somatic immaturity.

Nevertheless, there seems to be an approximate, although not universal, order of fusion of some skeletal elements in Triassic pterosaurs, which does not fully coincide with those of Kellner (2015). The extensor tendon process fused early to the wing phalanx 1, probably earlier than the co-ossification of scapula and coracoid (e.g. MCSNB 8950). Scapula-coracoid and ischium-pubis co-ossified before than ischiopubis-ilium and sacral vertebrae into a synsacrum. If distal carpals ever fused into a distal syncarpal, they did so after the formation of the proximal syncarpal. Proximal carpals could form a syncarpal later than the fusion of scapula and coracoid and ischium and pubis. Possibly, proximal tarsals fused to tibia at this stage, but obliteration of the suture occurred later (later than obliteration of sutures between the ilium and the puboischiadic plate). The sacrum fused with ilium later in ontogeny. Sutures between some mandibular elements disappeared relatively late in ontogeny too. Some skull bones and the mandibular rami are unfused also in the largest known individuals. As noted above, this is not necessarily indicative of the immature status of the individual. Sutures between skull bones are not obliterated during the ontogeny of the living archosaur *Alligator mississippiensis* (see Bailleul et al. 2016). Adult reptiles still preserving open sutures in composite skeletal elements occur also in the fossil record. For example, neural arches and caudal ribs are always unfused in non-plesiosaur eusauropterygians (Rieppel 2000).

Probably the neurocentral fusion in the vertebral column followed a pattern in pterosaurs, as it does in other diapsids (Brochu 1996; Irmis 2007). This fusion pattern was mentioned by Kellner & Tomida (2000), but not by Kellner (2015) and needs to be further investigated.

Kellner's six ontogenetic stages are an oversimplification of a very complex process. Ontogenetic features of different taxa that probably had distinct growth patterns have been grouped together into a sequence that Kellner (2015) considered to be valid for all pterosaurs. Furthermore, those stages have been based mainly on observations from large Cretaceous pterodactyloids, and then applied to Triassic specimens of basal pterosaur taxa. It is evident that the order of fusion of composite skeletal elements during ontogeny differs in pterodactyloids and early pterosaurs and there is no universal pattern that can be extrapolated to pterosaurs in general.

Systematic Palaeontology

DIAPSIDA Osborn, 1903
Pterosauria Kaup, 1834
Eudimorphodontidae Wellnhofer, 1978
(sensu Dalla Vecchia, 2014)
Carniadactylus Dalla Vecchia, 2009a

Carniadactylus rosenfeldi (Dalla Vecchia, 1995)
Specimen MPUM 6009
Figs 2, 3A and 4

1979 *Eudimorphodon ranzii* - Wild, pp. 179-180, 182, pls. 4-5, figs. 2, 5-7, 18, 24a, 26a, 27a, 28a, 29a and 42.
1994 *Eudimorphodon ranzii* - Wild, pp. 106, 112 and 115, fig. 13b, tabs. 1-2.
1998 *Eudimorphodon ranzii* - Dalla Vecchia, p. 357.
2001 *Eudimorphodon ranzii* - Jenkins, Shubin, Gatesy & Padian, pp. 151-152, 157 and 163, tabs. 1-2.
2002 *Eudimorphodon ranzii* - Dalla Vecchia, p. 46, fig. 10, tab. II.
2003 *Eudimorphodon ranzii* - Wellnhofer, pp. 8, 10-13, 15 and 17-19, tab. 1.
2003 the Milano specimen, which differs from the holotype of *Eudimorphodon ranzii* - Kellner, p. 116.
2003 *Eudimorphodon ranzii* - Dalla Vecchia, pp. 24, 26, 27-28, 37 and 40, tabs. 1-2.
2004a *Eudimorphodon* - Dalla Vecchia, pp. 50, 62, 65-67 and 69, figs. 5B and 6D, tab. I.
2004b I retain it in *Eudimorphodon*, but I consider dubious [*sic*] its conspecificity with MCSNB 2888 - Dalla Vecchia, p. 13, fig. 2.
2006 *Eudimorphodon* - Fröbisch & Fröbisch, p. 1087.
2008 *Eudimorphodon* sp. - Stecher, pp. 194-197, fig. 10d, tabs. 2-3.
2009a *Carniadactylus rosenfeldi* Dalla Vecchia - pp. 159-160, 168, 172-179 and 181-183, figs. 3D, 4D, 6B and 11B, tabs. 2-3.
2010 *Carniadactylus rosenfeldi* - Ősi, pp. 138, 140-141, 143-144 and 146, figs. 1F and 2I, tab. 1.
2010 *Eudimorphodon* - Bonaparte, Schultz & Soares, p. 66.
2013 *Carniadactylus rosenfeldi* - Dalla Vecchia, pp. 127, 133, 141 and 145, tab. 1.
2014 *Carniadactylus rosenfeldi* - Dalla Vecchia, pp. 160-162, 191-203 and 306, figs. 4.1.98B, 4.99.B-C, 4.100B, 4.1.137-146, tabs. 4.1.1-2, 4.1.6 and 4.1.17.
2015 *Bergamodactylus wildi* Kellner, p. 677 - pp. 677-683, figs. 3-4 and 5b, tabs I-II.

Description of MPUM 6009

MPUM 6009 is preserved on a thin limestone slab and lies on its right side. Although the skeleton was originally complete, most of its posterior part split away or was weathered leaving only a faint impression, or no impression at all (see Dalla Vecchia 2014: fig. 4.1.137). The preserved part of the skeleton is crushed and most of the bones as well as the teeth (see Dalla Vecchia 2014: fig. 4.1.140) are broken into many fragments. The bones were originally covered by a thin layer of minute whitish crystals (probably calcite, Wild 1979: 180), which can still locally be observed on the slab surface. As noted above, crystal growth is probably responsible of the pitted aspect of the bone surface of this specimen; for the same reason, the surface of the slab is also pitted where the thin layer split away.

Crushing is particularly evident in the skull, which is flattened and exposes its left lateral view (Fig. 2). Crushing caused some bones to twist with respect to their original position. Some bones partly split away when the specimen was collected in the field or when it was prepared. Some skeletal elements are partly overlapped by other elements. Furthermore, some palatal bones and possibly some elements of the right side are mixed with the lateral elements of the left side. The specimen was also covered with a lacquer that makes the bone surface shiny black like the enamel of the tooth crowns,

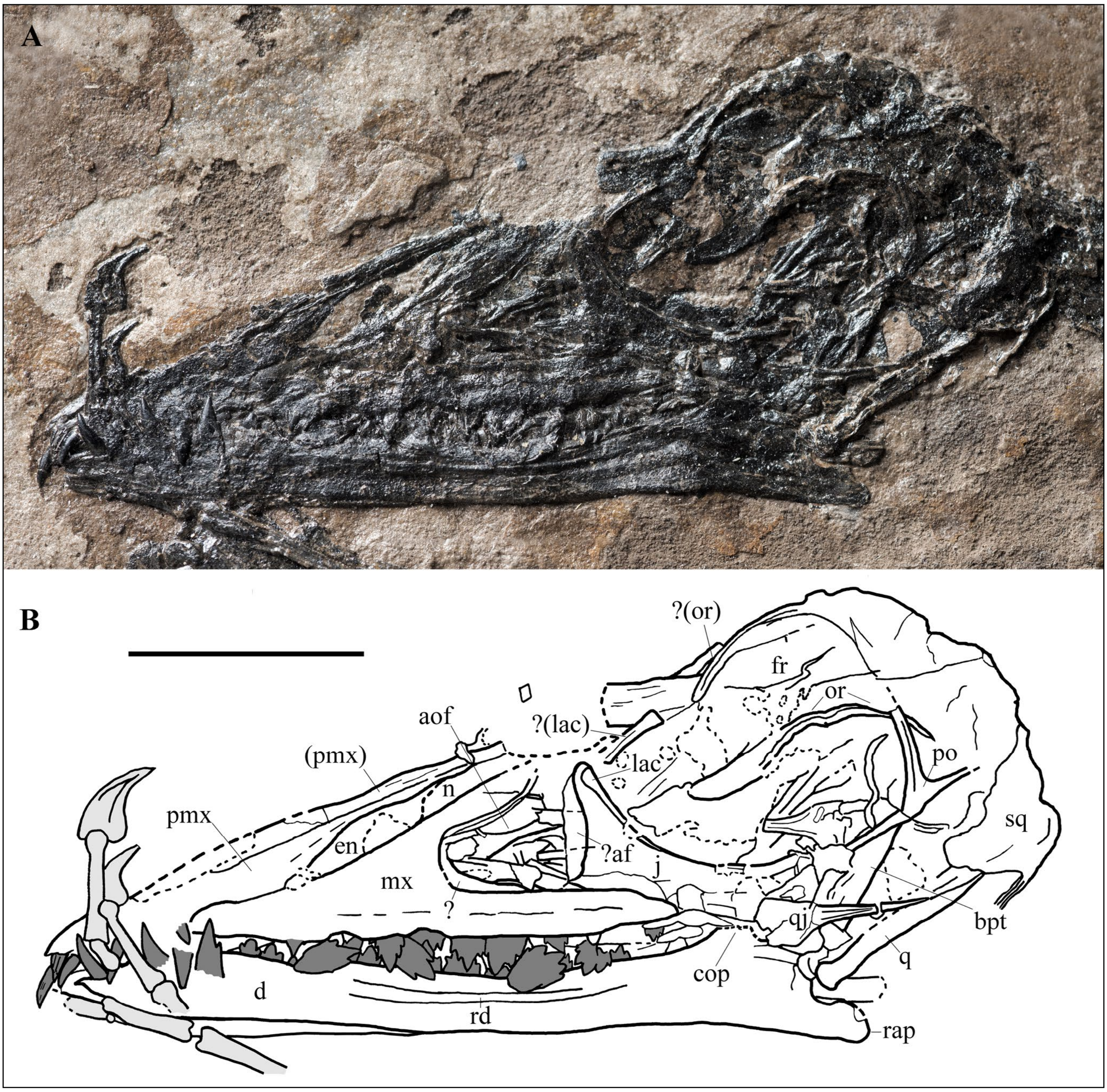

Fig. 2 - Skull and lower jaw of MPUM 6009. A) Photo; B) Drawing. Abbreviations: af, jugal antorbital fossa; aof, antorbital fenestra; bpt, basipterygoid process; cop, 'coronoid' process (surangular dorsal process); d, dentary; en, external naris; fr, frontal; j, jugal; lac, lacrimal; mx, maxilla; n, nasal; pmx, premaxilla; or, orbital rim of the frontal; po, postorbital; q, quadrate; qj, quadratojugal; rap, retroarticular process of the mandible; rd, ridge; sq, squamosal. Elements in parentheses are from the right side. Teeth are in dark gray; manus phalanges are in pale gray. The scale bar equals 10 mm.

sometimes making it difficult to distinguish a broken crown from a broken fragment of bone. This problematic state of preservation makes identification of single skull elements highly interpretative and sometimes prevents unambiguous interpretation of their morphology.

Wild (1979) published an interpretative drawing of the entire specimen (Wild 1979: pl. 5), an interpretative drawing of the skull and the skull reconstruction (Wild 1979: fig. 2), and an interpretative drawing of the left manus (Wild 1979: fig. 18). Dalla Vecchia (2014: figs 1.37B and 4.1.139B-C) published slightly modified versions of the interpretative drawings of the whole skeleton and skull by Wild (1979). Kellner (2015: fig. 4b-c) published his own interpretative drawing and reconstruction of the skull.

The following description supports the discussion of the ontogenetic stage of the specimen and the validity of *Bergamodactylus wildi*. Furthermore, mistakes in Kellner's (2015) interpretation of the specimen are corrected.

Skull and lower jaw (Fig. 2). Authors dealing with MPUM 6009 followed the interpretation and reconstruction of the skull by Wild (1979), mainly in the details that are more difficult to understand on the actual specimen. Dalla Vecchia (2009a; 2014: fig. 4.1.139) and Kellner (2015: fig. 4b-c) proposed alternative interpretations, but only for some skull bones. Dalla Vecchia (2014) revised the postcranium, but did not attempt a thorough revision of the skull and lower jaw, because of the difficulty of interpretation caused by its poor state of preservation. However, some points need to be clarified before arguing against the diagnostic features reported by Kellner (2015) for *Bergamodactylus wildi*.

The degree of fusion of the skull elements cannot be reliably established because of the general crushing. Fractures are barely distinguishable from sutures and can easily be incorrectly interpreted as such. The skull length/height ratio in the skull as preserved is 2.48 (41.5/16.75 mm; height as the distance between the highest point of the skull roof and the base of the quadrate condyle measured perpendicular to the main axis of the skull).

The external naris is relatively small (it is about 5.5 mm long and probably the smaller skull opening), rostroventrally to dorsoposteriorly elongated and probably with a sub-elliptical or sub-trapezoidal outline. The antorbital fenestra has a sub-triangular outline, but it is possibly distorted by crushing and its dorsal margin is not well defined. The orbit was sub-circular and by far the largest skull opening. The shape of the postorbital suggests that the upper temporal fenestra had the outline of an inverted tear drop.

The tip of the snout of MPUM 6009 is overlapped and partly covered by some phalanges of the right manus. The dorsal margin of the posterior two-thirds of the premaxillae split away, but the impression of the missing portion remains. The posterodorsal processes of the premaxillae rotated because of crushing and are both exposed in dorsal view; in this view, they are very narrow and are probably unfused (the midline is visible). They extend posteriorly to the level of the middle of the antorbital fenestra, but their posterior end is missing because a 5 mm-long portion of the dorsal margin of the skull at mid-skull split away. The rotation of the posterodorsal processes of the premaxillae reduced the apparent extent of the external naris. The premaxillary body and the premaxillary process of the maxilla are separated by a straight fracture starting from the rostral apex of the external naris. That fracture becomes an irregular line rostrally that is swollen along its ventral (maxillary) side and ends just posterior to the most distal premaxillary tooth. Thus, that line is the premaxillary/maxillary suture and the entire structure (fracture plus line) plausibly corresponds to the premaxillary/maxillary boundary. Therefore, the suture between the two bones is not obliterated and the premaxilla does not have a significant maxillary process bordering the external naris ventrally. However, the part of the premaxilla bordering the rostral apex of the external naris is damaged (Fig. 2), thus the extent of the participation of the premaxilla to the rostral margin of the external naris was estimated by Wild (1979: fig. 2b).

The outline of the triradiate maxilla is somewhat interpretative because of its fracturing, the fracturing of adjacent bones and the sometimes indistinct boundaries with them. The latter is the case of a shapeless element with the consistency of a film, which covers the central part of the external naris and partly overlaps the maxilla along its contribution to the ventral margin of the external naris (Fig. 2). The ascending process is plausibly that identified by Wild (1979: fig. 2a), but it is not as angled as depicted and its dorsal margin is straight. The ascending process is proportionally much thicker in lateral view than that of MCSNB 2888 and is lance-like instead of regularly tapering apically. Its apical termination is not preserved. Kellner (2015: fig. 4) drew the ascending process as more slender than it actually is. It is unclear which is the actual maxilla edge along the rostral and rostroventral margin of the antorbital fenestra (i.e., which are the margins of the posterior side of the base of the ascending process and the dorsal side of the proximal part of the jugal process), because there are two distinct, similar and parallel structures there. I opt here for the 'slender' maxilla option (Fig. 2B), chosen also by Kellner (2015), but I am unable to understand which other skeletal element the other, parallel, one could be. It apparently mimics the right maxilla (Fig. 2B), but it cannot be the right maxilla, because it lies on the presumed palatal elements. The posterior extent of the jugal process of maxilla is also problematic.

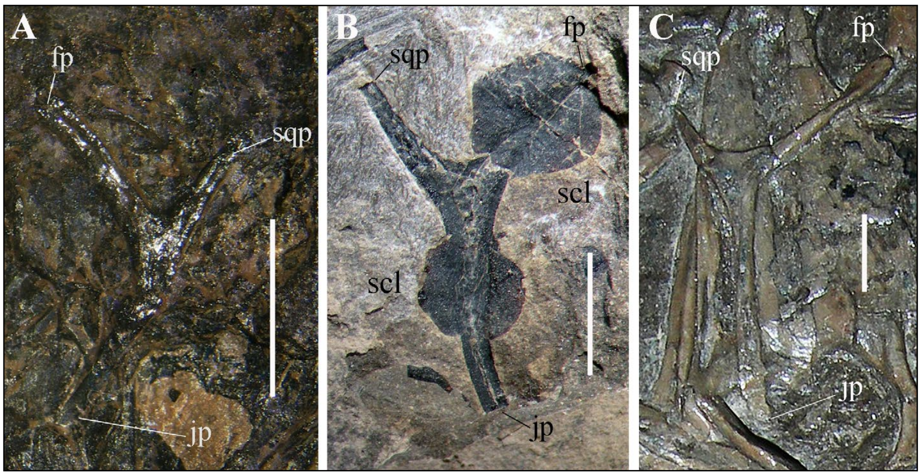

Fig. 3 - Postorbital of MPUM 6009 compared to those of *Austriadraco dallavecchiai* and *Campylognathoides liasicus*. A) Left postorbital of MPUM 6009; B) Left postorbital in medial view or right postorbital in lateral view of BSP 1994 I 51, holotype of *Austriadraco dallavecchiai*; and C) Right postorbital of *Campylognathoides liasicus* (SMNS 11879). Abbreviations: fp, frontal process; jp, jugal process; scl, sclerotic bone; sqp, squamosal process. Lines of the abbreviations point to the exposed extremities of the processes. The scale bars equal 3 mm.

For Wild (1979) and Kellner (2015), it reaches the level of the 'coronoid' process of the surangular. However, its actual posterior end is slightly rostral to the 'coronoid' process and about at the level of the mid-jugal and is abrupt, not tapering like that depicted by Kellner (2015). The upper and ventral margins of the jugal process are parallel for most of the length of the process. The jugal process is longer and shallower than the premaxillary process.

The nasal is a narrow strip of bone starting at the posterior end of the external naris. It is dorsally bordered by the posterodorsal process of the premaxilla and ventrally by the ascending process of the maxilla. Its rostral end, bordering the external naris, is damaged. It possibly has a small rostroventral process, but it is impossible to establish whether a rostrodorsal process like that of the nasal of MCSNB 2888 existed or not (contra Kellner, 2015: 681) because that part of the bone is missing. Its absence in skull reconstructions by the various authors is just a graphic compromise, not an anatomical feature. The posterior portion of the nasal is missing.

The jugal is probably tetraradiate and with a comparatively deep body like that of the jugals of *Eudimorphodon ranzii* and '*Raeticodactylus*' *filisurensis*. The rostrodorsal (lacrimal) process is probably complete and is the longest process of the jugal, while the rostroventral (maxillary) process is very small, but it could be laterally overlapped by the jugal process of maxilla. A film-like, vertical strip of bone rostral to the antorbital margin of the jugal, which was identified as a lacrimal by Wild (1979) and ignored by Kellner (2015), may be the bottom of a jugal antorbital fossa (as noted by Witmer 1997), like that occurring in the new and still undescribed Late Triassic pterosaur from USA (Britt et al. 2015; Britt et al. Submitted), although it is much broader in MPUM 6009. The antorbital margin (antorbital fossa excluded) is shallowly concave (i.e., nearly vertical). The orbital margin is broad and shallowly concave bordering ventrally the large orbit. The outline of the posterior termination of the jugal cannot be traced because of fracturing. The postorbital process is quite inclined posteriorly (the angle with the main axis of the skull is 152°); its distal extremity is not preserved and could be broken or still covered by rock. The quadratojugal process overlaps or is overlapped by the bone that, because of its position, was identified by Wild (1979) and Kellner (2015) as the left quadratojugal. The latter is a relatively large element (at least 6 mm long) with an expanded, flat and thin anterior extremity; it tapers to the posterior extremity, becoming rod-like and straight. It is impossible to establish the exact boundary between this bone and the left jugal. According to Dalla Vecchia (2014), that bone could alternatively be the broken and moved postorbital process of the jugal, but this appears to be improbable.

The Y-shaped postorbital (Fig. 3A) has slender squamosal and frontal rami forming an angle of about 70°. This indicates that the upper temporal fenestra had an unusually acute ventral margin. The jugal process is also slender and is slightly recurved (as is the frontal process). The distal ends of the squamosal and jugal processes are covered by other bones, while the distal end of the frontal process is broken. Therefore, the apparent length of these processes is not the true length. The left postorbital of MPUM 6009 is very similar to the postorbital of the holotype of *Austriadactylus dallavecchiai* (Fig. 3B), and moderately similar to that of the Early Jurassic *Campylognathoides liasicus* (Fig. 3C).

Kellner (2015) reported a relatively massive lacrimal along the orbital margin of the rostrodorsal process of the jugal, while Wild (1979) drew the element much thinner and identified it as the prefrontal. In both cases, it has the shape of an upside-down L. The bone has a thin shaft overlapping the thickened orbital margin of the jugal and a modest dorsorostral expansion that, as preserved, overlaps the apical part of the rostrodorsal process of the jugal. As preserved, the expansion is smaller than that figured by Wild (1979) and much smaller than that reconstructed by Kellner (2015). The shape of the shaft and the position of the bone are those of the lacrimals of the holotype of *Eudimorphodon ranzii* and '*Raeticodactylus*' *filisurensis*. Kellner (2015: fig. 4b) indicates the presence of a lacrimal in the drawing of the skull of MPUM 6009 with the abbreviation "la", but that abbreviation does not correspond with any bone in the figure. In that area, MPUM 6009 preserves a small, rod-like element that could be the right lacrimal, rotated at 90° counterclockwise from its original position (see Fig. 2A-B), but this bone is not drawn in Kellner (2015: fig. 4b).

The frontals were rotated because of crushing and are exposed in dorsal view. They appear as a misshapen, broad plate of bone that is broken into many fragments, some of which split away. Only the orbital margins have a defined outline, because they are thicker. There are no ridges on the dorsal surface of the frontals (unlike MCSNB 2888) and there is no evidence of a suture separating the right from the left frontal (contra Kellner 2015: fig. 4b). The outline of the parietals is indistinguishable; there are no evident ridges for the origin of the adductor musculature. Only the straight and thicker lateroposterior side of the left quadrate is exposed, with the distal lateral condyle that appears to be sub-spherical in lateral view. Possible traces of the medial lamella could be present too. The posterior slope of the left quadrate (135°) was somewhat exaggerated by the extreme crushing and flattening of the posterior part of the skull, which originally was transversely wide. The close rod-like bone that Wild (1979) identified as the right quadrate has a lower slope (about 120°). However, comparison with the holotype of '*Raeticodactylus*' *filisurensis* (see Dalla Vecchia 2014: fig. 4.1.160) suggests that this bone could be the left basipterygoid process of the basisphenoid.

At least six, apparently rod-like, and anteroposteriorly oriented bones cross the antorbital fenestra. At least some of them are plausibly palatal elements (Wild, 1979 identified the dorsal-most elements as the vomers or palatines), while the others could be parts of the elements of the right cheek side of the skull.

The mandibular ramus is slender with a length/height ratio of 17 (length is 34 mm and height is only two mm at mid-ramus). Its dorsal margin is slightly concave, while the ventral margin is nearly straight. Its height is constant along most of dentary length, but the ramus expands near the extremities. In fact, the ramus slightly flares by mandibular tooth 5 and tapers rostrally to tooth 2; the ramus reaches it maximum depth at the apical part of the 'coronoid' process and tapers toward the retroarticular process. The left mandibular ramus is slightly displaced posteriorly with respect to the right one, therefore the two rami were unfused at the symphysis. All mandibular elements appear to be fused, but possible sutures cannot be distinguished from cracks caused by crushing. The rostral tip of the ramus is sharply pointed, unlike the interpretation by Kellner (2015: fig. 4b-c), and the first fang-like tooth is close to the tip. An arched ridge that is bounded ventrally by a groove is present along the lateral side of the central part of the ramus (rd in Fig. 2B). It can also be observed in the holotype of *Austriadraco dallavecchiai* (BSP 1994 I 51), MFSN 21545 and also MFSN 1797 (as an impression). There is no external mandibular fenestra. The apex of the dorsal margin of the surangular (the 'coronoid' process) is overlapped and broken by another bone, probably the jugal (which overlapped the 'coronoid' process laterally in anatomical articulation). What appears to be the dorsal margin of the 'coronoid' process is a fracture line. Wild (1979: fig. 2b) recognized that the apical part of the 'coronoid' process is not exposed and traced it as a point. Wild's reconstruction is plausible since the opposite sloping of the dorsal margins of the surangular anterior and posterior to the broken part. Instead, Kellner (2015: fig. 5b) depicted the broken apical edge as if it were the actual apex of the surangular. This mistake biased the choice of one of the purported features supporting MPUM 6009 as a taxon distinct from *Carniadacty-*

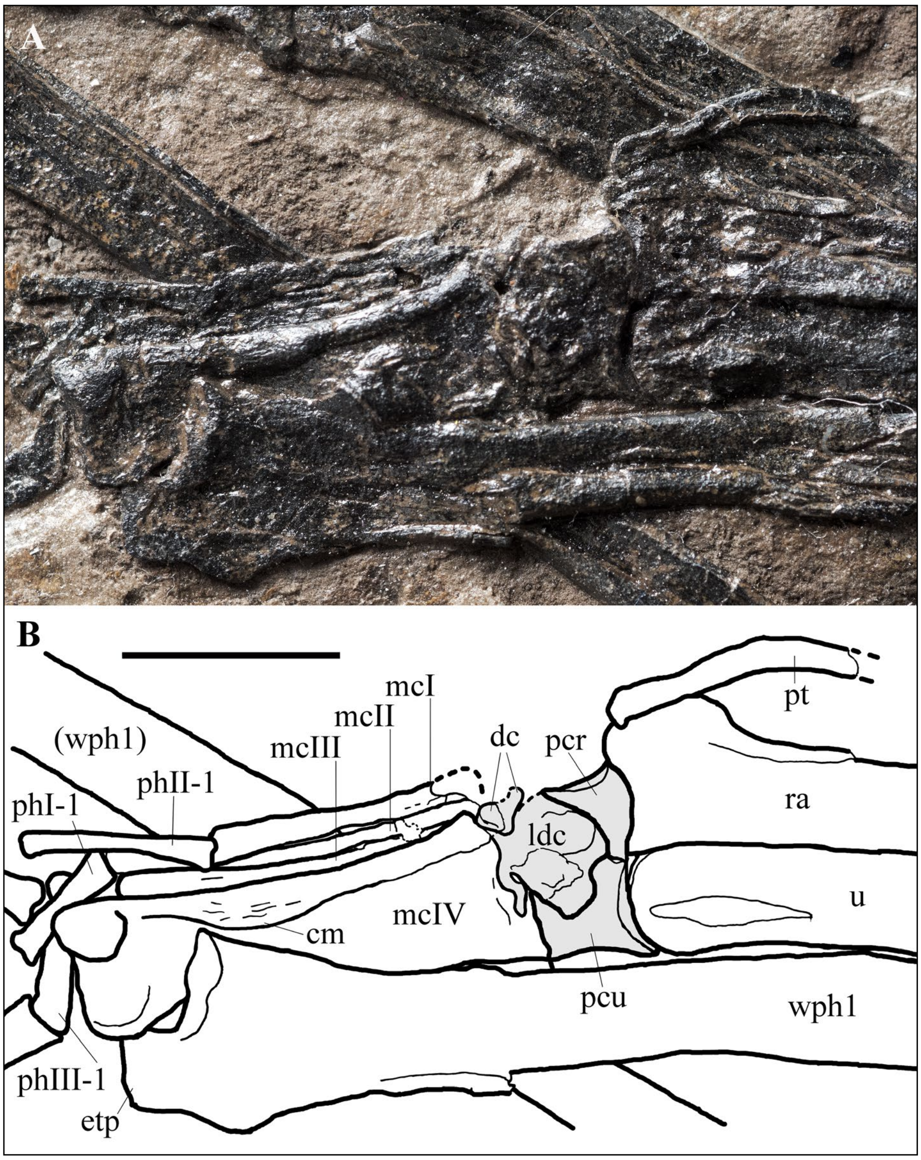

Fig. 4 - Left carpus of MPUM 6009 and adjacent bones in posterior (postaxial) view. A) Photo; B) Drawing. Abbreviations: cm, crista metacarpi; dc, distal carpal; etp, extensor tendon process of wing phalanx 1; ldc, large distal carpal; mcI-III, metacarpals I-III, mc IV, wing metacarpal; pcr, proximal carpal (radiale); pcu, proximal carpal (ulnare); ph, manual phalanges of digits I-III; pt, pteroid; ra, radius; u, ulna; wph1, wing phalanx 1. Elements in parentheses are from the right side. The carpals are in pale gray. The scale bar equals 5 mm.

lus rosenfeldi (see below). Kellner (2015) incorrectly drew the retroarticular process in his figure 5b as if it were entire, but actually the figured profile is clearly that of the broken process. The complete process had a more rounded profile in lateral view.

No one has attempted another reconstruction of the dentition or proposed an alternative tooth count to that of Wild (1979), probably because the teeth are poorly preserved and some of them are difficult to identify, with both Dalla Vecchia (2009a) and Kellner (2015) accepting Wild's interpretation. A more thorough analysis of the specimen shows that the most distal unambiguous mandibular tooth is the penultimate one in figure 2a of Wild (1979). Thus, the position of the last indisputable tooth is more distant from the apical part of the 'coronoid' process than previously supposed. The original incorrect interpretation biased the choice of one of the purported features to distinguish MPUM 6009 from the holotype of *C. rosenfeldi* (see below). Twelve left mandibular teeth can be recognized in situ: three are mesial laniaries (the first two monocuspid and the third bicuspid) and nine are smaller multicusped teeth. However, three segments of the dentary tooth row are covered by displaced maxillary teeth. Based on the mesiodistal length of a mid-row crown, the assumption that there are no interdental spaces (which is the case of the exposed crowns) and the position of the last unambiguous dentary tooth, my estimated tooth count is 17-18 (uncertainty in the count is caused by the different sizes of the multicusped crowns along the row, because the mesial and distal ones that are smaller than the others). Wild (1979) counted 17 mandibular teeth and Kellner (2015: fig. 4C) reported 16 teeth plus a probable empty alveolus distal to tooth 14; both authors included in the count the distalmost tooth that I am unable to find in the specimen.

Postcranium. The postcranium of MPUM 6009 was fully described by Wild (1979) and Dalla Vecchia (2014) and there is little need to replicate those descriptions here. Only details useful for discussing the validity of the characters used by Kellner (2015) to erect *Bergamodactylus wildi* and some additional details not previously described are reported here.

The vertebral column is articulated, but only the cervical segment is completely preserved. Eight cervical vertebrae are exposed, including the atlas-axis complex. The cervical-dorsal transition is covered by the left scapulocoracoid. Cervical vertebra 8 has a large pneumatic foramen (Dalla Vecchia 2014: fig. 1.1.141). The tail was long; the few preserved mid-tail caudal vertebrae have been described by Dalla Vecchia (2002).

Scapula and coracoid are fused without a suture (Dalla Vecchia 2014: fig. 4.1.99B-C). The shaft of the better preserved left coracoid is broad, flat and with nearly parallel anterior and posterior margins (i.e., it is not fan-shaped). Only the proximal portion of the left scapula is preserved. It is dorsoventrally low and with parallel dorsal and ventral margins (i.e. there is no evidence that the scapular blade was fan-shaped). The broad and flat sternal plate crops out from below the two humeri but its outline is unknown and its complete ossification cannot be checked, because it is mostly covered by appendicular bones.

The left humerus is complete; only the anterior margin of the 'squared' deltopectoral crest is slightly damaged (Dalla Vecchia 2014: fig. 4.1.142). Secondary centers of ossification cannot be identified at the extremities of humerus and ulna. The process for the insertion of M. triceps brachii on the ulna is moderately developed; no suture is visible between the process and the rest of ulnar epiphysis (Dalla Vecchia 2014: fig. 4.1.143). The right carpus is poorly preserved and the various elements cannot be reliably identified. The left carpus (Fig. 4) is better preserved, although it is partly damaged. The two proximal carpals (ulnare and radiale) are separated: there is a clear proximodistal line of separation between them (Fig. 4). This separation was noted by Wild (1979: fig. 18), but not by Dalla Vecchia (2009a, 2014). The distal carpus is composed of a large carpal corresponding with the wing metacarpal and one, or possibly two, much smaller carpals in correspondence of metacarpals II and III (Wild 1979: fig 18 reported two small distal carpals). The remainder of the carpus split away with the corresponding proximal portion of metacarpal I (Fig. 4). Although both carpi are articulated and also both pteroids are in situ, both preaxial carpals are missing. The pteroids have the same boomerang-like shape as those of MFSN 1797 (Dalla Vecchia 2009a: fig. 6; 2014: fig. 4.1.100). Their proximal ends contact the distal tubercle of their respective radii, which is the same position they have in the articulated holotypes of *C. rosenfeldi* and *E. ranzii*.

The left wing metacarpal has a prominent crista metacarpi. The extensor tendon process of wing phalanx 1 is fused with the phalanx (Dalla Vecchia 2014: fig. 4.1.144).

Only the preacetabular and postacetabular processes of the left ilium (Dalla Vecchia 2014: fig. 4.1.145) are preserved of the entire pelvis. Thus, the degree of fusion of the pubis and ischium in a single plate and fusion of the latter with the ilium cannot be checked.

Both femora are incomplete. The right femur lacks a small portion of the shaft and its distal extremity is damaged. Its proximal part is covered by a film of dark substance, thus it cannot be seen and its extent must be interpreted. Therefore, the length of the femora is an estimate (as acknowledged by Wild 1979: tab 1) and could be slightly higher than the 19 mm reported by Wild (1979) and the 18.5 mm reported by Dalla Vecchia (2014), although probably not much higher (i.e., 19.5-20 mm). Very little is preserved of the tibiae. Their distal articular ends are not preserved even as an impression. Thus, the length of the bone cannot be reliably estimated and it is impossible to establish whether the proximal tarsals were fused to the tibiae or not. Some phalanges of both pedes are preserved, including the ungual ones (Dalla Vecchia 2014: fig. 4.1.136). They are well ossified and the non-ungual phalanges have well-formed terminal ginglymi.

DISCUSSION OF KELLNER'S (2015) POINTS FOR A DISTINCT TAXON *BERGAMODACTYLUS WILDI*

The diagnosis of *Bergamodactylus wildi* includes the following purported autapomorphies (Kellner 2015: 678 and 680):

Tab. 2 - Wing span (in increasing order), wing metacarpal, humerus, ulna, wing phalanx 1 and femur lengths of *Dorygnathus banthensis* specimens and relative ratios. Measurements (in millimetres) are from Padian (2008a). The extreme values of each ratio are in bold. Anatomical abbreviations: f, femur; h, humerus; mc IV, wing metacarpal; u, ulna; wph1, wing phalanx 1; ws, wing span. Other abbreviations: nn = without museum number, st = stolen. Symbols: -, no measurement/ratio; +? = this bone " may not be quite complete" (Padian 2008: 19); * = based on approximate measurements.

Specimen	ws	mcIV	h	u	wph1	f	mcIV/h	mcIV/u	f/u	f/wph1
MH nn	665	19	38-39	60	44-45	30	0.49	0.32	0.50	0.67
SMNS 18880	820	25	51	68	59/60	38?	0.49	**0.37**	-	-
SMNS 50702	870	26	50	79	63	39	0.52	0.33	0.49	0.62
BSP 1938 I 49	890	25	51	82	60	42	0.49	0.30	0.51	0.70
MT lost	935	28.5	57.5	92	~75	48	0.50	0.31	**0.52**	0.64
SMNS 52999	960	29	51	-	65-72	42	**0.57**	-	-	0.65-**0.58**
SMNS 55886	~960	27	51	-	67	-	0.53	-	-	-
MNHU 1905.15	970	32	65	105	79	53	0.49	0.30	0.50	0.67
SMNS 51827	975	28	52	89	70	45	0.54	0.31	0.51	0.64
SMNS 56255	~990	29	56	-	71	-	0.52	-	-	-
SMNS 18969	~1000	29	57	94	78	47	0.51	0.31	0.50	0.60
SMNS 52998	~1000	-	47	-	-	37	-	-	-	-
U Lowen (st)	1025	28	60	93	72	48	0.47	0.30	**0.52**	0.67
UUPM R157	1030	29	61	98-100	71-73	50	0.475	**0.29**	0.50	0.69
U Zurich A/III493	~1050	26-27	~61	~92	~75	43-44	**0.43**	**0.29**	**0.47**	**0.58***
NHMW nn	1070	32	61	101	79	50	0.52	0.32	0.49	0.63
GPIT 1645/1	1085	30	60	101	80	48/49	0.50	0.30	0.48	0.61
SMNS 51826	~1150	29	-	-	76	-	-	-	-	-
SMNS 51106	1150	28	57	-	74	-	0.49	-	-	-
SMNS 50164	1150	33	75	105	74/76	55	0.44	0.31	**0.52**	**0.73**
Swedish Mus. nn	1150	34	65	103	81	-	0.52	0.33	-	-
NHMUK R10087	1285	36	-	112	90	57	-	0.32	0.51	0.63
MNHU 1920.16	1400	38	80	133	99	65	0.475	**0.29**	0.49	0.66
MNHU 1977.21	1690	42	84	142	110+?	70	0.50	0.30	0.49	-

A) Gracile postorbital with elongated frontal process;

B) Premaxilla not participating in the ventral margin of the external nares;

C) Wing metacarpal IV [*sic*] small, about 40% and 30% the length of the humerus and ulna, respectively;

D) Femur small, about half the length of the ulna and the first wing phalanx.

Autapomorphy (A)

This feature cannot be used to separate MPUM 6009 from MFSN 1797 (holotype of *Carniadactylus rosenfeldi*), because the postorbitals are not preserved or exposed in the latter (Dalla Vecchia 2009a), thus their shape is unknown. The holotype of *Austriadraco dallavecchiai* has a gracile postorbital, too (Fig. 3B). Wellnhofer (2003) did not mention it in his description of the specimen and Kellner (2015) followed the description by Wellnhofer (2003) without substantial improvements, thus he ignored this element. A similarly slender postorbital occurs also in MFSN 21545 (pers. obs.), which represents a still unnamed taxon with multicusped teeth from the Norian Dolomia di Forni Formation of NE Italy (Dalla Vecchia 2010, 2014) that is clearly distinct from MPUM 6009. As noted above, the processes of the postorbital of MPUM 6009 are all broken or covered by other bones, thus the relative elongation of the frontal process cannot be reliably established. In the postorbital of the holotype of *Austriadraco dallavecchiai* (Fig. 3B), all of the processes seem to be broken distally and the preserved part of the frontal process is as long as the squamosal process. In MFSN 21545, the frontal and squamosal processes are concealed distally by other bones, but the frontal process appears to be longer than the squamosal process. MPUM 6009 (Fig. 3A), the holotype of *Austriadraco dallavecchiai* (Fig. 3B) and MFSN 21545 share a slender and recurved jugal process. Also *Campylognathoides liasicus* has a gracile postorbital with an elongated frontal process (the frontal process is much longer than the squamosal process) as it can be observed in the complete right postorbital of SMNS 11879 (Fig. 3C; see also Padian 2008b: fig. 6). Therefore, the gracile postorbital with elongated frontal process is not autapomorphic of MPUM 6009.

Autapomorphy (B)

This feature cannot be used to separate MPUM 6009 from MFSN 1797 because neither premaxillae nor maxillae are preserved in MFSN 1797. Furthermore, this character is not autapomorphic of MPUM 6009 because it occurs in '*Raeticodactylus*' *filisurensis* (see Stecher, 2008, fig. 6) and probably also in *Dorygnathus banthensis* (see Arthaber 1921: 400; Wellnhofer 1978: fig. 2; Sangster 2003: fig. 2.2B; Padian 2008a: fig. 18; Ősi et al. 2010: fig. 3), *Scaphognathus crassirostris* (see Arthaber 1921: 406; Wellnhofer 1975b: fig. 34a and 36b; Unwin 2003: fig. 9c; Sangster 2003: fig. 2.2D), *Angustinaripterus* (see Sangster 2003: fig. 2.2E) and *Rhamphorhynchus muensteri* (see Arthaber 1921: 408; Wellnhofer 1978: fig. 2; Unwin 2003: fig. 9d).

Autapomorphy (C)

The wing metacarpal of the immature MCSNB 8950 (which is similar in size to MPUM 6009) is 35% the length of the humerus. The wing metacarpal is 43% the length of the humerus in the small specimen of *Austriadactylus cristatus* (MGC 332466), in the immature specimen MCSNB 3359 of *Peteinosaurus zambellii* and in the holotype (NHMUK R 1034) and smaller specimen (GSM 1546) of the earliest Jurassic *Dimorphodon macronyx* (see Sangster 2003). The wing metacarpal is 27, 31.4 and 32% the length of the ulna in MCSNB 8950, the small specimen of *Austriadactylus cristatus* (MGC 332466) and the holotype of *Dimorphodon macronyx*, respectively. Thus, the comparatively short wing metacarpal is not autapomorphic for MPUM 6009.

Wing metacarpal/humerus ratios are 0.50 and 0.39 (a difference of 28%) in MFSN 1797 and MPUM 6009, respectively. Wing metacarpal/ulna ratios are 0.38 and 0.29 (31%) in MFSN 1797 and MPUM 6009, respectively. As noted by Padian & Wild (1993: 67), the wing metacarpal is "the least accurate indicator of length ratios". Wing metacarpal/humerus and wing metacarpal/ulna ratios range 0.43-0.57 (n = 22; 33%) and 0.29-0.37 (n = 20; 28%), respectively, in a sample of the lower Toarcian (Lias ε II/1-6) *Dorygnathus banthensis* from southern Germany and France, with wing span ranging 665-1690 mm (Padian 2008a; see Tab. 2). Lias ε II/1-6 spans about from the middle of the Semicelatum to the lower third of the Elegans Ammonoid Subzones (Riegraf et al. 1984), which could correspond to less than 700 ky (Ogg et al. 2008), which is a relatively short span in geological time. There is no evident trend of the ratios related to wing span increase (Tab. 2), therefore the variability is probably not ontogenetic but intraspecific. The variability between ratios of MFSN 1797 and MPUM 6009 falls within the intraspecific variability observed in *Dorygnathus banthensis*.

A larger sample is available for the non-pterodactyloid *Rhamphorhynchus* (Wellnhofer 1975b) from the Solnhofen Limestone (Altmühltal Formation; Upper Jurassic, Malm Zeta 2; Riedense-Rueppelianus Ammonoid Subzones of the Tethyan realm, Schweigert 2007) of southern Germany. The stratigraphic interval corresponds to the lower 2/3 of the Hybonotum Zone, which is the first of the five Ammonoid Zones composing the Tithonian (Schweigert 2007); the Hybonotum Zone could represent about 1 million years (Ogg et al. 2008), thus the *Rhamphorhynchus* sample probably span less than one million years. All *Rhamphorhynchus* specimens were referred to a single species, *R. muensteri*, by Bennett (1995). They include juvenile, subadult and adult individuals with skull ranging 31-191.5 mm and are grouped into small, medium and large size classes (Bennett 1995; see SI, Tab. 1-3). Wing metacarpal/humerus and wing metacarpal/radius ratios (Wellnhofer 1975b does not report ulna length, but that is irrelevant here) range 0.34-0.79 (n = 68; 132%) and 0.22-0.48 (n = 71; 118%), respectively. There is no evident trend of the ratios related to body size increase (all of the variability occurs within the small-sized individuals; SI, Tab. 4), therefore the variability is probably not ontogenetic, but intraspecific. The variability between ratios of MFSN 1797 and MPUM 6009 falls within the intraspecific variability observed within *R. muensteri.*

A positive allometric growth of the wing metacarpal and a negative allometric growth of humerus and radius-ulna were reported by Codorniù & Chiappe (2004) in the South American pterodactyloid *Pterodaustro guinazui.*

Therefore, the wing metacarpal of MCSNB 6009 is not apomorphically small and the differences between wing metacarpal/humerus and wing metacarpal/radius ratios of MPUM 6009 and the holotype of *Carniadactylus rosenfeldi* can be due to intraspecific variability.

Autapomorphy (D)

The femur of MPUM 6009 is 53% or 51% (depending on its estimated length by Wild 1979 or Dalla Vecchia 2014) the length of ulna, but this percentage could be slightly higher, as explained above. The femur is 58, 56 and 53% the length of the ulna in MCSNB 8950, MCSNB 2887 (which has a pteroid unlike that of MPUM 6009), and in the holotype of '*Raeticodactylus*' *filisurensis*.

The femur is 51% or 49% (depending on its estimated length by Wild 1979 or Dalla Vecchia 2014) the length of the wing phalanx 1 in MPUM 6009. The femur is 49.5, 51 and 53% the length of the wing phalanx 1 in the small specimen of *Austriadactylus cristatus* (MGC 332466), the holotype of *Eudimorphodon ranzii* (using the estimate length of wing phalanx 1 by Wild, 1979) and MCSNB 2887, respectively. Thus, femur about half the length of the ulna and the first wing phalanx are not uniquely shared by MPUM 6009.

Femur/ulna ratio is 0.53 or 0.51 and femur/wing phalanx 1 ratios is 0.49 or 0.51 in MPUM 6009 (depending on its estimated length by Wild 1979 or Dalla Vecchia 2014), but these ratios could be slightly higher, as explained above. In MFSN 1797, femur/ulna and femur/wing phalanx 1 ratios are 0.67 (26% or 31% higher than that of MPUM 6009) and 0.58 (14% or 18% higher than that of MPUM 6009), respectively. Femur/ulna and femur/wing phalanx 1 ratios range 0.47-0.52 (n = 16; 11%) and 0.58-0.73 (n = 16; 26%) in the sample of *Dorygnathus banthensis* (Tab. 2). There is no evident trend of the ratios related to wing span increase, thus the variability is probably intraspecific, not ontogenetic. The difference between ratios of MFSN 1797 and MPUM 6009 falls within the intraspecific variability observed in *Dorygnathus banthensis* as for femur/wing phalanx 1 ratio, but it is higher for femur/ulna ratio. Femur/radius and femur/wing phalanx 1 ratios range 0.41-0.56 (n = 49; 37%) and 0.26-0.45 (n = 53; 73%), respectively, in the sample of *R. muensteri* mentioned above (see SI, Tabs. 1-3). There is no evident trend of the ratios related to body size increase; the whole range of variability occurs within the small-sized individuals and the mean of femur/radius ratio is practically the same among the three size classes (see SI, Tab. 4). Thus, variability is probably intraspecific, not ontogenetic, and the difference between ratios of MFSN 1797 and MPUM 6009 falls within the intraspecific variability observed in *R. muensteri.*

Therefore, the femur of MCSNB 6009 is not apomorphically small and its length with respect to the ulna and first wing phalanx does not support the taxonomic separation between MPUM 6009 and the holotype of *Carniadactylus rosenfeldi.*

Further distinctive features of *Bergamodactylus wildi*

According to Kellner (2015: 680), MPUM 6009 can be further distinguished from other "campylognathoidids" by a combination of characters that are listed and discussed below.

Character (A): "surangular dorsal process of moderate size (smaller than in *Carniadactylus rosenfeldi* but larger than in *Eudimorphodon ranzii*)". This is not the case. In the interpretation by Wild (1979: fig. 2b), the surangular dorsal process (= coronoid process) of MPUM 6009 has the same shape and size as that of MFSN 1797. The drawing of Kellner (2015: fig. 5B) is incorrect because it depicts the broken apical part of the process as if it were its actual apex. Nonetheless, the mandibular ramus is apomorphically high below the apex of the process in both MPUM 6009 and MFSN 1797 (Dalla Vecchia 2009a: 60 and fig. 11).

Character (B): "mandibular rami deeper than in *Carniadactylus*". The anterior two-thirds of the mandibular rami of MFSN 1797 are not preserved (Dalla Vecchia 2009a: fig. 2). The partial reconstruction of the right mandibular ramus of MFSN 1797 in Dalla Vecchia (2009a: fig. 11C) is tentative, based on the impression of the ramus remaining in the slab. Therefore, the drawing of the dentary portion of the ramus could appear slightly slimmer than the actual ramus because of perspective. In any case, the difference in depth of the mandibular rami of MPUM 6009 and MFSN 1797 is not substantial (see Dalla Vecchia 2014: fig. 4.1.98).

Character (C): "lack of enlarged maxillary teeth on the middle region of the maxillae (unknown in *Carniadactylus*)". As noted by Kellner himself, this feature cannot be used to distinguish between MPUM 6009 and MFSN 1797. Also the holotype of *Arcticodactylus cromptonellus*, MFSN 21545, *Campylognathoides* and all Jurassic pterosaurs lack enlarged maxillary teeth on the middle region of the maxillae.

Character (D): "dentition of the lower jaw extending more posteriorly than in *Carniadactylus*". This is an assumption based on the reconstruction of the dentition of MPUM 6009 by Wild (1979). According to the description in this paper (Fig. 2B), the most distal indisputable mandibular tooth is the penultimate one in figure 2a of Wild (1979). No further tooth remains can be identified distal to that tooth along the mandibular ramus. Thus, the position of the last mandibular tooth is more distant from the apical part of the surangular dorsal process than previously supposed. Furthermore, the upper margin of the mandibular ramus of MFSN 1797 just rostral to the surangular dorsal process is covered by a piece of matrix (see Dalla Vecchia 2009a: fig. 2A) that was not removed because it preserves some scientifically relevant conodonts. Teeth or alveoli could be preserved below that fragment. Thus, the posterior extent of the mandibular dentition is not a reliable feature to distinguish MPUM 6009 from MFSN 1797 taxonomically.

Character (E): "18 and 17 teeth on each side of the upper and lower jaw, respectively". This feature cannot be used to distinguish between MPUM 6009 and MFSN 1797, because the tooth count is unknown in the latter. No universal pattern exists for tooth count change through growth in diapsids (Brown et al. 2015). Therefore, tooth count should be used to diagnose a diapsid species only when a statistically adequate sample is available and the pattern for tooth count change through growth in related species is known (Brown et al. 2015). This has yet to be established for Triassic pterosaurs.

Character (F): "pteroid rod-like with a marked bend, having the proximal part shorter than in *Carniadactylus*". Small intraspecific differences in the morphology and proportions of the pteroids are expected. This is the case of *Rhamphorhynchus muensteri*: the pteroids are rod-like in all specimens, but they can be more or less elongated, slender and straight to gently curved (see Kuhn 1967: figs. 18 (12-13) and 21; Wellnhofer 1975a: fig. 12a-b; 1975b: figs. 19 and 21; pers. obs.). Relative size of the pteroid seems to increase with absolute size of the individual, i.e., small individuals have comparatively shorter pteroids (see Wellnhofer 1975a: fig. 12a-b). Thus, the minor difference between the pteroids of MPUM 6009 and MFSN 1797 probably falls within the intraspecific variability and perhaps the ontogenetic variability in particular. As underlined by Dalla Vecchia (2009a, 2014), the important point is that pteroids of MPUM 6009 and MFSN 1797 have a similar overall shape and that shape is not shared with other pterosaur taxa.

Character (G): "deltopectoral crest of the humerus comparatively more extended down the humerus shaft (this would not be expected in individuals of similar ontogenetic stages)". The deltopectoral crest extends along 28% and 23% (a difference of 22%) of the total humerus length in MPUM 6009 and MFSN 1797, respectively. Kellner (2015) considered that two individuals of the same age should have the same extension of the crest down the humerus shaft. However, they probably do not have the same ontogenetic age, as shown by the nonfusion of the proximal carpals in MPUM 6009 and their fusion in MFSN 1797. A more striking difference between the two specimens is in the total length : maximum proximal width of humerus ratio, which was unnoticed by Kellner (2015). The ratio is about 2.80 in MPUM 6009, while it is about 3.40 in the right humerus of MFSN 1797. i.e., the proximal part of humerus is proportionally less expanded in MFSN 1797. However, this ratio is variable even within the same individual pterosaur: the ratio of the left humerus is about 18% higher than the ratio of the right humerus in the holotype of *E. ranzii* MCSNB 2888 (Dalla Vecchia 2009a). The deltopectoral crest varied in shape with age in some taxa (e.g., *Rhamphorhynchus*, Wellnhofer 1975a; *Pterodaustro guinazui*, Codorniù & Chiappe 2004), becoming larger with respect to the total humeral length. Consequently, the humerus became stockier with age in *Rhamphorhynchus* and *Pterodaustro guinazui*, while the opposite is true for MPUM 6009 and MFSN 1797. However, the humerus of the holotype of '*Raeticodactylus*' *filisurensis* (BNM 14524; the largest partial skeleton of a Triassic pterosaur; see Tab. 1) has a very slender shaft, a deltopectoral crest that is comparatively short along the humerus respect to the total humerus length (Stecher 2008: fig. 10) and its total length : maximum proximal width of humerus ratio is 3.60. It is difficult to imagine a more slender humerus for a juvenile of '*Raeticodactylus*' *filisurensis*. Therefore, exceptions existed to the ontogenetic trend toward a stockier humerus in pterosaurs. Indeed, the humeri of MPUM 6009 and MFSN 1797 appear to be slightly different from each other and this might be taxonomically significative. However, the poor state of preservation of the crushed right humerus of MFSN 1797 (see Dalla Vecchia 2014: fig. 4.1.111; the left humerus is covered by other skeletal elements) suggests that a more cautious approach should be adopted when using those small differences to erect a new taxon. The possibility that small morphological differences could be due to intraspecific variability (individual, ontogenetic and sexual; see Verdù et al. 2015) cannot be discarded in a sample of only two individuals. Comparison between the ontogenetic differences within a sample of a highly derived tapejarid pterodactyloid taxon that lived in a Cretaceous desert and those of a primitive pterosaur that lived over 80 million years earlier in a coastal marine environment, as done by Kellner (2015: 681-682), should be carefully considered.

Ontogeny and size were also used to justify the taxonomic separation between MPUM 6009 and MFSN 1797. According to Kellner (2015), the different anatomical features and size between the two specimens cannot be ontogenetic because MPUM 6009 and MFSN 1797 belong to the same ontogenetic stage (OS5; considered in this case by Kellner 2015: 50 as "adult or "older" [*sic*] subadult"). However, the features used to establish the ontogenetic stage OS5 are not universally valid or cannot be observed in those specimens. Fusion of the proximal tarsals to tibia, fibula to tibia, pubis and ischium into a puboischiadic plate, and sacral vertebrae into a synsacrum and the presence of a suture between ilium and puboischiadic plate are unknown in MPUM 6009. The proximal tarsals are fused to tibia in MFSN 1797 and the suture is obliterated (contra Kellner 2015). A narrow transverse band of bone with a slightly different grain with respect the surrounding bone can be seen in the zone of tibia-proximal tarsal fusion only under the binocular microscope with high magnification and submerging the distal end of the tibiotarsus in alcohol. Instead, the suture is still visible in other Triassic specimens like the holotype of *Peteinosaurus zambellii* and MCSNB 3496 and even in the holotype of *Austriadraco dallavecchiai* (Fig 1A). MPUM 6009 is not a very young individual (scapula and coracoid are fused and the extensor tendon process is fused to wing phalanx 1), but the lack of fusion of the proximal carpals suggests that it is more immature than MFSN 1797.

Body size differences between MPUM 6009 and MFSN 1797 (humerus and ulna of MPUM 6009 are 63% and 65% the length of those of MFSN 1797, respectively) are indicative of taxonomic separation according Kellner (2015) because the two specimens belong to the same ontogenetic stage and should have similar sizes, if they are conspecific. However, MPUM 6009 is more immature than MFSN 1797, thus size difference is expected. Anyway, it is worth noting that a certain range of body size variability is expected among individuals at a same ontogenetic stage within a sauropsid population. As noted by Sebens (1987: 371) "Among the terrestrial vertebrates, significant differences in adult size may occur between populations of a single species...These size differences are caused by some amount of genetic differentiation between populations and by plastic ontogenetic responses to local conditions". Caution in using body size as a proxy for age is suggested also by the fossil record. Within the large sample of the hadrosaurid dinosaur *Maiasaura peeblesorum* (all specimens are from a single bone bed), some individuals considered to have been subadult when they died on histological evidence are larger than other individuals that are considered to be adult on the same basis (Woodward et al. 2015). A sample of the latest Cretaceous pterodactyloid *Bakonydraco galaczi* (all specimens of the sample are from a same stratigraphic horizon and locality) indicates high intraspecific variability in body size of histologically adult individuals (Prondvai et al. 2014). Therefore, individual maturity or the relative ontogenetic stage cannot be hypothesized only on the basis of absolute body size (as widely noted in literature, e.g., Andrews 1982; Bennett 1993; Woodward et al. 2011), although there is a general trend of increase in body size with age within a population.

MPUM 6009 and MFSN 1797 are evidently from different populations (Dalla Vecchia 2009a), thus size differences are not surprising, even if they died at the same ontogenetic stage. As noted by Sebens (1987), body size differences among individuals of a same species at the same ontogenetic stage may be a product of ecological factors in living terrestrial vertebrates. For example, in insular settings like those where probably nearly all the Triassic pterosaurs lived (cf. Jadoul et al. 1994; Gaetani et al. 2000), adult body size variability may be related to island area (e.g., Burness et al. 2001, Wikelski 2005) and changes in food availability (e.g., Wikelski 2005). The high intraspecific variability in adult body size within the sample of *Bakonydraco galaczi* (which lived on an island of the Late Cretaceous European Archipelago) was explained by the high degree of developmental plasticity related to a variation of the environment during the development

(Prondvai et al. 2014). A wide range of intraspecific adult size was considered to be relatively frequent in the Pterosauria by Prondvai et al. (2014).

Therefore, body size should not be a major criterion in the erection of a new taxon, unless supported by other robust evidence.

Geographic and stratigraphic provenances were also used by Kellner (2015) to justify the separation of MPUM 6009 from *Carniadactylus rosenfeldi*. The different geographic and stratigraphic provenance of MPUM 6009 and MFSN 1797 were stressed by Dalla Vecchia (2009a: 177), who wrote that MPUM 6009 and MFSN 1797 might "as an alternative ...belong to closely related but separate species, also because they lived in different localities in an insular palaeogeographic context" and concluded "this could be ascertained only with new material". As new material has not been found in the meantime, the matter remains hypothetical. MPUM 6009 and MFSN 1797 were found in localities that are now about 250 km apart (see Dalla Vecchia 2013: fig. 3) and they were on that order of distance also during the latest Triassic. Both localities were located on the shallow carbonate platform along the eastern margin of Pangaea far from a continental land mass (Dalla Vecchia 2014: figs 3.1.1-4), where the only emergent areas were probably low lying islands (Dalla Vecchia 2014). Living bird species can be endemic of each island of an archipelago (e.g., the famous Darwin's 'finches' of the Galápagos), but many species populate more than a single island. Sometimes, bird species are spread over wide geographical areas (for example, the columbid *Ptilinopus porphyraceous* lives in the Caroline, Marshall, Tonga, Fiji, Niue and Samoa islands; Baptista et al. 1997). Being flying diapsids, birds are probably the most appropriate candidates for comparison with pterosaurs employing the extant phylogenetic bracket principle (Witmer 1995). However, flying synapsids (Chiroptera, having wing patagia like pterosaurs, although with a substantially different structure) can also have wide geographical ranges (see for example, the continental and insular range of the Large Flying Fox, *Pteropus vampyrus*; Simmons 2005). Thus, a distance of a few hundred kilometres is not sufficient ground for taxonomic separation of MPUM 6009 and MFSN 1797 on palaeogeographic bases. Both specimens were deposited into intraplatform marine anoxic basins, although those basins were separated and their deposits received distinct formational names (Dalla Vecchia 2014). MPUM 6009 was collected from the upper part of the Calcare di Zorzino Formation that is referred to the upper part of the middle Norian (Alaunian 3) based on its palynomorph content (Jadoul et al. 1994), while MFSN 1797 comes from a level of the Dolomia di Forni Formation that was dated to the latest middle Norian too, but based on its conodont content (Roghi et al. 1995; Dalla Vecchia 2014). However, the biostratigraphic scales based on palynomorphs and conodonts cannot be correlated and the resolution of the Triassic biostratigraphy based on those microfossils is considerably lower than the Jurassic ammonoid biostratigraphy mentioned above for the pterosaurs from the Lower and Upper Jurassic of Germany. High resolution lithostratigraphic correlation between the Calcare di Zorzino and Dolomia di Forni formations is not possible. This means that MPUM 6009 and MFSN 1797 could be coeval as well as separated by several hundred thousand years. Thus, stratigraphic provenance is insufficient to prove per se the taxonomic separation of the two specimens.

CONCLUSIONS

Kellner's six ontogenetic stages are an oversimplification mixing ontogenetic features of different taxa that probably had distinct growth patterns. Finding commonality across all pterosaurs is impossible, because there is much variation in pterosaur ontogeny and the available sample is highly restricted.

The anatomical differences between MPUM 6009 and MFSN 1797 are too small to support the erection a new genus for MPUM 6009. MPUM 6009 and MFSN 1797 share at least four apomorphies (not just "some anatomical similarities" as reported by Kellner 2015: 686). The erection of a new genus based just on a few minor differences (a humerus slightly different in proportions, the more elongate proximal part of the pteroid; a proportionally smaller femur) within a sample of only two specimens, ignoring the shared apomorphic features, is hazardous. The risk is to use the normal intraspecific variability within a population and within distinct populations of a same species to create a new taxon. If used systematically, this procedure would produce a plethora of poorly supported taxa, inflating artificially the taxonomic diversity. The uniquely shared characters should be considered more important than minor differences in establishing taxonomic relationships. The erection of a new taxon does not appear as a better solution than retaining MPUM 6009 in *Carniadactylus rosenfeldi*, therefore it is here considered to be a specimen of this species and *Bergamodactylus wildi* must be regarded as a junior synonym until new and more solid evidence to the contrary is available.

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