

Feeding related characters in basal pterosaurs: implications for jaw mechanism, dental function and diet

RH: Feeding related characters in pterosaurs

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A comparative study of various feeding related features in basal pterosaurs reveals a significant change in feeding strategies during the early evolutionary history of the group. These features are related to the skull architecture (e.g. quadrate morphology and orientation, jaw joint), dentition (e.g. crown morphology, wear patterns), reconstructed adductor musculature, and postcranium. The most basal pterosaurs (*Preondactylus*, dimorphodontids and anurognathids) were small bodied animals with a wing span no greater than 1.5 m, a relatively short, lightly constructed skull, straight mandibles with a large gape, sharply pointed teeth and well developed external adductors. The absence of extended tooth wear excludes complex oral food processing and indicates that jaw closure was simply orthal. Features of these basalmost forms indicate a predominantly insectivorous diet. Among stratigraphically older but more derived forms (*Eudimorphodon*, *Carniadactylus*, *Caviramus*) complex, multicusped teeth allowed the consumption of a wider variety of prey via a more effective form of food processing. This is supported by heavy dental wear in all forms with multicusped teeth. Typical piscivorous forms occurred no earlier than the Early Jurassic, and are characterized by widely spaced, enlarged procumbent teeth forming a fish grab and an anteriorly inclined quadrate that permitted only a relatively small gape. In addition, the skull became more elongate and body size

increased. Besides the dominance of piscivory, dental morphology and the scarcity of tooth wear reflect accidental dental occlusion that could have been caused by the capturing or seasonal consumption of harder food items.

Key words: basal pterosaurs, heterodonty, dental wear, insectivory, piscivory

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Pterosaurs are the only known group of extinct tetrapods where several basal forms possessed complex, heterodont dentition while the last forms were edentulous (Wellnhofer 1991, Unwin 2003a, Fastnacht 2005). This irreversible transformation must have been controlled by constraints generated by the combination of various ecological parameters (e.g. climate, vegetation, other faunal elements in the ecosystem). During the 160 Mya of their evolution, pterosaur dentition varied dramatically among different taxa reflecting the appearance of distinct, specialized feeding techniques. Basal forms from the Late Triassic (*Preondactylus*, *Austriadactylus*, *Eudimorphodon*, *Caviramus*, *Carniadactylus*) often had strongly heterodont dentitions with a large number of teeth including conical, slightly curved premaxillary and anterior dentary teeth and multicusped or serrated posterior teeth that often bore an increasing of the number of cusps towards the back of the jaw (Wild 1978, 1994, Jenkins *et al.* 2001, Dalla Vecchia 1995, 2003a, b, 2004, 2009, Dalla Vecchia *et al.* 2002, Fastnacht 2005, Stecher 2008). The degree of heterodonty decreased in more derived forms of long tailed pterosaurs and disappears entirely in early pterodactyloids (some differences in the size of the anterior teeth in ornithocheirids, some gnathosaurines and *Cearadactylus* are known, but this is not homologous with that seen in Triassic forms, Unwin 2003a). As the closely spaced, short, multicusped teeth of basalmost pterosaurs became more elongate, recurved and more widely-spaced, tooth number was also reduced. Some forms, however, reversed this trend by developing extraordinary numbers of long, slender teeth (e.g. *Pterodaustro*, Bonaparte 1970; *Ctenochasma*, Jouve 2004, *Ganthsaurus*, Meyer 1834). The most derived forms (Pteranodontia and Azhdarchoidea) became edentulous with only a rhamphotecca covering a significant part of the elongated symphysis of their jaws was present (Frey *et al.* 2003a). This great variability in the dental apparatus of pterosaurs presumably reflects adaptations to various ecological niches and the

using of numerous different feeding strategies (Ósi 2009).

All pterosaurs used their teeth for capturing prey, with some using their teeth in an advanced manner by filtering small organisms from water or crushing hard-shelled food items (Wellnhofer 1991, Unwin 2006). Most of them, however, did not use active food processing including precise dental occlusion to cut or crush food. This unique feature appears to have been largely restricted to some basal forms possessing a heterodont dentition and, in some cases, was associated with a complex jaw mechanism. Some later pterodactyloids possessed unusual dentition such as *Istiodactylus* with the interlocked, labiolingually flattened teeth and razor edges. It was suggested that this form was able to cut and remove chunks of meat from prey and carcasses (Howse et al. 2001). Developed oral food processing with precisely occluding teeth, however, did not occur in *Istiodactylus*.

In the present study I compare the dentition of basal heterodont pterosaurs and on the basis of tooth morphology and dental wear pattern analysis I reconstruct the process of dental occlusion and jaw mechanism. Based on earlier reconstructions of cranial adductor musculature for various pterosaur taxa, possible inferences of skull structure on the cranial adductor musculature for these basal forms is discussed. When placed into a phylogenetic context the results demonstrate diversity of diet preferences among basal pterosaurs revealed by changes of feeding related features.

Institutional Abbreviations— **BMNH**, Natural History Museum, London, England; **BNM**, Bündner Naturmuseum, Chur, Switzerland; **MCSNB**, Museo Civico di Scienze Naturali di Bergamo, Italy; **MNHN**, Musée National d'Histoire Naturelle, Paris, France); **MPUM**, Dipartimento of Scienze della Terra dell'Università di Milano, Italy; **MTM**, Hungarian Natural History Museum, Budapest, Hungary; **PIMUZ**, Paläontologisches

Institut und Museum, University of Zürich, Zürich, Switzerland. SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

MATERIAL AND METHODS

This study is based mainly on specimens of Late Triassic pterosaurs, including *Eudimorphodon ranzii* Zambelli, 1973 (MCSNB 2888); *Carniadactylus rosenfeldi* Dalla Vecchia, 2009 (MPUM 6009); *Eudimorphodon cromptonellus* Jenkins, Shubin, Gatesy and Padian, 2001; *Peteinosaurus zambellii* Wild, 1978 (MCSNB 2886), *Preondactylus buffarinii* Wild, 1984; *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf and Reitner, 2002; *Caviramus schesaplanensis* Fröbisch and Fröbisch, 2006 (PIMUZ A/III 1225), and ‘*Raeticodactylus filisurenensis*’ Stecher, 2008 (BNM 14524). In accordance with Dalla Vecchia (2009), I consider *Raeticodactylus* to be a junior synonym of *Caviramus* based on the following interpretation of anatomical differences between the two taxa listed by Stecher (2008):

- 1) *Absence of quinticusped teeth in Caviramus*. Only one complete and one broken tooth is known in this genus, thus the presence of quinticusped teeth in the whole tooth row can neither be supported nor excluded.
- 2) *Presence of seven cup-shaped structures on the anterior part of the mandible for attachment of the rhamphoteca*. The detailed morphology of the frequently rugose surface on the anterior part of the jaws covered by a fleshy or horny beak (Fröbisch & Fröbisch 2006) can vary considerably even in one species and also during ontogeny (Frey *et al.* 2003a).

- 3) *In contrast to Caviramus, Raeticodactylus possesses a keeled, concave lower edge of the mandible.* The lower mandibular edge of *Caviramus* is indeed not as concave as seen in *Raeticodactylus*. However, at its anterior part a slight dorsoventral extension of the mandible indicates a weakly developed ventral mandibular crest was present. This suggests that this animal also possessed a slightly keeled mandible that was likely to be morphologically variable throughout ontogeny (Frey *et al.* 2003a).
- 4) *Caviramus has oval foramina located lateral to every 2nd tooth alveolus in contrast to those of every 3rd tooth alveolus in Raeticodactylus.* I suggest that, as with tooth count changes during ontogeny (Edmund 1969), the foramina transpassing nerves and blood vessels may also change with ontogeny.

These features further suggest that the fragmentary jaw of *Caviramus* represents a **skeletally** immature specimen of *Raeticodactylus*. Its ontogenetic status, however, cannot be entirely ascertained because none of the size-independent criteria listed by Bennett (1993) are **preserved**.

In addition to Triassic specimens, some Jurassic and Cretaceous forms such as *Campylognathoides liasicus* (Quenstedt 1858) (SMNS 18879, 50735), *Dimorphodon macronyx* (Buckland 1829) (NHM 43486-7, 41212-13), *Dorygnathus banthensis* (Theodori 1830) (SMNS 50184, 50914, uncatalogued specimen), as well as *Scaphognathus crassirostris* (Goldfuss 1831), (SMNS 59395), *Anurognathus ammoni* Döderlein, 1923 (Bennett 2007), and *Ornithocheirus mesembrinus* (Wellnhofer 1987) were used in this study for comparative purposes. Inventory numbers refer to those specimens **studied by the author** and in most cases casts have been taken from the teeth.

For comparison of the pterosaur teeth with those of extant lizards the following

specimens of the Osteological and Comparative Anatomical Collection of the Natural History Museum of Paris were used: *Iguana iguana* (MNHN 1974.129) *Ameiva* (MNHN 1887.875) *Ctenosaura acanthura* (MNHN 1909.524), *Iguana delicatissima* (MNHN 1941.215), *Cyclura cornuta* (MNHN 1964.144) and *Macroscincus coctei* (MNHN 1907.344).

For the dental wear pattern analysis in pterosaurs, the surfaces of in situ teeth were studied along with the morphology of the wear facet and macrowear and microwear patterns. Macrowear is defined here as a wear feature larger than 0.5 mm and microwear features are below this size. Wear patterns are represented by scratches and pits. For mapping details of the wear features a Hitachi S-2360N scanning electron microscope (SEM) was used. High resolution molds were taken from the teeth and prepared following procedures described by Grine (1986) for hominids. Specimens were first cleaned with cotton swabs soaked with ethyl alcohol, after which moulds were made using Coltene President Jet Regular (polysiloxane vinyl) impression material, of which casts were made with EPO-TEK 301 epoxy resin. This technique allows the reproduction of features with a resolution of a fraction of a micron (Teaford & Oyen 1989; El-Zaatari *et al.* 2005). After light microscopy examination, casts of specimens separated for further study were sputter-coated with approximately 5 nm of gold, and examined using SEM at 20 kV.

Hindlimbs of basal pterosaurs were filigrant indicating poor running ability that was further hampered by their flight membranes (Unwin 2006). New remains indicate a plantigrade stance and scansorial or perhaps arboreal habits rather than proficient terrestrial locomotion (Unwin 1988, Clark *et al.* 1998). Thus, I only discuss postcranial anatomy in those taxa where some aspects of the postcranial skeleton are unique and relevant to understand the feeding mechanism of the animal (see e.g. Anurognathidae).

A phylogenetic analysis was performed based on the taxon–character matrix of Unwin (2003b). *Caviramus* (based on Stecher 2008) and *Carniadactylus* (Dalla Vecchia 2009), two recently identified heterodont basal forms **are added** to the taxon list. The data matrix (53 characters, 18 taxa) was analyzed using the heuristic search algorithm of PAUP for Windows, version 4.0, Beta 10 (Swofford 2000). All characters have been treated as unordered and unweighted. Character state transformations were DELTRAN optimized. The analysis produced 13 most parsimonous trees with a length of 86 (CI=0.662, HI=0.337, RI=0.849, RC=0.563).

RESULTS

Feeding-related characters in basal heterodont pterosaurs

Skull and jaws

Compared to those of more derived pterosaurs, the skulls of basal **pterosaurs** are relatively short anteroposteriorly and high dorsoventrally, a shape that correlates well with a relatively high narial opening (Unwin 2003a). *Preondactylus* (MFSN 1770) has a lightly built skull which generally **appears to be** similar to that of *Campylognathoides* (Wild 1984, Dalla Vecchia 1998, **but see Unwin 2003 for a newer interpretation**). The disarticulated rostral elements indicate the lack of strong bony ossification in this region: this, however, could also be related to the skeletal immaturity of the animal (Dalla Vecchia 2003a). The quadrate orientation is ambiguous and the lower jaw is straight and weak (Fig. 1A).

Dimorphodon macronyx has a relatively large, high and short skull with a dorsally convex rostral margin and large, dorsoventrally-high external naris and antorbital fenestra

(Owen 1870, Wellnhofer 1978, Padian 1983). Laterally, the margins of these cranial openings formed by various processes of the rostral bones are thin. The occipital region and the quadrate are nearly vertically directed indicating a high angled orientation of the external adductor muscles. The proximal left quadrate of NHM 41212-13 shows a well-developed condylus cephalicus. This **articulation** is slightly elongated mediolaterally and well-expanded anteroventral–ventrally indicating a flexible joint with the squamosum and suggesting a possible streptostyly similar to *Eudimorphodon* (Wild 1978, see below). If *Dimorphodon* was streptostylic then the quadrate must have had ball joint or sliding contacts with its connecting bones, such as dorsally with the **squamosal**, medioventrally with the pterygoid and lateroventrally with the quadratojugal or, if the latter is fused with the quadrate, a sliding contact should have appeared between the jugal–quadratojugal. Due to the poor preservation of all *Dimorphodon* specimens possessing a skull (e.g. NHM 41212-13, NHM R 1035), however, only the jugal–quadratojugal connection can be determined as strongly ossified.

The lower jaw of *Dimorphodon*, especially the symphyseal region and posterior part, is deeper dorsoventrally (Fig. 1G) than that of *Preondactylus*. *Peteinosaurus*, the only other known dimorphodontid genus, is solely known by two fragmentary mandibles (MCSNB 2886; Wild 1978). Here, the dentary is straight and elongate (Fig. 1E) **as in** *Preondactylus*, but the postdentary part is more elevated.

The skull of anurognathids is unique among pterosaurs in being wider than long, box-like, and it is extremely lightly constructed (Wellnhofer 1975, Unwin *et al.* 2000, Dalla Vecchia 2002, Bennett 2007). Except for the skull roof, most cranial elements are rod-like with slender contacts to each other. In the very short skull, the quadrate is oriented

vertically (Bennett 2007). Similarly to *Preondactylus* and dimorphodontids, the lower jaw is straight and slender and without developed coronoid process (Fig. 1C).

Except for the cranial crest, the general shape of the skull of *Austriadactylus* is similar to that of *Eudimorphodon*. The orientation of the quadrate is uncertain (contra Fastnacht 2005) because the elements of the temporal region (e.g. squamosal, quadrate, lateral temporal arcade) are disarticulated (Dalla Vecchia *et al.* 2002). The anterior part of the mandible is straight and weak (Fig. 1D), similarly to *Preondactylus* or *Peteinosaurus*. The postdentary part, however, is more massive and elevated, **as in** dimorphodontids.

The quadrate of *Eudimorphodon* is **not** directed vertically or subvertically as in *Dimorphodon* and anurognathids, but rather inclined approximately 60° relative to the occlusal plane. This will slightly increase the moment arm of the external adductors (Fig. 1B) and decrease the velocity of jaw closure: this, however, could have been compensated by **the supposed retraction of the a streptostylic quadrate** (Fig. 1B). Wild (1978, p. 248) noted the presence of condylus cephalicus proximally on the quadrate of *Eudimorphodon*, and suggested streptostyly as a consequence. The pterygoid process of the quadrate is connected with the pterygoid, but other details of this joint are obscured by overlying bones. In the lower temporal arcade of the holotype neither the jugal–quadratojugal nor the quadratojugal–quadrate are fused, further suggesting the possibility of quadrate rotation during opening **and** closing of the mouth. The mandible is straight and its postdentary part bears an obvious but weakly-developed coronoid **process**.

The quadrate of *Carniadactylus* is strongly similar to that of the holotype of *Eudimorphodon* in being inclined approximately 60° relative to the occlusal plane (Wild 1994). Based on MFSN 1797 the mandible is **distinct** in having a well developed, triangular dorsal margin of the postdentary part of the mandible (Dalla Vecchia 2009; Fig. 1F).

In contrast to the aforementioned basal, heterodont pterosaurs, *Caviramus* (based on ‘*Raeticodactylus*’ BNM 14524) has strongly inclined (40°) occipital and temporal region relative to the occlusal plane. The quadrate is strongly fused (no condylus cephalicus can be observed) with the squamosal **preventing streptostyly**. Along with the lower temporal arcade the postdentary region of the mandible slopes posteroventrally (Fig. 1H) to produce a strongly elevated insertion area for the external adductor musculature. In contrast to *Eudimorphodon*, the mandibular symphysis is strongly fused with a deep, convex keel ventrally. Both on the holotype (PIMUZ A/III 1225) and the more complete specimen (BNM 14524, Stecher 2008) bear “cup-shaped” structures on their anterior dentaries: these have been proposed to be depressions housing nutritive vessels supplying and anchoring soft tissue in this region (Fröbisch & Fröbisch 2006).

Dentition and extant analogues

By all means, the most fundamental feeding adaptation of basal pterosaurs is their complex dentition. In almost all basal pterosaur taxa, the anterior teeth are relatively large, and fang-like, often with slight curvature and smooth surfaces (but striated in *Eudimorphodon* [Wild 1978] and *Caviramus* [Stecher 2008; Fig. 2M]). **They usually lack carinae (except for *Dimorphodon*)**. In *Caviramus* (BNM 14524) the anterior ‘fang’-like teeth are robust and more closely spaced than in **most** other taxa. An exception to this general heterodont pattern of basal forms is *Anurognathus* where the dentition is isodont **comprising** narrow, slightly (or strongly in *Batrachognathus*) recurved teeth that have a roughly cylindrical base and sharp, pointed tips (Döderlein 1923, Wellnhofer 1978, Bakhurina & Unwin 1995, Bennett 2007; Fig. 2E).

Posterior tooth row crown morphology is much more variable among most basal pterosaurs. *Preondactylus* and *Austridactylus* have coarsely serrated teeth of different sizes that are triangular, pointed and labiolingually flattened with a relatively sharp apical angle (45°, Fig, 2A, B; Dalla Vecchia *et al.* 2002, Dalla Vecchia 2003a:fig. 5). Denticles are similar or slightly smaller compared to those seen in many dinosaurs and crocodylians with similar, labiolingually flattened, triangular teeth (e.g. the ziphosuchian crocodylian *Doratodon* Company *et al.* [2005] or the basal theropod *Richardoestesia*, Currie *et al.* [1990]).

The posterior maxillary teeth of *Dimorphodon* are large (6–8 mm), widely spaced and triangular - similar to those of *Austridactylus* - and less curved distally (Fig. 2C). In contrast, the opposite teeth in the dentary are small (1–3 mm) closely spaced, labiolingually flattened and triangular (Owen 1870, Padian 1983; Fig. 2C). The apical angle of the teeth ranges between 30–50°, giving most teeth relatively sharp points (Fig. 2C). The teeth of *Peteinosaurus* are widely spaced and pointed, with single cusps that form a sharp apical angle of 40–45°. In addition, some distal teeth bear mesial and distal cusples (Dalla Vecchia 2003a, pers. obs.), but they are not as well developed as in other multicusped forms (Fig. 2F). The general morphology and the widely spaced arrangement of the teeth of *Peteinosaurus* are similar to the smaller teeth of *Preondactylus*.

Dentition in forms with multicusped teeth (*Eudimorphodon*, *Caviramus*, *Carniadactylus*) are diagnostic for each taxon. They are closely spaced but lack the cingulum seen in thyreophoran dinosaurs with similar, labiolingually compressed teeth with denticulate carinae (Vickaryous *et al.* 2004). In these forms, the posterior section of the tooth row resembles a long cutting blade with zig-zag occlusal surface. This is especially

true of the posterior part of the mandibular dentition which, in contrast to that of the maxilla, lacks enlarged teeth (Wild 1984, Dalla Vecchia *et al.* 2002).

The teeth of *Eudimorphodon* are labiolingually compressed, tri- and quinticusped and often possess longitudinal enamel ridges (Fig. 2G, H). Generally, the central tooth cusp is the largest with a sharp apical angle of 40°, but the mesial and distal accessory cusps are also well-developed. The teeth of *Carniadactylus* (Fig. 2I) resemble the teeth of *Eudimorphodon* (MCSNB 2888), but, based on MPUM 6009, the posterior teeth are non-bulbous tri- or quinticuspid with smooth labial and lingual surfaces. Furthermore, the the third mandibular alveolus of *Carniadactylus* has a labiolingually compressed bicuspid tooth with a small accessory cusp present behind the main cusp; this tooth type is absent in *Eudimorphodon*.

In *Caviramus* the crowns of the preserved, posterior dentary teeth (9th–19th) overlap each other (Fig. 2N) in a similar manner to those of thyreophoran dinosaurs (Coombs & Maryanska 1990, Ősi & Makádi 2009). Both tricusped and posteriorly quinticusped teeth occur among the anterior portion of the tooth row. The main cusps of both the maxillary and dentary teeth have apical angles of 70–75°, much higher than those of other previously discussed taxa. Irregular ridges are present in the enamel on the lingual surface of various maxillary teeth (Fig. 2M).

Various authors (e.g. Evans & Sanson 1998, Herrel *et al.* 2004, Kosma 2004) emphasized that the reduction of contact area between tooth and food is required for penetrating and crushing hard food items (such as the exoskeleton of insects). Accordingly, narrower, pointed teeth are more useful for this than cuspidate or blunt teeth. The teeth of *Preondactylus*, dimorphodontids, and anurognathids correspond well to these criteria and suggest a dominantly insectivorous diet. By contrast, labiolingually compressed, sharply

pointed, triangular teeth with serrated carinae (as seen in *Preondactylus*) do not occur among extant lepidosaurs (Schwenk 2000, Kosma 2004). Some extant lizards, e.g. *Iguana iguana* (MNHN 1974.129) possess labiolingually compressed lance-shaped teeth with serrated carinae (Fig. 3G) but also bear much broader apical angles than those of *Preondactylus*. Thus, serrated carinae and differences of tooth size in the tooth row may also indicate a more diverse diet including small vertebrates and carcasses for some forms.

Various forms of extant lizards, possess multicusped (mostly bi- or tricuspid) teeth posteriorly. The insectivorous teiid *Kentropyx calcarata* has tricuspid teeth where the main cusp is often longitudinally striated (Kosma 2004) in a manner similar to that of the teeth of *Eudimorphodon*. Different species of the dominantly insectivorous teiid *Ameiva* (MNHN 1887.875, Fig. 3A, B) and *Cnemidophorus* have tricuspid teeth that closely resemble the teeth of *Carniadactylus* (MPUM 6009). Most taxa with tricuspid teeth are mainly insectivorous, but some species are more opportunistic and also consume small vertebrates or vegetables (Kosma 2004). Quadri- or quinticusped teeth are rarer in extant lizards but occur in the gerrhosaurid *Angolosaurus* (Kosma 2004), in the omnivorous iguanid *Ctenosaura acanthura* (MNHN 1909.524, Fig. 3C, E), in some herbivorous iguanids such as *Iguana delicatissima* (MNHN 1941.215), *Cyclura cornuta* (MNHN 1964.144, Fig. 3D), and the extinct herbivorous scincid *Macroscincus coctei* (MNHN 1907.344). Teeth of *Angolosaurus* are similar to those of *Caviramus* in their overlapping arrangement that is not present in *I. delicatissima*, *Cyclura*, *Macroscincus*, or *Ctenosaura*. These labiolingually flattened, more than tricuspidate teeth are interpreted as an adaptation to a herbivorous diet (Kosma 2004).

These extant analogues lend some support to the possible dietary preference of heterodont basal pterosaurs. However, there are several differences between the

multicuspid teeth of pterosaurs and **those of** extant lizards, most notably that of size: in most cases, pterosaur teeth are two or three times larger than those of extant lizards mentioned here (excluding *Cyclura*). In addition, marked dental wear as preserved in *Eudimorphodon* and *Carniadactylus* (see below) can not be observed in extant lizards, although some apical wear also occurs.

Tooth wear

In accordance with their widely-spaced teeth and general tooth morphology (pointed, **monocuspid** teeth) no developed tooth wear **has been** recognized in *Preondactylus*, dimorphodontids, anurognathids, or *Austriadactylus*. **Some apical wear has been recognized on the crowns of *Dimorphodon* (Mark Witton pers. comm.) that rather refers to tooth-food-tooth contact than to dental occlusion. By contrast,** dental wear occurs more frequently in forms with closely **spaced teeth** and multicuspid teeth. Wild (1978) reported extensive wear facets on the teeth of the holotype of *Eudimorphodon*, showing that the tips of the anterior fang-like teeth are usually **worn (Fig. 2G, H)**. The widely-spaced nature of these teeth excludes any effective tooth–tooth occlusion, suggesting the eroded tips were **most likely** formed by tooth–food contact during prey capture. Worn surfaces of the tips on the posterior, multicuspid teeth are also frequent and, on the posteriormost, quinticuspid teeth, they extend much further compared to the anterior teeth (Wild 1978:fig. 8; pers. obs.; Fig. **2G, H**). Here, the mesiodistally positioned secondary cusps are also more frequently worn. Besides the apical wear, nearly vertical wear facets are present on the labial and lingual surfaces of the multicuspid teeth (**Fig.2H**). On the basis of the lack of longitudinal enamel surface striations, slightly eroded surfaces can be recognized on the labial sides of the 5th, 6th, 7th, 8th, 11th left dentary teeth of MCSNB 2888. Much heavier labiolingual wear is

present more posteriorly. It appears that on numerous teeth not only the occluding side (labial on the mandibular teeth, lingual on the maxillary teeth) became eroded, but also the other side (Wild 1978). This heavy erosion of the non-occluding side indicates that not only tooth–tooth contact but also food particles **abraded** the crown surfaces during feeding. Unfortunately, **For this study the worn surfaces of the teeth could not be examined using a scanning electron microscope**, thus the pit/scratch ratio and orientation of scratches in *Eudimorphodon* **remains** unknown. No tooth wear has been described in *E. cromptonellus* (Jenkins *et al.* 2001).

Although *Carniadactylus* **does** possess multicuspid teeth, MPUM 6009 does not show any indication of dental wear (pers. obs.) and no tooth wear has been reported for MFSN 1797 (Dalla Vecchia 2009; **Fig. 2I**). Stecher (2008) described extensive tooth wear on both the maxillary and dentary teeth of *Caviramus*, **where** facets occur both apically and on the labial side of **the** mandibular teeth. Wear facets on the labial side of the multicusped dentary teeth are almost vertically orientated and situated on the middle, thickest part of the crown, or, more rarely, on the distal half of the crown (Fig. 2O–Q). In the latter case, the distal accessory cusps are also steeply eroded. These wear facets are limited and the enamel–dentine interface can clearly be **seen**. Due to acid preparation of the specimen (Ulrich Schneppat, pers. comm.) the original surface of the wear facets were eaten away, thus no scratches or pits can be studied that **might indicate the direction** of jaw movement. Wear can be observed also on both the mesial and distal accessory cusps of the anterior tooth of the *Caviramus* **holotype** (Fig. 2L): the mesial cusp is eroded along a steeply inclined, elongated wear facet on its mesial–labiomésial side, while the distal cusp shows almost horizontal wear **facet**. **The** enamel–dentine interface can be easily identified on the distal cusp. Numerous short scratches are present on the dentine and are roughly parallel **to**

the longer axis of the wear facet. Except for some isolated uncertain scratches, no significant wear has been found on the central cusps.

Jaw joint and musculature

Along with dental features and wear pattern, the form of the quadrate condyles and the glenoid surface can reflect different types of jaw movement (orthal, palinal, propalinal, transverse) during jaw opening and closure. **In all pterosaurs**, the glenoid is deeply concave, **short** anteroposteriorly. Usually, a transverse ridge between the glenoid and the retroarticular process prevents anteroposterior movement of the quadrates. Furthermore, the quadrate condyles, where they can be seen (e.g. *Dimorphodon*, *Eudimorphodon*, *Caviramus*), are clearly separated by a deep intercondylar groove **that prevents** transverse movement.

In addition to its form, the position of quadrate–articular joint relative to the occlusal plane can be also an important factor **for** reconstructing the work of adductor muscles and **determining** the velocity of jaw closure (see e.g. Smith 1993, Ősi & Weishampel 2009). Forms with highly elevated jaw joint (e.g. ungulate mammals) usually work with weakly advanced adductors originating from the temporal region and responsible for rapid jaw closure. On the other hand, **the** deeply positioned jaw joint ensures a shorter distance between the origin and insertion surfaces of these adductors, thus providing **rapid** jaw closure.

In *Preondactylus*, *Dimorphodon* (the postdentary part of *Peteinosaurus* is poorly preserved), anurognathids, and *Austriadactylus* the jaw joint is situated on or close to the level of the occlusal plane (Wild 1984:fig. 3; Bennett 2007; Fig. 1A, C, D, G). In these forms, especially in anurognathids, the quadrate and the pterygoid are relatively thin (rod-

like in *Anurognathus* Bennett 2007:figs. 3, 4) and the postdentary region of the mandible are filigant without a well-developed coronoid process. These features reflect relatively small origin and insertion areas for the cranial adductors, especially for the pterygoid muscles [MPT] and m. adductor mandibulae posterior [MAMP]. As in most other pterosaurs, parts of the external adductors (MAME/S/M/P) responsible for rapid jaw closure (Iordansky 1964, Endo *et al.* 2002, Mueller-Töwe 2006) could have been the dominant jaw closers (Witton and Naish 2008) that originated from the margin of the supratemporal fenestra and most of their bundles inserted along the dorsal edge of the surangular (Holliday & Witmer 2007; Fig. 3A, C). This may have been an important factor in capturing flying insects.

In contrast to these forms, *Eudimorphodon*, *Carniadactylus* and especially *Caviramus* have a jaw joint well below the level of the occlusal plane (Fig. 1B, F, H) and the prominent coronoid processs indicating a well-developed insertion surface for the external cranial adductors (MAMES and MAMEM) responsible for rapid jaw closure (Fig. 1). This elevated insertion area for the external adductors (Fig. 1F), the deeply positioned jaw joint and the strongly inclined occipital and temporal regions provide an almost vertical direction for these adductors relative to their insertion area, thus providing an increased moment delivered to the quadrato-articular joint (Herrel *et al.* 1999).

Feeding mechanism and possible diet

Based on tooth morphology, wear pattern analysis, quadrate morphology, and jaw joint mechanics it can be concluded that no basal pterosaurs used transverse jaw movements during feeding. The labiolingually flattened, triangular teeth would make the transverse motion of the lower jaws impossible when the jaws were close to occlusion and, in all taxa,

the quadrate fits precisely into the glenoid. This latter feature excludes well developed palinal or propalinal mandibular movements. *Preondactylus*, dimorphodontids, anurognathids and *Austriadactylus* show no dental wear (due to occlusion) and these features, at least in these latter taxa, suggest a precision shear bite (isognathous orthal jaw movement) that was completed with interlocking of the lower and upper anterior teeth. In *Preondactylus* and *Austriadactylus* this is highly supported by the finely serrated carinae and, along with their lightly built skulls and pointed, finely serrated teeth (Evans & Sanson 1998), a dominantly insectivory can be inferred. The enlarged teeth between the naris and the antorbital fenestra probably served to crush hard food substrates such as exoskeleton of insects while the serrated carinae were ideal for dismembering prey and removing bite-sized chunks as in some carnivorous and necrophagous extant lizards. In the latter carnivorous taxa, however, teeth are usually distally curved as in some *Varanus* species (Fig. 3F). Serration on the sharply pointed triangular teeth of *Austriadactylus* and *Preondactylus* were better able to penetrate and then to section the food item (e.g. hard chitinous exoskeleton of arthropods).

On the basis of tooth morphology and reconstructed cranial biomechanics, Fastnacht (2005) described a snap and hold function for the dental apparatus of *Dimorphodon* and suggested a low penetration capability of the teeth. The information on the adductor musculature, discussed here, corresponds well with this idea. The advanced, almost vertically oriented external adductors produced a rapid closure of the mandibles (thereby permitting a high closing velocity for the lower jaws, Fastnacht 2005), and the relatively short and high skull ensured a great mechanical advantage during jaw closure. These features and the larger, narrow and pointed anterior teeth together with the smaller, triangular posterior teeth suggest a dominantly insectivorous habit for *Dimorphodon* (and

possibly for *Peteinosaurus*) that could have been acquired during flight. This, however, does not exclude the possibility of temporary consumption of other food resources, such as small vertebrates and carcasses. This would be supported by the relatively high but lightly constructed skull that would be more resistant against bending stresses during penetrating flesh than those of rhamphorhynchids and campylognathoidids, thereby allowing them to handle relatively large or feisty prey (Mark Witton pers. comm). In addition, we have to take into account that, similarly to other vertebrates such as sauropod dinosaurs (Fiorillo 1998), crocodiles (Ósi & Weishampel 2009) or mammals (Walker *et al.* 1978), seasonal climate, different ontogenetic stages or any kind of change in the ecological niche might result in a higher portion of other food resources (e.g. flesh, molluscs, plants etc.) in *Dimorphodon* but also in other pterosaurs.

Fastnacht (2005, p. 179) correlated the *Anurognathus* skull with low torsional loads that is either “due to the intake of only small-sized food or absorbed by a possible cranial kinesis”. Various authors have suggested that anurognathids were aerial insectivores because of their large, anterolaterally directed eyes, wide mouth with a large gape, and a sharp, isodont dentition suitable for holding prey (Döderlein 1923, Wellnhofer 1975, Bakhurina & Unwin 1995, Bennett 2007). Bennett (2007, p. 391) argued that “the posterolaterally directed retroarticular process would not interfere with the inward slanting of the quadrate when the mandible was depressed, and so would permit depression of at least 90° producing a large gape”. These cranial and muscle constructions are absolutely advantageous for catching small-bodied flying prey with the help of wide opening and fast closing mouth. Besides cranial features, those of the postcranium also support aerial insectivory for anurognathids. Bennett (2007, p. 394) concluded that the construction of the flight apparatus (with voluntarily flexed interphalangeal joints in the wing finger, low wing

loading, short tail) allowed “slow, highly maneuverable flight”. Indeed, anurognathids were among the smallest pterosaurs with a wing span of generally shorter than one metre (Dalla Vecchia 2002) and possessed a wing ecomorphology that well correlates with modern aerial hawkers (Witton 2008).

Eudimorphodon is one of the few pterosaurs that certainly used oral food processing during feeding. This was most probably completed by extensive dental occlusion which, on the basis of dental wear, was most significant in the posterior region of the tooth row. This corresponds well to the simple physical constraint that mechanical food processing is more effective closer to the adductors (i.e. rotation point of the jaw) (Fastnacht 2005). Although the mandibles of the holotype are not preserved as functionally articulated (i.e. closed jaws, Wild 1978) and the exact original relations between the upper and lower teeth cannot be observed, the closely spaced teeth and the heavy dental wear on the tip of both the main and accessory cusps indicate that the main cusps of the upper teeth occluded with the distal and mesial accessory cusps of two neighbouring lower teeth and vice versa. The presence of heavy wear facets on both the apical and labiolingual regions (fig. 2G, H) of the teeth may indicate the absence of a simple, precise shearing bite as seen in thyreophoran dinosaurs (Barrett 2001, Rybczynski & Vickaryous 2001, pers. obs.) or in numerous extant herbivorous lizards. They rather suggest a slight mobility of the mandibles in the transverse plane that was most probably facilitated by the unfused mandibular symphysis. In this case, a thin fibrocartilaginous pad may have lain in the symphysis, separating the two mandibles (Lieberman & Crompton 2000) and allowing them to rotate slightly about their long axis as it is known in several mammalian lineages (Mills 1967, Crompton & Hiiemae 1970, Crompton 1995). This could provide shearing contact between the lingual and labial sides of the upper and lower teeth respectively, while also allowing direct contact between the

tips of the cusps. This, however, does not necessarily refer to an ordinary transverse movement of the jaws. Wear facets of the lingual side of the dentary teeth and those on the labial side of the maxillary teeth can not be the result of dental occlusion rather they are a result of food particles abrading the crown surfaces during feeding.

If streptostyly was present in *Eudimorphodon* (and perhaps in *Dimorphodon*), then it must have caused a decrease in bite force for these taxa compared to an animal that possesses a rigid skull and thus a higher bite force, because cranial kinesis weakens the skull as a frame for adductor muscles. However, this “derived weakness” might have turned into a functional advantage (Herrel et al. 2000) so that, for example, the speed of closure of the mandibles became faster.

Wild (1978) noted the abundance of ganoid fish in the same beds where *Eudimorphodon* occurred and also ganoid scales in the gut content of MSCSNB 2888, and suggested piscivorous habits for *Eudimorphodon*. The pointed morphology of the teeth, the heavy wear on various parts of the tooth crowns and a presumed kinetic system (see Metzger 2002) support this hypothesis. Nevertheless, it can not be excluded that seasonal climate could have caused variation in food sources resulting different stages of wear on the teeth.

Dalla Vecchia (2009, p. 159) noted that “no definitive evidence of a juvenile stage occurs in the two specimens” of *Carniadactylus*. This might suggest that *Carniadactylus* was small bodied animal and its teeth are similar in size to those of extant analogues. Although the teeth of *Carniadactylus* strongly resemble those of *Eudimorphodon*, great size difference present between the two taxa may explain the lack of dental wear in *Carniadactylus* through a difference in feeding habits (this is further supported by the lack

of enamel wrinkles in the latter). Based on the lack of dental wear it can be assumed that *Carniadactylus* consumed softer food (e.g. worms, larvae) than *Eudimorphodon*.

Stecher's (2008) suggestion that in *Caviramus* the upper and lower teeth occluded during feeding is supported by the dental wear features (Fig. 2O–Q). The steep inclination of the distinct wear facets and their presence on the distal part of the tooth crown suggests precise contact of the upper and lower multicusped teeth and reflect a shearing bite. This is further supported by a transverse ridge posterior to the glenoid on the right articular that prevents any anteroposterior dislocation of the quadrate condyles or mandibles. Conversely, apical wear facets (“horizontal wear” of Stecher [2008]) and heavy erosion of maxillary teeth raises the question of their generation: were they produced by direct tooth–tooth contact, tooth–food–tooth contact or both? In contrast to *Eudimorphodon*, however, no wear can be detected on the labial side of the upper teeth that could have been caused by the consumption of hard shelled food. This indicates that dental wear facets formed simply by tooth–tooth occlusion.

Stecher (2008, p. 13) discussed the possibility that *Caviramus* caught fish by skimming and provided numerous features which would support this idea (e.g. laterally compressed upper and lower jaws with bladelike horny covering; large cervical vertebrae to anchor developed neck musculature; large cranial adductor musculature). However, comparative biomechanical studies of different pterosaur taxa and the extant skimmer, *Rynchops niger cinerascens* pointed out numerous adaptations that appear to be essential for skimming but missing in the investigated pterosaur taxa (Humphries *et al.* 2007). Among these, one of the most important requirements is the “extreme lateral compression and pronounced horny extension of the mandibular symphysis” (Humphries *et al.* 2007, p. 5). *Caviramus*, indeed, possesses a laterally compressed symphysis (along with short, massive and dorsoventrally

high mandibular rami), but its anterior tip is too short (approximately 5 mm) **to support** an extended rhamphotea that functionally corresponds to that of *Rynchops*. In addition, this short tip is pointed anterodorsally instead of ventrally as seen in skimmers (Humphries *et al.* 2007). Another difficulty could be the presence of large and massive, relatively closely packed teeth in the anterior part of the mandible which would increase the hydrodynamic drag on the lower jaw of *Caviramus* and **therefore** the energetic costs of flight. Although several osteological features of this pterosaur seem to meet the skim-feeding requirements, it is unlikely that *Caviramus* would have been able to use skim fishing during powered flight. Instead of this, it could have **caught** fish via dip-feeding, a strategy employed by various sea birds today and proposed for *Anhanguera* and *Ornithocheirus* (Wellnhofer 1991). This is supported by its strong but highly flexible neck, the enlarged recurved fang-like teeth, and the developed **external** adductor musculature that produced a powerful and rapid jaw closure. This idea is also supported by the medial crests both on the mandible and the premaxilla that could have helped to stabilize the head during fishing **in a similar way it was supported by for ornithocheirids by** (Veldmeijer *et al.* 2006). Consuming fish, however, does not necessarily require such specialized dentition and does not produce significant dental wear thus *Caviramus* may have had a more variable diet including fish, arthropods, and plant food.

DISCUSSION

Unwin (2006, p. 232) suggested correlation between the development of active flight in “protopterosaurs” and the great abundance of insects at the beginning of the Mesozoic, supposing “that insects powered pterosaurs to a true flapping flight ability”. Indeed, after

the end-Permian extinction a radical change can be recognized in the evolutionary history of insects that was characterized by the decrease of diversity of the Palaeozoic Insect Fauna, followed by an increase in modern family level diversification that commenced from the late-Middle to Late Triassic (Labandeira & Sepkoski 1993, Labandeira & Eble 2000, Grimaldi 2003). Pterosaurs are the only known actively flying vertebrates of the Triassic and most probably became one of the most important predators of the new generation of flying insects. Even without direct evidence to support an insect–pterosaur trophic relationship, various anatomical features related to feeding suggest that the most basal pterosaurs could have been predominantly insectivorous animals. It is noteworthy to mention that there could be another scenario to explain the development of flapping flight ability: it may evolved simply as a transportation mechanism first and was only coopted for food acquisition by more derived forms later (e.g. anurognathids) (Mark Witton, pers. comm.).

Although differing in their structure, the contrasting phylogenetic context of Bennett (2007) and Unwin (2003a) infer that basal pterosaurs (*Preondactylus*, dimorphodontids and anurognathids) had all necessary abilities to feed on insects during flight. All these taxa were small-bodied animals with a wing-span usually of 40 to 80–90 cm (*Dimorphodon* was rather a medium sized animal with a wing span of 1.4 m, Mark witton, pers. comm.) capable of producing the slow, highly maneuverable flight essential for catching flying insects. These early forms had a vertically or subvertically oriented quadrate relative to the occlusal plane (“posteriorly placed quadrate–articular joint” of Bennett [2007]; Fig. 1, 4) that permitted depression of the mandibles to a high angle (80–90°), producing a wide gape. The wide gape is a typical adaptation of insectivory and is seen in microchiropteran bats but also in several birds such as wrens (Troglodytidae), swallows (Hirundinidae), Old

World flycatchers (Muscicapidae) and nightjars (Caprimulgidae) among others (Wellnhofer 1991, Bennett 2007). Other important features of these basal forms such as dentition, jaw morphology and reconstructed external **jaw** adductor mechanics are also strong indicators of a dominantly insectivorous feeding habit.

Using the data matrix of Unwin (2003b) *Carniadactylus* and *Caviramus* were included in a phylogenetic analysis of basal pterosaurs (Fig. 5). The analysis showed that they belong to the Lonchognatha (Unwin 2003a) and that *Caviramus* is the sister taxon of the Rhamphorhynchidae+Pterodactyloidea. On the other hand, *Carniadactylus* and *Caviramus* are closely related to other heterodont forms with multicusped teeth and active oral food processing. This suggests that, among the earliest but not the most primitive forms (currently known in Campylognathoidae+*Carniadactylus*+*Caviramus*), specialized dentition with multicuspid teeth appeared allowing more effective exploitation of a **wider** variety of **food through active oral** processing. Thus, these forms could have been opportunists. Just as in other distant relatives of pterosaurs (e.g. crocodylians, ornithischian dinosaurs), this feature evolved independently in several lineages of the Pterosauria. In *Caviramus* dental wear occurs apically (Stecher 2008) but, in contrast to *Eudimorphodon*, is found more frequently on the labial side of the mandibular teeth. This suggests the presence of a more precise shearing bite and a diet **distinct** from that of *Eudimorphodon*. Anteriorly, the massive recurved fang-**like** teeth, the massive construction of the mandibles, the strongly developed external adductors, the deeply positioned jaw joint and the massive cervical vertebrae indicate an adaptation to fishing, but precision shear of the teeth suggests a food processing mechanism where food is cut or chopped up before swallowing. These taxa with multicusped teeth (*Eudimorphodon*, *Carniadactylus*, *Caviramus*) **appears to be restricted to the Late Triassic and probably they were still not predominantly piscivorous**

forms. They possess some cranial characters (e.g. heterodont, relatively closely spaced dentition, perpendicular or subperpendicular orientation of external adductors relative to the insertion area) relating them to the plesiomorphic, predominantly insectivorous forms, but in other aspects (e.g. occipital region extends posteriorly with anteriorly inclined quadrates, body size) they are similar to the more derived taxa.

Among Jurassic and Cretaceous lonchognathans the occipital region became more inclined (Fastnacht 2005; Fig. 1I, 4), thus the external adductors are composed of relatively more elongated bundles and anchored at an acute angle relative to the occlusal plane. *Campylognathoides* is less derived in having a straight weak mandible, lightly constructed skull similar to *Preondactylus*, and teeth that are more closely spaced and rather triangular, compared to the elongate, recurved teeth of more derived forms. The earliest forms (e.g. *Dorygnathus*, *Scaphognathus*, *Rhamphorhynchus*) with a dominantly piscivorous habit might have appeared no earlier than the Early Jurassic. They possess slightly bowed mandibles posteriorly and widely spaced, enlarged procumbent teeth forming a fish grab (Fig. 1I, 4B–D, 5, but there are some exceptions e.g. scaphognathines Mark Witton, pers. comm.). Besides dental morphology, the anteriorly inclined quadrate (especially in lonchognathan forms; see Fig. 1I, 4B, D) corresponds well with having a different feeding habits than those of basal, insectivorous forms. The skull of more piscivorous forms became elongated anteroposteriorly and the wingspan/body size generally increased (but see *Arthur dactylus*, David Martill, pers. comm). In more derived representatives with strongly elongate skull, the inclined position of the quadrate does not allow as large gape for the mandibles as in anurognathids and probably in dimorphodontids, because the retroarticular process is stopped by the quadrate shaft in a fully opened position (Fig. 4). Here, the maximum gape could not be larger than 60–70° (see e.g. *Ludodactylus*, Frey *et al.* 2003b).

However, these animals **primarily fed on small food items, and most of them consumed dominantly** aquatic organisms (fishes, arthropods, molluscs, planktonic animals) and did not need to operate with a completely opened mouth (Wellnhofer 1991).

Pterosaurs with widely spaced teeth could not use active oral food processing and dental occlusion as some earlier heterodont forms did, but nonetheless dental occlusion accidentally produced heavy tooth wear (e. g. in *Rhamphorhynchus*, BMNH R37002 [Mark Witton, pers. comm.], *Dorygnathus* cf. *banthensis*, SMNS 81840; uncatalogued specimen; Fig. 6) similar to that of various theropod dinosaurs or extant reptiles (Schubert & Ungar 2005). Schubert & Ungar (2005) described spalled surfaces and wear facets as the result of probably serendipitous contact between the upper and lower teeth. Wear facets on the anterior teeth of *Dorygnathus* (Fig. 6) are short and conchoidal, extending to the apex of the tooth with scratches on the **worn** surface heterogeneously oriented. They resemble the spalled surfaces recognized in tyrannosaurids more than a wear facet prepared by shearing contact of the upper and lower teeth seen e. g. in *Caviramus*. Spalled surfaces, however, reflect “flaking of enamel resulting from forces produced during contact between tooth and food” (Schubert & Ungar 2005, p. 93). **If this can be demonstrated**, then it could be supposed that *Dorygnathus* and perhaps other lonchognathan pterosaurs fed on hard shelled prey (e.g. molluscs, crustaceans) besides fish.

It is noteworthy to mention that basal pterosaur phylogeny is still controversial with numerous different schemes proposed by different authors (see e.g. Dalla Vecchia 2009, Lü et al. 2009; Andres et al. 2010). Using for example the systematic works of Dalla Vecchia (2009) or Andres et al. (2010) they included some recently published taxa but the latter work does not include *Preondactylus*, *Caviramus* or *Carniadactylus* in the analysis. These two works concluded (contra Kellner 2003, Unwin 2003b, Bennett 2007) that

anurognathids are the sistergroup of the Pterodactyloidea. Applying this topology we cannot see the above described main trend, namely that insectivorous forms were dominantly among the most basal taxa. Results of Andres et al. (2010) rather indicate that similarly to the heterodont dentition with multicusped teeth, insectivorous forms also evolved independently in several lineages of the Pterosauria. Hopefully, additional material and future works helps to clarify this controversy.

The foregoing analysis demonstrates a significant change of numerous feeding related characters in the evolution of basal pterosaurs that most probably correlates with the differentiation of various feeding strategies among pterosaurs. However, it is important to emphasize that the fossil record of basal pterosaurs is far from complete: the first 35 million years of their history (Middle Norian to the end Toarcian) is represented by less than a dozen genera. Hopefully, with future discoveries of new material of already known but poorly preserved taxa and new forms additional information can be provided that will help clarify the diversification of feeding strategies in basal pterosaurs.

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Figure captions:

Figure 1. Mandibles with the articulated quadrate in closed position in different pterosaurs scaled to the same size. A, *Preondactylus buffarini*, modified from Dalla Vecchia (2003a). B, *Eudimorphodon ranzii* (MCSNB 2888). C, *Anurognathus ammoni* modified from Bennett (2007). D, *Austriadactylus cristatus*, modified from Dalla Vecchia *et al.* (2002). E, *Peteinosaurus zambellii* (quadrate position is hypothetical) F, *Carniadactylus rosenfeldi* (after specimens MFSN 1797 and MPUM 6009 and Dalla Vecchia 2009). G, *Dimorphodon macronyx* (NHM 41212-13). H, *Caviramus schesaplanensis* (based on BNM 14524). I, *Ornithocheirus mesembrinus* (after Wellnhofer 1987). Arrow shows the distance between the occlusal plane (continuous line) and the jaw joint (broken line), dotted area shows the relative size of insertion surface of the external adductors.

Figure 2. Dentition and wear patterns of basal heterodont pterosaurs. A, enlarged maxillary tooth with serrated carinae of *Preondactylus buffarini*, modified from Dalla Vecchia (2003a). B, Serrated teeth of *Austriadactylus cristatus*, modified from Dalla Vecchia *et al.* (2002). C, pointed dentary teeth and a maxillary tooth of *Dimorphodon macronyx*. D, pathologically bicusped tooth in the middle part of the dentary tooth row of *D. macronyx* (NHM 41212-13). E, mandibular dentition of *Anurognathus ammoni* modified from Bennett (2007). F, mandibular dentition of *Peteinosaurus zambellii* (MCSNB 2886). G,

eroded upper and lower posterior multicusped teeth of *Eudimorphodon ranzii* (MCSNB 2888). H, multicusped dentary tooth (14th) of *E. ranzii* with wear facets. I, unworn multicusped tooth of the ‘Milano specimen’ of *Carniadactylus rosenfeldi* (MPUM 6009). J, 10th tooth of *Caviramus schesaplanensis* (PIMUZ A/III 1225), K, 7th tooth of *C. schesaplanensis*. L, wear facet on the mesial part of the 7th tooth of *C. schesaplanensis*. M, enamel wrinkles on the lingual surface of a maxillary tooth of *Caviramus schesaplanensis* (BNM 14524). N, 10th to 19th left dentary teeth of *C. schesaplanensis* (BNM 14524) in labial view. O, wear facet on the 14th tooth. P, wear facet on the 15th tooth. Q, wear facet on the 16th tooth. Abbreviations: ew, enamel wrinkle; wf, wear facet.

Figure 3. Dentition of some different extant lizards. A, *Ameiva ameiva* (MNHN 1887.875) left dentary in medial view. B, *Ameiva festiva* posterior tooth in lingual view (after Kosma 2004) C, *Ctenosaura acanthura* (MNHN 1909.524) posterior part of tooth row in the left dentary in lateral view; D, *Cyclura* sp. (MNHN 1964.144) posterior part of tooth row in the left dentary in medial view; E, *Ctenosaura acanthura* (MNHN 1909.524) left dentary in lateral view; F, *Varanus komodoensis* upper and lower teeth of the left lateral side, G, *Iguana iguana* (MNHN 1974.129) right maxilla in medial view. Except for Fig. 3B, F photos courtesy of László Makádi.

Figure 4. Diagrammatic sketch of the skull, mandible and the main cranial adductor and depressor muscles in *Anurognathus ammoni* (A, C; after Bennett 2007) and *Ornithocheirus mesembrinus* (B, D; after Wellnhofer 1987) in lateral view. A and C, closed position. B and D, opened position. Abbreviations: MAMEP, m. adductor mandibulae externus profundus; MAMP, m. adductor mandibulae posterior; MDM, m. depressor mandibulae; MPT,

musculus pterygoideus dorsalis and ventralis. Note that in *Anurognathus* the quadrate is in a vertical position and the maximum gape of the mandible can reach an angle of 90°, whereas in *Ornithocheirus* the quadrate is strongly inclined anteriorly thus the maximum gape can not be larger than approximately 60°.

Figure 5. Phylogenetic context of basal pterosaurs used in this work. Character–taxon matrix is based on Unwin (2003b). This cladogram shows the main changes of feeding related characters observed in basal pterosaurs and suggests the process of possible alteration in their feeding strategies. (Politomy appeared among anurognathids.)

Figure 6. Wear facets on the teeth of *Dorygnathus* cf. *banthensis*, SMNS 81840. These wear facets are most probably spalled surfaces resulting from forces produced during contact between tooth and food.

Table 1.

Taxon/specimen	Tooth morphology	Tooth wear pattern	Quadratum	Orientation of external adductors relative to insertion area	Jaw joint	Reference
<i>Preondactylus buffarinii</i> Wild, 1984 (MSFN 1770)	Anterior teeth recurved, labiolingually flattened, fang teeth; enlarged serrated teeth below the ascending process of the maxilla	No data	No data	No data	In or slightly above the level of the occlusal plane	Wild 1984, Wellnhofer 1991, Dalla Vecchia 1998, 2003a, b
<i>Dimorphodon macronyx</i> (Buckland 1829), (NHM R1034)	Large, labiolingually compressed, recurved fang teeth (laniaries) anteriorly; widely spaced large triangular teeth in the maxilla, closely packed, small triangular teeth posteriorly in the dentary	No indication of wear	Subvertically positioned	Nearly perpendicular relative to mandible	Slightly above the occlusal plane	Owen 1870, Padian 1983, Unwin 2003a, pers. obs.
<i>Peteinosaurus zambellii</i> Wild, 1978 (MCSNB 2886)	Recurved, fang teeth anteriorly; small closely-spaced monocusped slightly	No indication of wear	No data	No data	Slightly above the occlusal plane	Wild 1978, Dalla Vecchia 1998, pers.

	curved teeth backwards					obs.
<i>Austriadactylus cristatus</i> Dalla Vecchia, Wild, Hopf et Reitner, 2002 (SMNS 56342)	Recurved fang premaxillary teeth; enlarged triangular, labiolingually flattened, serrated teeth beneath the ascending process of the maxilla, short, triangular multicusped teeth posteriorly	No indication of wear	Vertically positioned	70–90° relative to mandible	In the level of the occlusal plane	Dalla Vecchia <i>et al.</i> 2002
<i>Eudimorphodon ranzii</i> Zambelli, 1973 (MCSNB 2888, BSP 1994I 51)	Vertically striated, recurved fang teeth anteriorly; enlarged, multicusped teeth beneath the ascending process of the maxilla; tricusped and quinticusped teeth posteriorly with longitudinal enamel ridges	Labial and lingual wear facets on the multicusped teeth, on the posterior teeth, the top of the cusps are eroded	Subvertically positioned	60–70° relative to mandible	In the level of the occlusal plane	Zambelli 1973, Wild 1978, Dalla Vecchia 2003a, b, 2004, Wellnhofer 2003, pers. obs.
<i>Eudimorphodon cromptonellus</i> Jenkins, Shubin, Gatesy et Padian, 2001 (subadult)	Smooth, multicusped teeth in the maxilla and the dentary; no enlarged teeth beneath the ascending process of the maxilla	No indication of wear	Quadrangle slopes forward	No data	No data	Jenkins <i>et al.</i> 2001
<i>Carniadactylus rosenfeldi</i> Dalla Vecchia, 2009 (MFSN 1797, MPUM 6009)	Mono- and quinticusped teeth	No indication of wear	Quadrangle slopes forward	No data	Slightly below the level of the occlusal plane	Wild 1994, Dalla Vecchia 1995, 2009

<p><i>Caviramus schesaplanensis</i> Fröbisch et Fröbisch, 2006 (PIMUZ A/III 1225) (BNM 14524).</p>	<p>Large, recurved fang teeth anteriorly, multicusped teeth posteriorly, with longitudinal enamel ridges</p>	<p>Labial and lingual wear facets on the multicusped teeth, on the posterior teeth</p>	<p>Quadrate slopes forward</p>	<p>Nearly perpendicular relative to mandible</p>	<p>Below the level of the occlusal plane</p>	<p>Fröbisch and Fröbisch 2006, Stecher 2008, pers. obs.</p>
<p>Jurassic and Cretaceous lonchognathan pterosaurs</p>	<p>Dominantly widely-spaced conical, recurved teeth</p>	<p>Spalled facets apically (in <i>Dorygnathus</i>, SMNS 81840)</p>	<p>Quadrate slopes forward</p>	<p>Ranging from 10–60°</p>	<p>In or slightly below the level of the occlusal plane</p>	<p>Wellnhofer 1978, 1991; Unwin 2003a, pers. obs.</p>