

Pterosaurs in Mesozoic food webs: a review of fossil evidence

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Abstract: Understanding the ecological roles of pterosaurs is a challenging pursuit, but one aided by a growing body of fossil evidence for their dietary preferences and roles as food sources for other species. Pterosaur foraging behaviour is represented by preserved gut content, stomach regurgitates, coprolites and feeding traces. Pterosaurs being eaten by other species are recorded by tooth marks and teeth embedded in their fossil bones, consumer gut content and regurgitate, and their preservation entangled with predatory animals. This palaeoecological record has improved in recent years, but remains highly selective. The Jurassic rhamphorhynchid *Rhamphorhynchus*, Cretaceous ornithocheiroid *Pteranodon* and azhdarchid pterosaurs currently have the most substantial palaeoecological records. The food species and consumers of these taxa conform to lifestyle predictions for these groups. *Rhamphorhynchus* and *Pteranodon* ate and were eaten by aquatic species, matching expectations of these animals as sea-going, perhaps partly aquatic species. Possible azhdarchid pterosaur foraging traces alongside pterosaur tracks, and evidence that these animals were eaten by dinosaurs and Crocodyliformes, are consistent with hypotheses that azhdarchids foraged and lived in terrestrial settings. Fossil evidence of pterosaur palaeoecology remains rare: researchers are strongly encouraged to put specimens showing details of dietary preferences, foraging strategies or interactions with other animals on record.

Pterosaur science is currently enjoying a sustained period of heightened interest, discovery and development (Hone 2012). An outcome of this is that flying reptile lifestyles and possible ecologies have started to receive detailed assessment after relative neglect by previous generations of pterosaur researchers. Historically, pterosaurs were classified as highly volant marine fishers, skim-feeders and seabird analogues, irrespective of size, skeletal proportions, detailed anatomy or geological context (e.g. Wellnhofer 1991). An appreciation that well-established links between form and function must apply to pterosaurs as much as other fossil taxa and discovery that their fossil record is not as skewed to marine habits as previously suspected have led to a more complex appreciation of their ecomorphology, foraging biomechanics, habitat preferences and likely lifestyles (e.g. Bennett 2007; Humphries *et al.* 2007; Veldmeijer *et al.* 2007; Witton & Naish 2008, 2015; Habib & Cunningham 2010; Witton & Habib 2010; Ōsi 2011; Witton 2012, 2013, 2015; Butler *et al.* 2013; Martill 2014). It is increasingly apparent that pterosaurs were suited to a variety of lifestyles, many of them only partly reliant on flight, and adapted to tackle a range of diets in varied environments (see Witton 2013 for a review).

In addition to these functional and taphonomic investigations, rare pterosaur fossils have helped shed light on their place in Mesozoic food webs. These remains, representing both body and trace fossils, join a rich palaeoecological record for other

Mesozoic animals (Kelly *et al.* 2003) comprising healed wounds from predatory acts (Carpenter 1998), toothed-scarred and partially digested gut content (Varricchio 2001; Forrest 2003), coprolites with identifiable food remains (Chin & Gill 1996; Chin *et al.* 2003) and purported traces of predators pursuing prey (Thomas & Farlow 1997). Palaeoecologically informative specimens remain relatively rare for pterosaurs compared with more abundant, robust Mesozoic tetrapods such as dinosaurs (e.g. Farlow & Holtz 2002), but their record is sufficient to augment theoretical discussions of pterosaur foraging methods and ecology. Beyond providing basic data on ancient trophic interactions, these fossils also serve as tests of the theoretical dietary preferences and foraging mechanics indicated by functional studies. These are invaluable given the unfamiliar nature of some pterosaur morphologies, the increasing recognition of ecological plasticity in modern animals (e.g. facultative fruit-eating in crocodylians, Brito *et al.* 2002; and predatory acts by cervids, Pietz & Granfors 2000) and ongoing controversies over some flying reptile foraging behaviours (e.g. Humphries *et al.* 2007). Direct evidence of pterosaur foraging behaviour and dietary preferences are provided by their coprolites, regurgitates, gut content and foraging traces. Tooth marks, embedded teeth, gut regurgitates and carnivore-consumed associations provide evidence of pterosaurs as food for other Mesozoic species. These data are reviewed and appraised here.

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Institutional abbreviations

ALMNH, Alabama Museum of Natural History, USA; AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; EME, Transylvanian Museum Society, Cluj–Napoca, Romania; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Los Angeles County Museum, USA; LEIUG, University of Leicester Department of Geology, Leicester, UK; LH, Museo de las Ciencias de Castilla–La Mancha, Cuenca, Spain; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MIC, Museo Interactivo de Ciencias, Universidad Nacional de San Luis, San Luis, Argentina; MM, Museum auf dem Maxberg, Germany; MPC-D, registered number of dinosaur specimens stored at the Paleontological Laboratory of Paleontological Center, Mongolian Academy of Science, Ulaanbaatar, Mongolia; MCSNB, Museo Civico di Scienze Naturali in Bergamo, Italy; NMV, Museum of Victoria, Melbourne, Australia; PTH, Philosophisch-Theologische Hochschule, Naturwissenschaftliche Sammlungen, Eichstätt, Germany; RMM, Red Mountain Museum (collection curated at the McWane Center), Birmingham, Alabama, USA; SDMS, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; SMNK, Staatliche Museum für Naturkunde Karlsruhe, Germany; SMNS, Staatliche Museum für Naturkunde Stuttgart, Germany; SOS, Jura Museum (Solnhofen Sammlung), Eichstätt, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; WDC, Wyoming Dinosaur Centre, Thermopolis, Wyoming, USA.

Systematic nomenclature

Pterosaur systematics are currently complicated by the existence of contrasting, sometimes incompatible interpretations of clade content, definition and nomenclature (see [Witton 2013](#) for discussion). This paper follows pterosaur systematics and nomenclature as presented by [Lü *et al.* \(2012\)](#).

Pterosaurs as foragers

Gut content and stomach regurgitates

Gut content is known from a number of pterosaur specimens, but their state of preservation is highly variable. Among the poorest quality are masses of calcite crystals preserved in the posterior trunk regions of some articulated Solnhofen Formation

pterosaurs. These are suspected to represent diagenetically altered stomach remains, but they present no characteristics allowing identification of ingested content (e.g. [Bennett 2014](#); [Hone *et al.* 2015](#)). Other examples are of sufficient quality to permit identification of the consumed species and even the state of digestion before the death of the pterosaur individual.

The geochronologically oldest record pterosaur gut content is that of MCSNB 2888 ([Fig. 1a](#)), the holotype of the Triassic (Norian), Italian (Zorzino Limestone Formation) pterosaur *Eudimorphodon ranzii* ([Wild 1978](#)). MCSNB 2888 is a partial but articulated skeleton with partly digested bone preserved within the abdominal cavity. The preservation of the alleged food items within the dorsal rib cavity and their etched texture indicative of digestive acids confirms the identification of these remains as gut content. Mild disruption of the torso has distributed the remains throughout the trunk region, and the largest and most concentrated remains are clustered into a mass 8 mm long by 7 mm wide. Additional food remains are represented by smaller fragments of bone and indeterminable debris. Most of the remains cannot be identified but ganoid scales preserved within the gut cavity have been attributed to the fish genus *Parapholidophorus* ([Wild 1978](#)).

As will become apparent throughout this review, fossils of the relatively abundant Jurassic (Tithonian), German rhamphorhynchid *Rhamphorhynchus muensteri* provide a wealth of information about the interactions of this species with other animals. Several specimens have been cited as showing gut content in the last century and, although not all are considered valid examples today, this species still offers the most complete and detailed picture of dietary preferences in any pterosaur. The best known *Rhamphorhynchus* gut content belongs to the Solnhofen Formation specimen SOS 4599 ([Fig. 1d](#)), a complete skeleton with large, partly articulated and somewhat digested fish remains in the trunk skeleton immediately anterior the pelvis ([Wellnhofer 1975, 1991](#), p. 160). The relative extent of the gut content is impressive, it occupying much of the torso alongside five lunate structures that may be either additional food items ([Wellnhofer 1975](#)) or gut tissues ([Unwin 2005](#)). There is no doubt that this specimen records genuine gut content as the pterosaur torso is articulated, the fish remains are enclosed by ribs and they have etched textures consistent with other partly digested fossil remains. The caudal fin morphology can still be determined in the gut content and shows that the prey item was swallowed whole and head-first. The fish remains provide data on the size of the *Rhamphorhynchus* gut: at 30.3 mm long, they occupy 60% of the torso length (taken as the length from acetabulum to

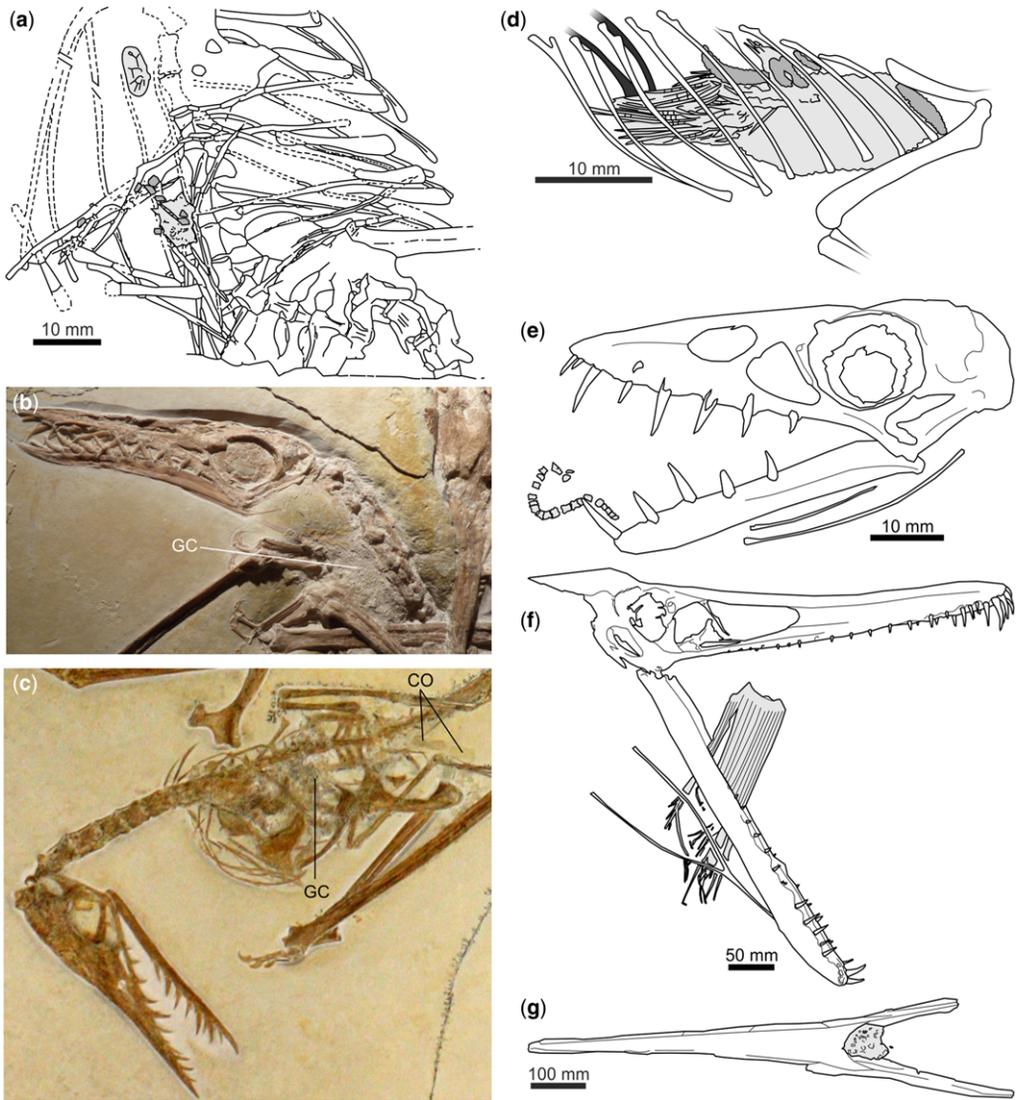


Fig. 1. Evidence of pterosaur foraging and digestion. (a) *Eudimorphodon ranzii* torso (MCSNB 2888) with fish scales and other gut content; (b–d) *Rhamphorhynchus muensteri* gut content and coprolites; (b) skull and neck of WDC CSG 255, showing partial fish remains in the throat region; (c) upper body of TMP 2008.41.001, showing poorly preserved gut content (GC) and a coprolite (CO); (d) SOS 4599 torso with substantial, part-digested fish remains; (e) *Scaphognathus crassirostris* skull and mandible with associated fish axial column (SMNS 59395), interpreted as regurgitate; (f) possible catastrophic feeding of *Ludodactylus sibbicki* (SMNK PAL 3828); (g) *Pteranodon* sp. mandible with fish regurgitate preserved between mandibular rami (AMNH 5098). Grey shading indicates ingested prey items. (a) After Wild (1978); (b) from Frey & Tischlinger (2012); (c) from Hone *et al.* (2015); (d) after Wellnhofer (1975); (e) after Bennett (2014).

anteriormost dorsal vertebra), suggesting that much of the *Rhamphorhynchus* abdomen could be occupied by ingested food. The relatively enormous gut content of SOS 4599 suggests that *Rhamphorhynchus* must have possessed highly mobile and

distensible throat tissues, much like those of modern fish-eating birds (Witton 2013).

Additional gut content has been found in the throat region of WDC CSG 255 (Fig. 1b), a complete and fully articulated *Rhamphorhynchus*

notable for its close association with a predatory fish (see below; Frey & Tischlinger 2012). This gut content comprises a small and complete fish skeleton similar in morphology to the common Solnhofen teleost *Leptolepides*. It is proportionally much smaller than that seen in SOS 4599, but was also swallowed head-first. The fish skeleton is preserved in close association with the cervical vertebrae, suggesting it was in the throat region – perhaps being swallowed – when the pterosaur died. This interpretation is supported by its lack of etched textures (Frey & Tischlinger 2012). Hone *et al.* (2013) identified further evidence of fish prey for *Rhamphorhynchus* from piscine teeth and scales preserved around the ventral torso margin of the complete *Rhamphorhynchus* specimen CM 11427. Another *Rhamphorhynchus* with gut content, reported by Hone *et al.* (2015), is the articulated and virtually complete skeleton TMP 2008.41.001 (Fig. 1c). The arrangement of the ribcage, enveloping of the gut remains by the pterosaur skeleton and excellent articulation of the torso verify that these remains are genuine stomach content. However, what this ingested material represents is mysterious as it is not well preserved. It seems to be composed of bone, and thus represents a small vertebrate, but further identification is difficult.

Rhamphorhynchus is not the only Solnhofen Formation pterosaur known with dietary remains. SMNS 59395 (Fig. 1e), a complete skeleton of the Solnhofen species *Scaphognathus crassirostris*, preserves an articulated, but relatively poorly defined piece of gut regurgitate (Bennett 2014). This is represented by an articulated vertebral column preserved in a loose spiral adjacent to the mandibular tip of the pterosaur, as if ejected from the animal during the decay process. So far as can be established, this represents a small individual of the common Solnhofen fish *Leptolepides*. The exact size of the fish is not known as the vertebral column is not complete, but the proportions of the vertebrae suggest that it was much smaller, relatively, than that devoured by the SOS 4599 *Rhamphorhynchus*.

Compelling evidence of gut content is rare among pterodactyloid pterosaurs. Perhaps the only incontrovertible dietary remains from this group pertain to specimens of the Late Cretaceous (Santonian), North American ornithocheiroid *Pteranodon*. The best known example is AMNH 5098 (Fig. 1g), an isolated mandible from the Niobrara Formation with regurgitated gut content between the mandibular rami, probably held in place by throat tissues before burial. This specimen is the longest-known example of pterosaur dietary remains still considered valid (Brown 1943) and was initially reported as comprising ‘backbones of two species of fishes and the joint of a crustacean’ (Brown 1943).

However, a reanalysis by Bennett (2001) suggests that only fish vertebrae are present. It is assumed that these jumbled, partly digested fish remains represent gut content regurgitated during death throes (Bennett 2001), as occurs in modern animals (Wings 2007). The bolus comprises disarticulated vertebrae, most of which are small (c. 7 mm in length), save for at least two that are much larger (c. 15 mm) and probably represent a second consumed species. Even these large vertebrae would have belonged to comparatively small fish, however, contrasting with the relatively enormous fish found in the gut of the SOS 4599 *Rhamphorhynchus*. Additional discoveries of possible *Pteranodon* gut content pertain to two specimens (SDSM 45719 and SDSM 69040) associated with *Enchodus* fish vertebrae from the Campanian Pierre Shale (Hargrave 2007). It is not uncommon for *Pteranodon* fossils to be associated with fish bones and these may represent additional dietary remains (Bennett 2001), although the widespread occurrence of fish fossils throughout the Niobrara and Pierre Shale deposits (Hargrave 2007) makes the palaeoecological significance of these associations uncertain.

Stomach content is known from two partial skeletons of the Cretaceous (Albian) ctenochasmatoid *Pterodaustro guinazui*, MIC-V263 and MIC-V243 (Codorníu *et al.* 2013). These Argentinian (Lagarcito Formation) remains are not food however, but sand and gravel interpreted as geogastroliths (Codorníu *et al.* 2013). The enclosure of these clasts within the body cavity of the pterosaur specimens, their distinction from local lithologies and evidence of a consistent diagenetic history all support their identification as inorganic gut content. It is thought that gastroliths were used by these pterosaurs to digest tough food items filtered from water through their unusual, sieve-like dentition. They remain the only pterosaur specimens known with gastroliths, despite the global distribution and relative abundance of pterosaurs with elongate, fine dentitions also potentially indicative of suspension-feeding.

Coprolites

The sole known pterosaur coprolite is associated with a complete *Rhamphorhynchus* specimen mentioned above, TMP 2008.41.001 (Fig. 1d; Hone *et al.* 2015). It is closely associated with the skeleton, being preserved immediately posterior to the pelvic region. Presumably, it was ejected from this individual shortly after it settled on the bed of the Solnhofen lagoon. The coprolite is small, broken into two roughly quadrangular pieces and variably composed of calcite masses (proximally) and hundreds of submillimetre, spike-shaped objects (distally). What the latter represent is not clear.

A vertebrate identification is unlikely given that they do not conform to obvious vertebrate anatomy or mineralogy typical of Solnhofen vertebrate fossils. Cephalopod hooklets have been intimated as a possible, albeit problematic identification (Hone *et al.* 2015). The potential effects that a complete digestive process will have on the recognizability of these remains has been noted (Hone *et al.* 2015).

Jaw and prod marks

Several pterodactyloid trackways are thought to show evidence of pterosaurs feeding in a wader- or shorebird-like manner (Fig. 2). Shallow, paired, rounded impressions interpreted as beak traces are associated with Jurassic *Pteraichnus* footprints from the Del Monte Mines, Utah (Fig. 2b; Summerville Formation, Oxfordian; Lockley & Wright

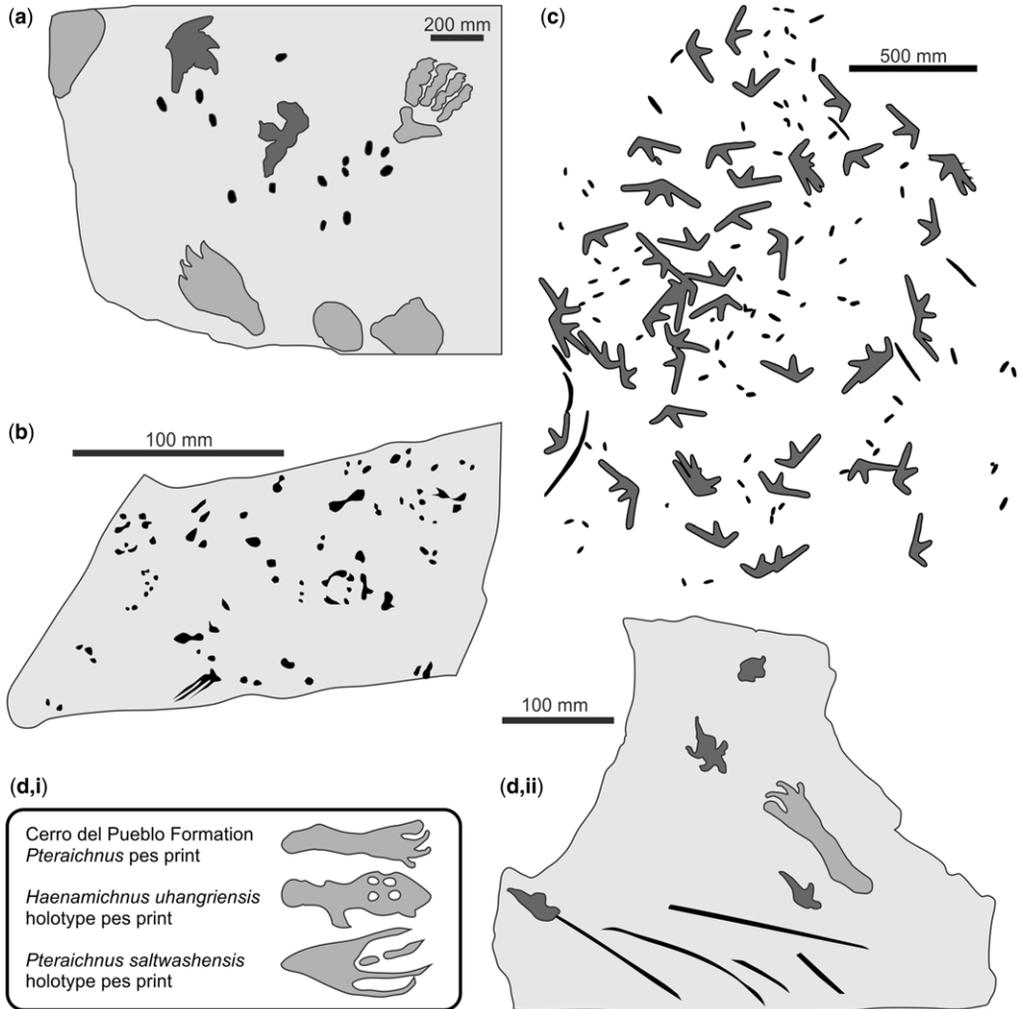


Fig. 2. Possible pterosaur feeding traces. (a) Early Cretaceous *Purbeckopos pentadactylus* tracks from the Purbeck Limestone Formation, England; (b) Late Jurassic foraging marks from the Del Monte Mines, Utah; (c) Late Cretaceous Blackhawk Formation tracks, Utah; (d) *Pteraichnus* sp. tracks and possible beak scrapes from the Late Cretaceous Cerro del Pueblo Formation, Mexico, argued here as more akin to the azhdarchid track *Haenamichnus* than the pterodactyloid track *Pteraichnus* (inset (d, i)). Shading represents trace identification: lighter grey shading shows pes prints; dark grey shading shows manus prints; and black shading shows possible foraging marks. (a) Modified from Wright *et al.* (1997); (b) modified from Lockley & Wright (2003); (c) modified from Parker & Balsley (1989); and (d) after Rodriguez-de la Rosa (2003).

2003), Lower Cretaceous *Purbeckopus pentadactylus* tracks from Dorset, England (Fig. 2a; Berriasian; Wright *et al.* 1997) and pterosaur tracks from the Late Cretaceous Blackhawk Formation, Utah, USA (Fig. 2c; Campanian; Wright *et al.* 1997; Mazin *et al.* 2003). Some controversy surrounds the track-maker identity of two of these tracks. *Purbeckopus* has been considered pterosaurian by most (e.g. Wright *et al.* 1997; Lockley *et al.* 2008), but not universally (Billon-Bruyat & Mazin 2003). The Blackhawk Formation tracks, which lack pes prints, have been suggested as pertaining to Hesperornithes (Parker & Balsley 1989) rather than pterosaurs, but the triradial morphology of these traces shows strong similarity to pterosaur manus prints and suggested a pterosaurian origin to Unwin (1997) and Mazin *et al.* (2003). The lack of pes prints at this site has been attributed to the ‘manus-only’ ichnological phenomenon known from several pterosaur track sites (Mazin *et al.* 2003; see Lockley *et al.* 1995; Li *et al.* 2015).

That pterodactylid tracks might be associated with foraging traces is not surprising given that modern animals often leave feeding traces when foraging on flat, muddy substrates. Traces left by birds pecking at soft substrate are very similar to those intimated for pterosaurs in being rounded, paired depressions which have profiles reflecting the track-maker’s bill tip anatomy. It remains possible that non-pterosaurian animals could have produced these marks (perhaps common pterosaur prey, as suggested by Lockley & Wright 2003) but this would require the second animal to leave no additional evidence of its presence and coincidentally produce tracks closely resembling those of pecking beaked animals. Such a hypothesis is not as parsimonious as explaining these marks as being made by foraging pterosaurs.

As well as pecking, sweeping movements of pterodactylid jaws may also be recorded in the pterosaur track record. These are long, shallow, sometimes curving channels in substrate closely associated with pterosaur manus or footprints. They are known from the Blackhawk Formation tracks mentioned above as well as alongside *Pteraichnus* prints from the Campanian Cerro del Pueblo Formation of North Mexico (Fig. 2d; Rodriguez-de la Rosa 2003). Similar, but broader marks attributed to sweeping pterosaur jaws are known from the Del Monte Mines tracksites (Lockley & Wright 2003). These marks were interpreted as ‘tail drags’ by Parker & Balsley (1989) rather than impressions of moving jaws, while those from the Cerro del Pueblo Formation were labelled as ‘tail drags of unknown origin’ by Rodriguez-de la Rosa (2003). If these traces were indeed made by pterodactylid pterosaurs, tail drags are an unlikely explanation. The caudal series of pterodactylids are

characteristically short compared to their limb lengths, and unlikely to contact the ground without adoption of a pronounced crouch. In contrast, the long jaws of pterosaurs could easily reach ground level from a standing pose (Witton & Naish 2008, 2015).

The palaeoecological insight offered by pterosaur foraging traces is limited by the current inability to allocate pterosaur tracks to specific clades. Thus, while these tracks demonstrate that pterodactylids sometimes fed terrestrially (e.g. Unwin 2005; Witton 2013), they provide little information about the habits of specific pterosaur groups. An exception to this problem might be the Cerro del Pueblo Formation tracks. Pterosaur pes prints from this formation are noted for being proportionally elongate compared to typical *Pteraichnus* prints (Rodriguez-de la Rosa 2003), a feature which characterizes pes prints of the Santonian/Campanian Korean pterosaur ichnotaxon *Haenamichnus uhangriensis* (Hwang *et al.* 2002). Further similarities between these prints are their distribution of padding around the heel and distal metatarsals, the lack of curving claw impressions and relatively short digits (Fig. 2di). These morphologies make the Cerro del Pueblo Formation tracks better approximations of *Haenamichnus* than *Pteraichnus*, and might suggest a similar track-maker. *Haenamichnus* is an exceptional pterosaur ichnotaxon in that a compelling case has been made for it belonging to a specific group, the Azhdarchidae, a group of often long-necked and gigantic edentulous pterodactylids which dominated Late Cretaceous pterosaur evolution (Hwang *et al.* 2002). If elongate pes prints are characteristic of azhdarchids, the Cerro del Pueblo Formation tracks and possible jaw prints might also be referable to this group and present direct evidence of azhdarchid foraging behaviour.

Doubtful or uncertain evidence of pterosaur foraging

A number of specimens intimated as recording pterosaur foraging behaviour can be considered uncertain, suspect or flawed. Issues associated with these specimens include a lack of evidence for flying reptiles being associated with certain trace fossils, misidentification of gut content or loss of specimens.

One such report concerns the earliest report of pterosaur gut content. This specimen of ‘*Pterodactylus propinquus*’ from the upper Jurassic of Germany (Broili 1938) is now lost (Wellnhofer 1970), but was said to preserve disarticulated fish debris in and around the region of the gular pouch, including a 10 mm-long series of articulated vertebrae and fin debris. The association of this material with the throat region of the pterosaur suggests that they

might represent fish remains regurgitated from the gut during death. However, the unknown whereabouts of this specimen makes the validity of these claims difficult to ascertain.

Two specimens of *Rhamphorhynchus* once suggested to possess gut content have since been reinterpreted. Döderlein (1929) suggested that the *Rhamphorhynchus* specimen BSP AS 1 772 preserved regurgitated gut content in its throat region, indicating a broad diet of fish, crinoids and crustaceans. Reanalysis of this specimen by Wellnhofer (1975) revealed no trace of these elements and cast doubt on Döderlein's observations. Wellnhofer (1975) suggested that the maxilla, several ribs and vertebrae of a small *Leptolepis*-like fish were found among the disarticulated torso skeleton of PTH 1954.39b (now SOS 2819). These elements have now been reinterpreted as sternal ribs belonging to the pterosaur, and not the remains of a second animal (Claessens *et al.* 2009).

Sanz *et al.* (2001) described a gastric pellet comprising four partial skeletons of juvenile birds, representing at least three different species, from the Early Cretaceous (Barremian) Las Hoyas Lagerstätte of Spain (LH 11386). The articulation of the skeletons within the pellet are said to rule out a mammalian or fish origin, and the size of the pellet is too large to have stemmed from known avian or lizard taxa from this locality. This regurgitate is therefore suggested to have originated with a pterosaur or small theropod dinosaur (Sanz *et al.* 2001). Evidence from *Rhamphorhynchus* specimens verifies that at least some pterosaurs swallowed small animals whole and adds credence to this hypothesis, but the identity of this pellet-maker cannot be conclusively established at this stage.

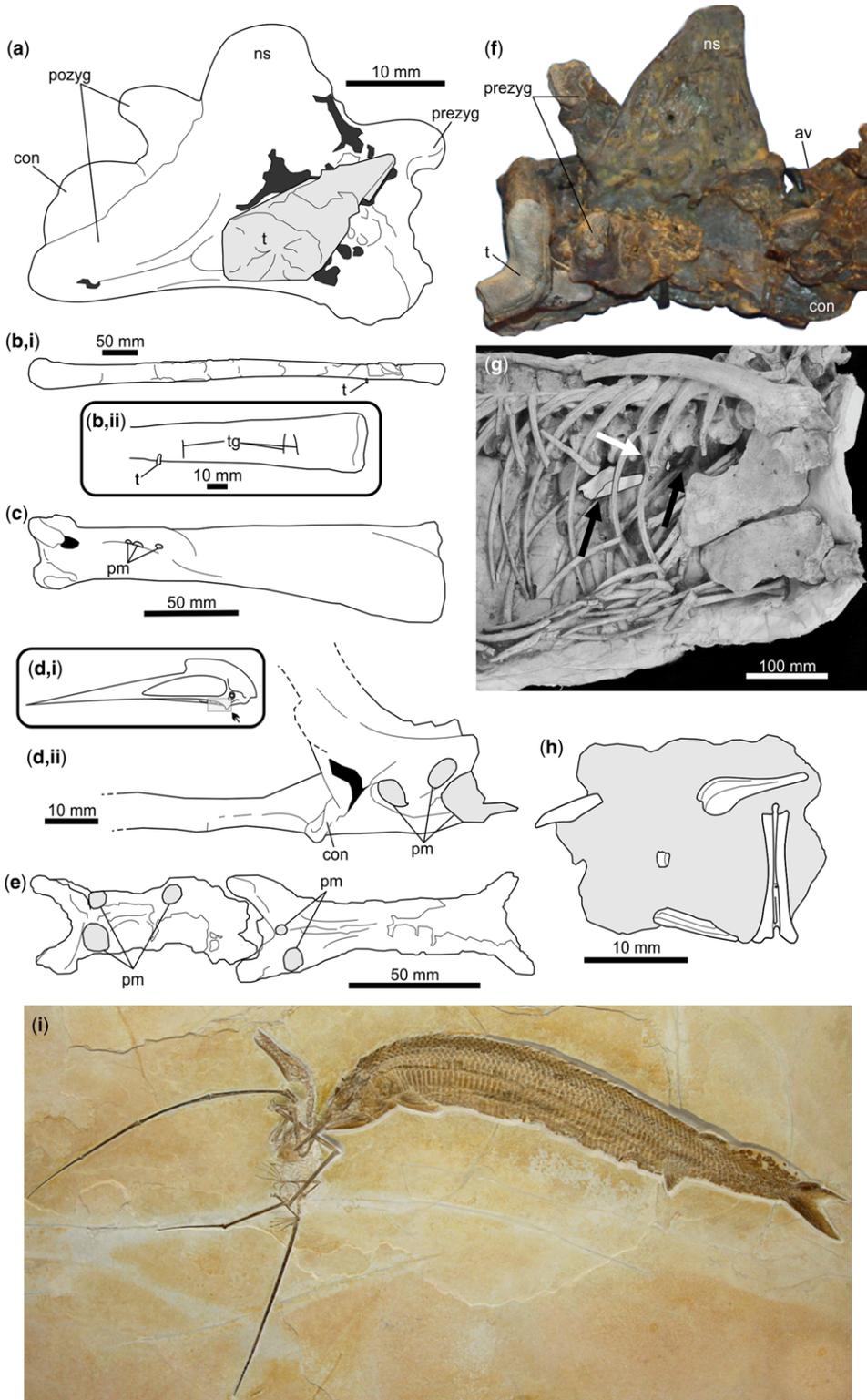
Ambiguous gut content is preserved in IVPP V14377, the Aptian, Jiufotang Formation holotype specimen of '*Nemicolopterus crypticus*' (Wang *et al.* 2008; a case for this specimen representing a juvenile of a contemporary tapejarid pterosaur species is made in Witton 2013). This comprises 'yellow coloured matrix occasionally forming rounded structures' thought to represent decayed soft tissues or amorphous gut content.

Aberrant evidence of possible pterosaur foraging is the association of a large leaf between the mandibular rami of the Early Cretaceous (Aptian) Brazilian pterosaur *Ludodactylus sibbicki* (SMNK PAL 3828, Fig. 1f; Frey *et al.* 2003). This Crato Formation specimen represents an articulated cranium, mandible and hyoid apparatus. Frey *et al.* (2003) argue that the likelihood of this leaf associating so intimately with the pterosaur fossil through taphonomic processes is low, suggesting that the animal must have apprehended the leaf when feeding. Given that the spear-like dentition of *Ludodactylus* appears better suited to piscivory than herbivory,

this association has been interpreted as a fossilized calamity: the pterosaur mistook the leaf for a component of its regular diet or apprehended the leaf with other food items, after which its sharpened fronds became lodged in the gular pouch. The frayed leaf margin in the gular region of the pterosaur fossil is interpreted as evidence of attempts to dislodge the leaf from the gular pouch, and the pterosaur's inability to do this led to its death (Frey *et al.* 2003). This explanation is not untenable, but there are attributes of the specimen which seem peculiar within this scenario. For instance, the hyoid apparatus is preserved on top of the leaf rather than enveloping it. Evidently at least this part of the jaw apparatus – which supports much of the throat tissue supposedly stabbed and stuck to the plant material – was not significantly attached to the leaf itself. A discussion could be had about the likelihood of the hyoid breaking free after the leaf was embedded, how detachment of the skull from the body might have disrupted the throat region, and so on. However, this would be no more testable than existing interpretations of this specimen, and therefore of little value to those wanting to understand pterosaur behaviour, diets and foraging methods. It may be most sensible to consider any explanation of this unusual fossil association as conjectural: this pterosaur may have made a fatal mistake when attempting to swallow a leaf, or it may not.

The damaged wings of two fossil insects have been ascribed to pterosaur predation by Tischlinger (2001). These specimens, representing the odonatan *Cymatophlebia longialata* (accessioned in a private collection) and the neuropteran *Archegetes neuropterum* (MM P.V. 1, 1/16), are both from the Jurassic Solnhofen Formation and are perfectly preserved except for the removal of the posterior right wingtip in the odonatan and anterior left wingtip in the neuropteran. The odonatan also demonstrates minor damage to the posterior margin of the right anterior wing which is confluent with the damage seen elsewhere on the specimen, suggesting a common cause. The broken wing margins of the odonatan specimen cut across the venation pattern to suggest that the wings were sheared rather than torn, while the damage inflicted on MM P.V 1, 1/16 appears to have largely resulted from tearing or ripping.

There are a number of reasons to entertain the idea that pterosaurs might have antagonized these insects. The damage suffered by these wings is greater than that produced by typical insect wing wear. At most, this may reduce wing area by 10% (Hedenström *et al.* 2001). The excellent quality of the insect fossils suggests that they were not transported far before burial and thus are unlikely to have been damaged during taphonomic relocation. Aggressive acts from other organisms seem a likely cause of these pathologies, and the fact the insects



are perfectly preserved other than their damaged wings might suggest that they were not attacked by an aquatic predator – it is unlikely that an aquatic animal would immediately ignore wounded, submerged prey after partly successful strikes. These points imply aggressive acts taking place above, rather than in, the Solnhofen lagoon. All three specimens share damage to their wing tips, matching areas considered likely to record failed feeding traces by modern birds predating lepidopterans (Wourms & Wasserman 1985), and the general extent of damage to each specimen might betray the involvement of a relatively large predator. Pterosaurs are perhaps the most suitable animals in the Solnhofen palaeobiota to predate volant insects and some taxa from these deposits – such as *Anurognathus ammoni* – seem specifically adapted for this form of predation (Wellnhofer 1991; Bennett 2007; Witton 2013). All this said, there is a limit to what damaged and torn insect wings can reveal about their origins, and direct evidence of pterosaur involvement with these insects remains wanting. Moreover, other scenarios (e.g. intraspecific disputes between insect individuals) provide equally compelling explanations of these specimens. They cannot, therefore, be considered wholly reliable insights into pterosaur foraging behaviour.

Pterosaurs as food sources

A number of specimens reveal that flying reptile tissues were eaten by a range of Mesozoic animals (Fig. 3). These comprise bite marks on pterosaur bones, teeth embedded in pterosaur specimens, gut regurgitate containing pterosaur wings and, most remarkably, pterosaurs preserved entangled with their predators.

Bite marks and shed teeth

Many vertebrate specimens from Late Cretaceous Chalk deposits of North America are associated with the teeth and tooth marks of carnivorous vertebrates, particularly those of sharks and other predatory fish (e.g. Schwimmer *et al.* 1997; Shimada 1997; Everhart 2005; Everhart & Ewell 2006). Several fossils of the Santonian pterodactyloid *Pteranodon* bear characteristic tooth gouges made by the serrated teeth of *Squalicorax* and the teeth of this shark are often found alongside *Pteranodon* specimens (Bennett, pers. comm. 2007). Full details of many of these specimens remain unpublished, but Ehret *et al.* (2015) have recently outlined two Mooreville Chalk Formation *Pteranodon* wing bones (RMM 3274 and ALMNH 2014.1.200) with serrated bite marks probably attributable to the shark *Squalicorax kaupi*. The ALMNH *Pteranodon* also bears bite marks from a second fish, presumed to be a saurodontid such as *Saurodon* or *Saurocephalus*. The anterior cervical vertebra of the *Pteranodon* specimen LACM 50926 (Niobrara Formation) is preserved with a *Cretoxyrhina mantelli* tooth wedged between vertebral processes (Fig. 3f), providing evidence that this large lamiform shark also ate pterosaurs. Work on this specimen, including a full description and determination of the relationship between shark tooth and pterosaur bone, is currently underway (D. Hone, pers. comm. 2015).

Several accounts of theropod dinosaurs biting or ingesting pterosaur bone are known (Fig. 3). Two of these are represented by tooth material embedded in pterosaur specimens, allowing identification of these animals to species level in both cases. Currie & Jacobsen (1995) reported an embedded tooth tip and several tooth gouges from the dromaeosaur *Saurornitholestes langstoni* in the tibia of TMP 92.83

Fig. 3. Utilization of pterosaur remains by other Mesozoic species. (a) Ornithocheirid cervical vertebrae with embedded spinosaurid tooth (WDC-SFB-001c, Santana Formation, Brazil, Early Cretaceous); (b) azhdarchid tibia (TMP 92.83, Dinosaur Park Formation, Canada; Late Cretaceous) with tooth gouges and embedded dromaeosaur tooth (see inset (b, ii) for detail); (c) ornithocheirid wing metacarpal with unidentified puncture marks (NMV P197962; Toolebuc Formation, Australia; Early Cretaceous); (d) *Quetzalcoatlus* sp. skull with puncture marks on posterior surface of quadrate (TMM 4422-30, Javelina Formation, USA, Late Cretaceous) (inset (d, i) shows region and point of view of (d, ii)); (e) *Eurazhdarcho langendorfensis* cervical vertebrae with crocodyliform puncture marks (EME VP 312, Sebeş Formation; Romania, Late Cretaceous); (f) *Pteranodon* sp. cervical vertebra with intimately associated *Cretoxyrhina mantelli* tooth (LACM 50926, Niobrara Formation, USA, Late Cretaceous); (g) *Velociraptor mongoliensis* torso with possible azhdarchid pterosaur gut content (white arrows, black arrow shows pathological rib) (MPC-D100/54; Tugrikin Shireh aeolian sandstones, Mongolia, Late Cretaceous); (h) gut regurgitate including *Rhamphorhynchus* bones (SMNS Inv.-No. 63990, Nusplingen Limestone, Germany, Late Jurassic); (i) associated *Rhamphorhynchus muensteri* and *Aspidorhynchus acutirostris* (WDC CSG 255, Solnhofen Formation, Germany, Late Jurassic; the *Aspidorhynchus* is 80 cm in length, measured from the tip of the snout the base of the caudal fin (see López-Arbarello & Schröder 2014)). Abbreviations: av, anterior vertebra; con, condyle; pm, puncture mark; postzyg, postzygapophysis; prezyg, prezygapophysis; t, tooth; tg, tooth groove. (a) After Buffetaut *et al.* (2004); (b, i) after photograph provided by Liz Martin-Silverstone; (b, ii) after Currie & Jacobsen (1995); (c) after Kellner *et al.* (2010); (d) after Kellner & Langston (1996); (e) after Vremir *et al.* (2013); (f) modified from a photograph provided by Dave Hone; (g) from Hone *et al.* (2012); (h) after Schweigert *et al.* (2001); (i) from Frey & Tischlinger (2012).

(Fig. 3b), a partial azhdarchid skeleton from the Late Cretaceous (Campanian) Dinosaur Park Formation, Canada. Buffetaut *et al.* (2004) demonstrated that larger theropods also ate pterosaurs with a spinosaurid tooth driven into an ornithocheirid cervical vertebra from the Early Cretaceous (Albian) Santana Formation of Brazil (WDC-SFB-001c, Fig. 3a). This tooth matches those described for the spinosaurid *Irritator challengeri*, also known from the Santana Formation (Sues *et al.* 2002). Owing to the lack of acid etching on the pterosaur material, it is suggested the vertebra was bitten, but not consumed, by this dinosaur.

Other animals known to have consumed pterosaurs include Crocodyliformes. Bite marks from these reptiles are recorded on the Romanian holotype specimen of the azhdarchid *Eurazhdarcho langendorfensis* (EME VP 312, Sebeş Formation, Maastrichtian), specifically the cervical vertebrae and distal metacarpal IV (Fig. 3e; Vremir *et al.* 2013). These rounded punctures, breaks and regions of crushing are reminiscent of marks left by biting Crocodyliformes, and such traces are common to bones from this formation (Vremir *et al.* 2013).

A series of tooth marks are seen on an isolated, Australian ornithocheirid wing metacarpal (NMV P197962, Fig. 3c) from the Early Cretaceous (Albian) Toolebuc Formation (Kellner *et al.* 2010). These shallow punctures, associated with slight crushing, are aligned in a row along the anterodorsal margin of the bone. The identity of the animal which created these bite marks is not known. A further possible record of pterosaur tissue consumption was reported by Kellner & Langston (1996), who suggested that three unusual openings in the quadrate of the azhdarchid, *Quetzalcoatlus* sp. specimen TMM 4422-30 (Fig. 3d; Javelina Formation, Maastrichtian), may record puncture wounds. Unfortunately, these openings also reveal little about the identity of the animal which produced them.

Pterosaurs as gut content

Pterosaur bone has also been found within the abdominal cavity of MPC-D100/54 (Fig. 3g), a specimen of the Campanian Mongolian dromaeosaur *Velociraptor mongoliensis* (Hone *et al.* 2012). The pterosaur material comprises only scant remains – fragments of limb bone shafts – but demonstrates the very thin bone compacta characteristic of Cretaceous pterodactyloids and is enclosed by ribs within the fully articulated dinosaur skeleton. Circumstantial evidence suggests that an azhdarchid identity is likely for the pterosaur material because, although it is too fragmentary to be linked with any specific pterodactyloid clade, azhdarchid pterosaurs

seem to have dominated latest Cretaceous faunas and are present in contemporary east-Asian deposits (Hone *et al.* 2012).

Pterosaur-consumer gut regurgitates

Fossil gut regurgitate containing pterosaur remains is rare, although a number of examples, now considered doubtful, have been reported (see below). Presently, only a gastric pellet from the Kimmeridgian Nusplingen limestones of Germany (SMNS Inv.-No. 63990, Fig. 3h) seems to be a valid example of a regurgitated pterosaur. This is thought to represent the partly digested remains of a *Rhamphorhynchus* (Schweigert *et al.* 2001), the specimen including at least a wing metacarpal, caudal vertebrae and wing finger fragments. It has been suggested that the regurgitate originated with a marine crocodylomorph or large predatory fish, both of which are known from the same deposit. Regurgitates of modern crocodiles do not contain any bony material but are instead composed of keratinous tissues such as hair and claw sheaths (Fisher 1981). If these characteristics were true for Mesozoic crocodylomorphs, a piscine origin for SMNS Inv.-No. 63990 seems more likely.

Pterosaurs preserved with their predators

A set of fossils from the Tithonian Solnhofen Formation show associated, complete skeletons of *Rhamphorhynchus muensteri* and the much larger predatory ganoid fish *Aspidorhynchus acutirostris* (Frey & Tischlinger 2012; Weber 2013). These associations, of which five are known, are believed to be the result of predatory acts from the *Aspidorhynchus*. Accessioned examples of these specimens belong to the Wyoming Dinosaur Centre (WDC CSG 255; Fig. 3i, described in detail by Frey & Tischlinger (2012)) and Bergér Museum (no specimen number), with the three remaining specimens being housed in private collections. All five examples are illustrated by Weber (2013). That these specimens are not just chance associations but have palaeoecological significance is suggested by several points. Associations between large vertebrates are very rare in the Solnhofen plattenkalk, making the recovery of five associations with identical taxonomic compositions unlikely to be a chance occurrence. All skeletons in these associations are in the same state of excellent preservation and articulation (soft-tissues occur in at least two of the pterosaurs – Weber 2013), suggesting the associated animals have similar taphonomic history. The arrangement of the associations is also consistent in that the pterosaurs are always located around the skull and jaws of their respective *Aspidorhynchus*. In some examples (e.g. WDC CSG 255) the wing

bones of the *Rhamphorhynchus* are preserved under the jaws of the neighbouring fish. These details point to the pterosaurs being seized, carried by and ultimately preserved with *Aspidorhynchus* individuals. That five near-identical examples of the same phenomenon are known suggests that interactions between *Rhamphorhynchus* and *Aspidorhynchus* may have once been common occurrences.

Doubtful or uncertain instances of pterosaurs as food sources

A specimen of Triassic gastric ejecta (MFSN no. 1891), once thought to contain remains of cf. *Preondactylus*, has traditionally been regarded as the stratigraphically oldest evidence of a predator–pterosaur interaction (Dalla Vecchia *et al.* 1989). Successive re-examination of the remains has seen their pterosaurian nature look increasingly doubtful, however. Dalla Vecchia (2003) thought them no more diagnosable than Pterosauria *incertae sedis*, and more recently Holgado *et al.* (2015) provided detailed, compelling evidence for the pellet comprising the bones of a protorosaurian archosauromorph. A further regurgitated pterosaur skeleton from Barremian/Aptian deposits of southern Mongolia was described by Kurochkin (1991), but subsequent analysis has revealed that bones within the specimen are far more bird-like than pterosaurian (Bakhurina & Unwin 1995). The association of two preserved feathers with the pellet corroborates this observation, and the specimen is now regarded as a small, possibly enantiornithine bird (Bakhurina & Unwin 1995).

Evidence of Santonian plesiosaurs ingesting pterosaurs in the Western Interior Seaway was recorded by Brown (1904). The plesiosaur specimen AMNH 5803, from the Campanian Pierre Shale Formation of South Dakota, was reported as having gut content containing broken pterodactylid limb elements. However, the specimen is badly weathered and the alleged pterosaur material is poorly preserved, casting some doubt over its identity (C. Mehling, pers. comm. 2007). An additional case of a marine reptile consuming a pterosaur was reported by Martill (1986) based on the discovery of delicate, hollow bones in the gut region of the Oxford Clay (Callovian) marine crocodile *Metrirhynchus* (LEIUG 90985). Subsequent analysis has suggested these bones may have belonged to a fish rather than a pterosaur (Forrest 2003).

Kellner *et al.* (2010) suggested that insect borings had been found in pterosaurs, citing the skull description of *Quetzalcoatlus* sp. authored by Kellner & Langston (1996) as evidence of this fact. This suggestion is confusing as no insect borings were mentioned in this description or other documentation of *Quetzalcoatlus* remains, and they may be

erroneous. Confirmed utilization of pterosaur tissues by invertebrates is known in the form of invertebrate rasping traces, possibly representing activity by bone-consuming osteopeltid gastropods, on pterosaur bones from the Albian Cambridge Greensand Formation (Unwin 2001). Encrusting organisms in the form of serpulid worms and remnants of oyster shells also occur on pterosaur fossils from this unit. All cases reflect the use of settled, probably long-dead pterosaur carcasses and therefore provide relatively little information concerning the lifestyles of flying reptiles, although they are notable for being rare examples of invertebrates utilizing pterosaur bones.

Discussion

Palaeoecologically informative pterosaur fossils have been considered extremely rare even in recent years (Wellnhofer 1991; Veldmeijer *et al.* 2007; Frey & Tischlinger 2012). While this remains generally true, increased discovery rates of pterosaur fossils and an elevated interest in their palaeobiology has augmented this record to the extent that these fossils should not be considered as scant as they once were. This improved palaeoecological pterosaur record is biased and selective, however. Factors that might be expected to play a role in providing palaeoecological data, such as raw abundance of fossils, or the recovery of pterosaur fossils from Konservat Lagerstätten, show little correlation with the current spread of pterosaur palaeoecological data (Fig. 4a). Notably, several newly discovered, major sources of pterosaur fossils – Brazilian and Chinese Konservat Lagerstätten – have made little impact on this dataset. Of the dozens of fossils described from these sites since the 1970s, only two Brazilian fossils are palaeoecologically informative, and one these is of questionable significance (Frey *et al.* 2003; Buffetaut *et al.* 2004). Contrarily, azhdarchid pterosaurs – which have a good, but not exemplary, fossil record, and no occurrences in fossil Lagerstätten – have a relatively good palaeoecological record. Correlation between fossil abundance and the pterosaur palaeoecological record is, at best, a loose one. For example, ctenochasmatoid pterodactyls are very well represented globally, and their record is augmented by their relative abundance in a number of Jurassic and Cretaceous Lagerstätten. However, this lineage provides no palaeoecologically informative fossils. The comparably represented lineages Ornithocheiroidea and Rhamphorhynchidae are also largely bereft of such fossils, save for certain genera (*Pteranodon* and *Rhamphorhynchus*, respectively) with substantial palaeoecological representation.

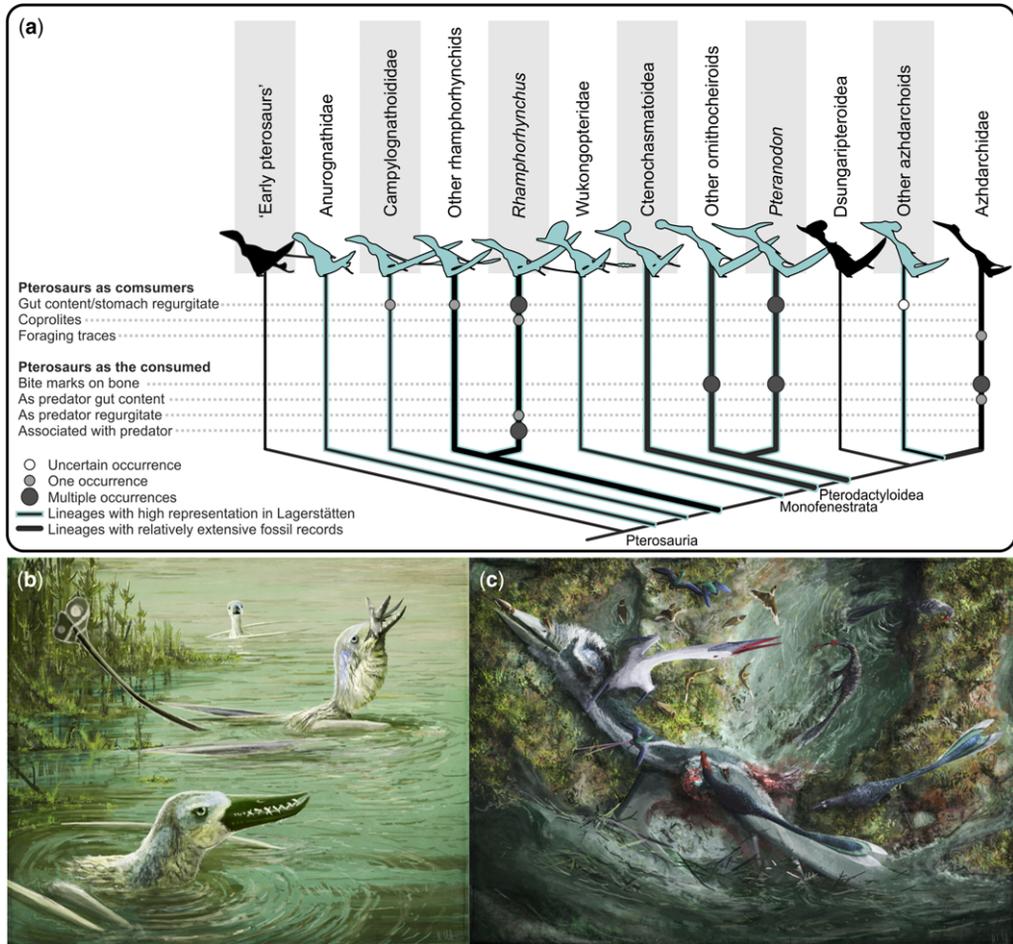


Fig. 4. Overview of the pterosaur palaeoecological record, and palaeoartistic scenes inspired by the fossils reviewed in this text. **(a)** Highly simplified phylogeny of pterosaurs with palaeoecological data mapped to clades, factored against abundance of fossils and taxon distribution in fossil Lagerstätten. Topology slightly modified from Lü *et al.* (2012); **(b)** restoration of *Rhamphorhynchus muensteri* as an aquatically adapted pterosaur, foraging for fish while immersed in water (the individual in the middle-distance is based on the SOS 4599 specimen); **(c)** a 6 m wingspan azhdarchid is eaten by several different components of an inland Mesozoic ecosystem, including the dromaeosaurid *Saurornitholestes langstoni* (scene based on TMP 92.83).

These observations suggest that factors other than fossil abundance and exceptional preservation are shaping the pterosaur palaeoecological record. It may be that the specific behaviours and habits of pterosaurs themselves are important here. For instance, it is increasingly thought that pterosaur diets may have been varied (see Witton 2013 for a review), and many food types now discussed for these animals have low preservation potential (examples include invertebrates and nutritious plant matter). Moreover, recent proposals of pterosaur foraging habits suggest that many taxa were feeding in habitats unsuited to rapid burial and

fossilization. Modern concepts of pterosaur foraging strategies are diverse (Unwin 2005; Ósi 2011; Witton 2013) and include dedicated scavenging (Witton 2012; Martill 2014), insectivory (Bennett 2007), terrestrial foraging (Witton & Naish 2008, 2015; Witton 2015), frugivory (Wellnhofer & Kellner 1991), piscivory (Veldmeijer *et al.* 2007) and suspension feeding (e.g. Chiappe *et al.* 2000). Many of these strategies are best employed in terrestrial habitats which are unconducive to high-quality fossilization. Pterosaur anatomy may be a factor, too. Tooth marks or embedded teeth have yet to be reported from small pterosaurs, or the more delicate

components of larger species, perhaps reflecting an inability of small, fragile pterosaur bones to record predatory acts rather than simply breaking when handled by consumers. The selective nature of the pterosaur palaeoecological record may reflect a complex interplay of preservational, behavioural and anatomical factors that are only fully countered by a minority of pterosaur lineages.

Pterosaurs in Mesozoic foodwebs

An obvious question concerning the fossils reviewed here is whether they represent predatory acts on living pterosaurs, or scavenging acts on dead ones. It seems likely some of these examples represent genuine predation. Specifically, the multiple *Aspidorhynchus* and *Rhamphorhynchus* associations, which are perfectly preserved, consistently arranged and of identical taxonomic composition probably record predatory behaviour. Frey & Tischlinger (2012) provide a plausible explanation for these fossils as failed predatory attempts from *Aspidorhynchus*. They suggest that, once apprehended, at least some *Rhamphorhynchus* were too large, complex or entangled for the fish to ingest, and that the animals died when mistakenly entering the toxic bottom waters ultimately responsible for the excellent preservation of Solnhofen fossils. Frey & Tischlinger (2012) invoke skim-feeding as a possible reason for *Rhamphorhynchus* to be close enough to water to be seized by a fish. Numerous authors have been critical of the skim-feeding pterosaur hypothesis (e.g. Chatterjee & Templin 2004; Humphries *et al.* 2007; Witton & Naish 2008, 2015) and it seems unreasonable – and unnecessary – to invoke the involvement of this behaviour here. A less speculative interpretation is simply that *Rhamphorhynchus* routinely entered aquatic settings and their surroundings, perhaps entering water directly (see discussion, below), and were potential prey for aquatic predators.

Circumstances surrounding other examples of pterosaurs being ingested by carnivorous animals are less clear. It is apparent that the pterosaurs recorded in these specimens were dead or dying when being eaten because none show evidence of recovery from their wounds. All records of theropods feeding on pterosaurs are suggested to be acts of scavenging rather than predation. Currie & Jacobsen (1995) cite the size disparity between the 2 m-long dromaeosaur *Saurornitholestes* and a 6 m wingspan azhdarchid as reason for assuming that the dinosaur was eating carrion. The Brazilian pterosaur vertebra associated with an *Irritator* tooth reverses this scenario with a large theropod and comparatively small pterosaur (Buffetaut *et al.* 2004), but scavenging is still cited as favourable over active predation. Greater equality of size is

represented by the *Velociraptor* and azhdarchid specimen described by Hone *et al.* (2012), the pterosaur being thought to span 2–3 m across the wings and the dromaeosaur being of similar length. Hone *et al.* (2012) suggest that the pterosaur would have been a challenging prey item for *Velociraptor*, despite the estimated 44% weight advantage given to the dinosaur, and conclude that this specimen also represents scavenging behaviour. Shark feeding traces on *Pteranodon* bones are also interpreted as scavenging behaviour owing to the lack of healing exhibited on the pterosaur fossils (Ehret *et al.* 2015). The relatively small size of *Squalicorax* (typically less than 3.0 m long) is often used as reasoning for its bite marks representing scavenging behaviour on contemporary marine animals (Schwimmer *et al.* 1997).

How pertinent these conclusions are remains uncertain, as equally compelling arguments could be made for these specimens representing predatory scenarios. Volant animals are routinely killed by terrestrial or even semi-aquatic animals of all sizes in modern times (e.g. Emmons 1986; Hutton 1987; Pérez-Higareda *et al.* 1989; Thorbjarnarson 1990; Wang 2002), and it is not unreasonable to suppose that dromaeosaurid and spinosaurid theropods might have been capable of subduing pterosaurs. Likewise, the mass disparity between even large *Pteranodon* and sharks such as *Squalicorax* and *Cretoxyrhina* was probably tremendous: using modern shark masses as a guide, Witton (2013) suggested that even a modestly sized, 3 m-long Mesozoic shark would weigh between 100 and 250 kg, considerably more than the highest reasonable mass estimates for large *Pteranodon* (Witton & Habib 2010). Such a discrepancy in mass suggests that, so long as they could reach them, these large, sharp-toothed predators would not struggle to overpower swimming or floating *Pteranodon*. A modern equivalent of this behaviour is seen when living seabirds are attacked and eaten by sharks (Wetherbee & Cortés 2004), suggesting that this scenario is not implausible for ancient communities. Ultimately, ascertaining the predatory or scavenging nature of these specimens is difficult, perhaps impossible, from scraps of ingested bone, rare bite marks and solitary embedded teeth.

A similar conclusion might be drawn about the preserved gut content of pterosaurs themselves. Being mostly disarticulated fish bones, they provide little insight into whether these pterosaurs preyed or scavenged their meals. Exceptions are the SOS 4599 and WDC CSG 255 *Rhamphorhynchus* and SMNS 59395 *Scaphognathus*. The articulated dietary remains of these specimens suggest that they were eaten whole, or nearly whole, and imply that the pterosaurs in question were either involved in killing the ingested animals or able to scavenge

them relatively quickly after their death from other causes.

Less speculative use of the pterosaur palaeoecological record is using its basic data – such as the nature of the predatory animals eating pterosaurs, or the dietary preferences of pterosaur species – to test functional and biomechanical hypotheses of flying reptile habits. The predicted lifestyles of *Rhamphorhynchus* as a soaring-adapted, marginal marine predator of pelagic prey and of *Pteranodon* as a sea-going specialist (e.g. Wellnhofer 1975; Bennett 2001; Unwin 2005; Tütken & Hone 2010; Witton 2013) are entirely consistent with their palaeoecological records. Both demonstrate multiple interactions with pelagic species, showing them both as consumers and the consumed in their respective ecosystems in the manner predicted by functional studies. Recent studies have shown that these animals have numerous adaptations for efficient take-off from aquatic settings (including reduced hindlimbs, small torsos, ‘hatchet-shaped’ or ‘warped’ deltopectoral crests and others – see Habib & Cunningham 2010), suggesting they may have routinely entered water (Fig. 4b). This may account for their relatively good palaeoecological records, elevated quality of fossil preservation and common encounters with piscine carnivores (also see Lockley & Wright (2003) and Hone & Henderson (2014) for discussions of pterosaur swimming).

The azhdarchid palaeoecological record also matches lifestyle predictions for this group made through functional studies. The habits of these pterosaurs have long been controversial, but recent, seemingly largely accepted work on azhdarchid functional anatomy and taphonomy suggests that they foraged for small animals in terrestrial environments (Witton & Naish 2008, 2015). The Mexican pterosaur trace fossils and associated possible beak scrapes, suggested here to belong to azhdarchids, might record a member of this group engaging in ground-based foraging. This possible feeding trace has further significance in demonstrating that azhdarchids could reach the ground with their beak tips, despite their relatively inflexible necks. Neck arthrology has been a point of contention for many azhdarchid lifestyle hypotheses (see discussions in Witton & Naish 2008, 2015), making possible trace fossils of azhdarchid jaw tips useful evidence for the terrestrial foraging hypothesis. Additional support for this idea comes from examples of azhdarchid bodies being eaten by typical ‘terrestrial’ Mesozoic faunas, such as dinosaurs and Crocodyli-formes (Fig. 4c). This meets taphonomic assessments showing that the azhdarchid record is biased towards inland, continental habits and not waterways or seas (Buffetaut *et al.* 1996; Witton & Naish 2008).

Studies of pterosaur lifestyles remain in their infancy, but the fossils reviewed here provide useful tests of palaeoecological hypotheses proposed for these often controversial animals. The expansion of this dataset through new discoveries and reappraisals of historic remains should be pursued by those wanting to understand the role of pterosaurs in Mesozoic ecosystems. To that end, curators, collectors and researchers are encouraged to carefully check for and record pterosaur specimens with evidence of their places in Mesozoic food webs.

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