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Research Paper

Beneath the waves: Extraordinary dietary insights from a dismembered ichthyosaur from the lower Cretaceous

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ABSTRACT

Marine reptile lineages thrived throughout the Mesozoic era and are known to have performed diverse roles in marine ecosystems. Ichthyosaurs are characterized by their often dolphin-like convergences and thunniform bodies, having evolved a variety of forms and sizes that presumably represent niche diversity within their bauplan. Here, we report a spectacular discovery from the Lower Cretaceous of Australia: a dismembered adult ichthyosaur, *Platypterygius australis* (~6–7 m in length), with preserved gut contents alongside massive bite marks on its skeleton that together, illuminate its role as both predator and prey within the Eromanga Basin marine ecosystem.

Numerous bite marks are preserved on the vertebral centra of the ichthyosaur; some are split with corresponding halves missing, suggesting evidence of oral processing. Given their size, the bite marks were likely inflicted by the largest marine predator in the region, the pliosaur *Kronosaurus queenslandicus*. The gut contents of the *P.australis* specimen were preserved as globular concretions, likely formed from the ichthyosaur's spilt digestive tract. Neutron tomography NT scanning revealed one of these concretions contained fragments of fish, cephalopods, and two pterosaur bones, including a dentary fragment. The pterosaur dentary fragment was identified as a near-exact match to a previously unnamed taxon within Ornithocheiroidae. This discovery provides the first definitive evidence of food web interactions among these three groups and marks the first recorded instance of an ichthyosaur consuming a pterosaur or part thereof.

1. Introduction

Ichthyosaurs were a highly successful group of Mesozoic marine tetrapods. Their diets, particularly among Jurassic forms from Lyme Regis, Dorset, England (Buckland, 1836) and surrounding areas, are well known from gastric masses and coprolites, which reveal squid and fish as primary food sources (Pollard, 1968; Keller, 1976; Massare, 1987; Böttcher, 1989; Lomax, 2010). Evidence for ontogenetic dietary shifts has been identified in Lower Jurassic specimens of *Stenopterygius quadriscissus*: juveniles preferred burst-swimming fish, subadults consumed both fast-moving fish and cephalopods, and larger adults predominantly preyed upon cephalopods (Dick et al., 2016). While evidence of ichthyosaurs preying on other animals is rare, the Cretaceous ichthyosaur *Platypterygius australis* (McCoy, 1867) McGowan, 1972, from the Toolebuc Formation, central Queensland, Australia, suggests that this later species may have had a more opportunistic diet. This conclusion is supported by the discovery of gut contents from one individual (QM F16811), which included remains of actinopterygian fish, hatchling-sized marine protostegid turtles, and enantiornithine bird remains (Kear et al., 2003).

In this study, we report the scattered remains of a mature *P.australis* (estimated to be 6–7 m), from the Toolebuc Formation, Richmond, Queensland Australia. The scattered remains of this *P.australis* specimen show evidence of deep bite marks on several vertebrae, indicating predation or scavenging and carcass dispersal over > 10 m. The size and morphology of the marks implicate a large pliosaur, most plausibly

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Kronosaurus queenslandicus Longman, 1924—known to have been among the region's largest marine predators. Pliosaur bite marks are seemingly rare, with few documented examples (e.g., on an *Eromangasaurus* skull (Thulborn and Turner, 1993); on a small *K.queenslandicus* skull and plesiosaur propodials (Clarke and Etches, 1991), and an isolated ichthyosaur vertebral centrum (see Fig. 6 Martill, 1996).

Associated nodules were recovered among the disarticulated elements between the skull and scattered trunk region; one nodule contained partially exposed bones that were mechanically prepared and scanned by neutron tomography. Mechanical preparation revealed two pterosaur fragments, while neutron tomography revealed several belemnites and isolated fish remains (vertebrae and ribs). The location amongst the KK F1435 remains and the structure of one of these concretions appears to represent a globular mass that we have hypothesized was once soft tissue that encapsulated stomach content. As such, pterosaurs could be potentially added to the diverse food range of *P. australis* alongside birds, hatchling protostegid turtles, belemnites and fish (Kear et al., 2003).

In accepting that the pterosaur fragments are in fact gut content, it provides the first direct evidence of trophic interactions linking pterosaurs, ichthyosaurs and pliosaurs.

2. Methods

2.1. Neutron tomography scanning

The *P.australis* skeleton was excavated and divided into six separate plaster casts, which are now showcased at Kronosaurus Korner Museum (KKM), Richmond Queensland. Most of the associated skeletal material remains in their original relative positions. Additionally, a section preserving four globular nodules was located directly behind the ichthyosaur's skull on the same bedding plane as the skull and the scattered postcranial remains. A nodule identified as potentially containing gut contents was imaged using the thermal-neutron tomography instrument DINGO at the Australian Nuclear Science and Technology Organization's (ANSTO) (Garbe et al., 2015). For this measurement, the instrument was configured in high-fluz mode, with a collimation ratio (*L/D*) of 500. A ZWO ASI2600MM Pro CMOS camera (liquid-cooled, 16-bit, 6248 × 4176 pixels) coupled with a Makro Planar 24 mm Carl Zeiss lens and a 50 μm thick ZnS/^{6}LiF scintillator screen (RC Tritec AG). This configuration yielded a pixel size of 45.45 × 45.45 μm and a field of view of 200 × 200 mm^2. As the specimen was larger than the instrument field-of-view, the specimen was imaged in two successive scans separated by a vertical translation of 150 mm. Each of the two scans consisted of 1250 radiographic projections, acquired equiangularly as the specimen was rotated 180° about its vertical axis. To improve signal-to-noise, each radiograph consisted of 3 × 8 s exposures (Mays et al., 2017). Total measurement time was 20 h. The raw radiographs were denoised, averaged and binned to a voxel size of 90.9 × 90.9 μm in post-processing using ImageJ, reconstructed with Octopus Reconstruction 8.8.1, and the reconstructed data segmented and visualized using *Dragonfly* v.2022.2 (Comet Technologies Canada Inc). Images and measurements of the partial mandibular rostrum of Ornithocheiroidae, gen. et. sp. indet. QM F44423 (Fletcher and Salisbury, 2010), suspected to be a direct match of the potential gut content, were captured using a Dino-Lite (5 MP AM7013MZT).

2.2. Surface scanning

The specimen is displayed in plaster jackets. We imaged it at multiple angles using a DJI Mavic 2 drone to produce 3D surface meshes. Because the pterosaur jaw (QM F44423) is small we captured close-up images with a Dino-Lite for 3D processing. AgiSoft PhotoScan Standard (Version 2.0.2.16404) was used to generate surface meshes from the drone and Dino-Lite images. Additionally, an Artec Space Spider handheld laser scanner (www.artec3d.com/portable-3d-scanners/artecspider-v2) was used to create surface scans of three ichthyosaur vertebral centra that show definitive bite marks; meshes were processed in Artec Studio Professional (www.artec3d.com/3d-software/artec-studio).

2.3. Pairwise analysis

Pairwise morphological variation analysis was employed to compare the potentially ingested pterosaur fragment with other Australian pterosaur specimens (White and Campione, 2021). To account for damage and/or distortion, we initially exported our 3D meshes as *.obj files into Zbrush 2023 (Pixologic Inc, USA). This software allowed for scaling, preliminary digital alignment and the digital removal of non-comparable features such as cracks and misalignments, preventing erroneous cloud-to-mesh C2M and cloud-to-cloud C2C results. The iterative closest point (ICP) algorithm (Besl and McKay, 1992; Pomerleau et al., 2015), implemented in the open-source software Cloud Compare (CC) v.2.9.1 (https://www.cloudcom-pare.org/main.html), was utilized to quantify our visual assessments.

Pairwise analysis comparisons were performed using point cloud-to-mesh (C2M), and cloud-to-cloud (C2C) methods. The distance for C2M or C2C comparisons was calculated as the absolute Hausdorff distance (also known as Pompeiu–Hausdorff distance) (Rockafellar and Wets, 2005), which was projected onto the target specimen using a 'heat-map'. Colder colour distributions indicate low distance values (indicating close matching between the target and reference specimens), while warmer colour distributions signify increasing distances (indicating greater variation) (White and Campione, 2021). This methodology has also been successfully employed to compare unguals of *Australovenator* (White and Campione, 2021), pterosaur femora (Pentland et al., 2022), Mesozoic mammal teeth (Rich et al., 2022), and humeri of *Megaraptor namunhuaiquii* (Calvo et al., 2025).

3. Locality and geology

3.1. Discovery site

The *P.australis* remains were discovered at 'Dig Site One', located approximately 12 km northwest of Richmond (−20.644575° S, 143.100564° E), Queensland, Australia (Fig. 1). The site consists of a highly weathered artificially exposed outcrops of the Toolebuc Formation, Lower Cretaceous, upper Albian (Tucker et al., 2013). These sediments were deposited in a cool to temperate inland shallow marine setting at a time when vast areas of Australia were covered by shallow seas (Frakes et al., 1987; Campbell and Haig, 1999; Richards et al., 2021). The Toolebuc Formation has an average thickness of ~ 15 m and covers roughly 300,000 km2 (Jiang et al. 2018). It consists of oil- and kerogen-rich shales, coquinitic and nodular limestones and minor labile sandstones, deposited under maximum flooding, fully marine conditions in an epeiric basin system (Henderson, 2004; Jell, 2013; Richards et al., 2021).

3.2. Fauna

The Toolebuc Formation is one of Australia's most prolific sources of Mesozoic marine fossils. Invertebrates are abundant and include molluscs (pelecypods, gastropods) ammonites and belemnites (Day, 1969; Exon and Senior, 1976; Henderson and Kennedy, 2002). Teleosts are well represented, for example the ichthyodectiforms *Cooyoo australis* Woodward, 1884 (Lees and Bartholomai, 1987) and *Dugaldia emmilta* Cavin and Berrell, 2019, the aspidorhynchid *Richmondichthys sweeti* Bartholomai, 2004, and the pachycormid *Australopachycormus hurleyi* Kear, 2007a. Marine tetrapods include protostegid sea turtles *Cratochelone berneyi* Longman, 1915, *Bouliachelys suteri* Kear and Lee, 2006, and *Notochelone costata* Owen, 1882; the endemic ichthyosaur *Platypterygius australis* (McCoy, 1867) McGowan, 1972; the elasmosaurid plesiosaur *Eromangasaurus australis* (Sachs, 2005), Kear, 2007b, and the

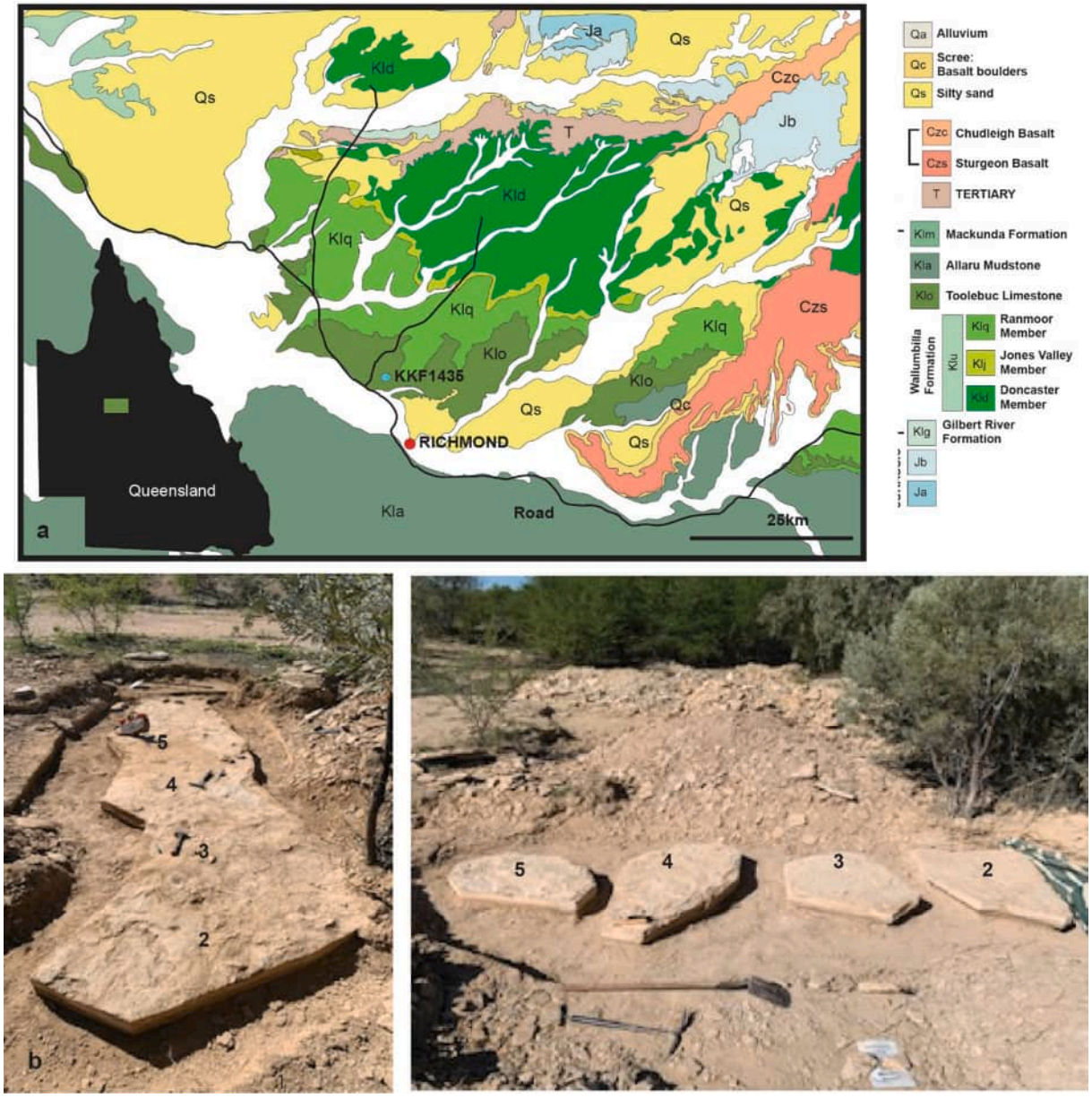

Fig. 1. Surface geology of the area where KK F1435 was discovered. (a) Black silhouette of Queensland, Australia, showing the geological units and the region where the specimen was discovered (Geoscience Australia 2021). (b) The slab or rock containing blocks 2–5 before being separated for transportation. (c) sectioned up slabs 2–4 insitu.

pliosaurid *Kronosaurus queenslandicus* Longman, 1924. Avian remains include the enantiornithean birds *Nanantius eos* Molnar 1986 and *Tenuicruris piscanexum* White et al., 2026. Pterosaurs recovered from the formation include *Aussiedraco molnari* Molnar and Thulborn, 1980, *Haliskia peterseni* Pentland et al., 2024, *Mythunga camara* Molnar and Thulborn, 2007, *Thapunngaka shawi* Richards et al., 2021, 2024 and an indeterminate ornithocheiroid specimen QM F44423 (Fletcher and Salisbury, 2010). Only rare, fragmentary terrestrial dinosaurs are recorded, typically interpreted as 'bloat and float' carcasses: the ornithopod *Muttaburrasaurus langdoni* Bartholomai and Molnar, 1981, and an indeterminate titanosauriform (Molnar, 1991; Molnar and Salisbury, 2005; Poropat et al., 2017).

4. Results

4.1. Identity of the ichthyosaur KK F1435

Platypterygius has long been regarded as a 'waste-basket' genus for Cretaceous ichthyosaurs whereby it was considered the only genus present until late-surviving Jurassic genera and new genera from the Barriasian to Cenomanian were increasingly being reported by the mid 2000′s onwards (Zammit, 2010; Fischer, 2016; Cortes et al., 2021). There has also been considerable debate regarding the identification of *Platypterygius* specimens within Australia. Early studies had been hindered by poor locality recordings, descriptions and figures through lack of direct side-by-side comparisons to support whether the named species *P.australis*, *P.longmani* and *P.marathonensis* should be synonymized. That debate was summarised by Kear (2003) and Zammit (2010), who concluded that *P.australis* should be recognised as a single valid species based on cranial and limb characters. Zammit (2010) also designated a

neotype (NMV P12989) because the original type material is presumed lost. Numerous ichthyosaur discoveries from the Eromanga Basin, particularly around Richmond, have been reported since those assessments, so additional material that could refine the diagnosis is now available. Detailed taxonomic revision is beyond the scope of this report but based on the anatomical overlap between KK F1435 and the diagnostic features listed for *P.australis* (Zammit, 2010), we identify KK F1435 as *P.australis*.

4.2. Diagnosis

The following diagnostic characters for *P.australis* are derived from Wade (1990), Kear (2002) and Zammit et al. (2010). KK F1435 is a large ichthyosaur, estimated at ~ 6–7 m in length. The skull has been extensively fractured by impact from the deadfall; therefore, accurate assessment of morphological overlap with the skull characters is limited. The humerus has a tapering crest-like dorsal trochanter and three distinct distal facets for articulation with the ulna, radius, and preaxial accessory element. One of the trunk vertebral centra was preserved with its neural spine, which was clearly divided into anterior and posterior peaks by an asymmetric V-Shaped apical notch. The caudal centra from the tail stock region bears weakly developed haemal arch facets.

Ophthalmosauridae Baur, 1887.

Platypterygius von Huene, 1922.

Platypterygius australis (McCoy 1867) McGowan, 1972.

4.3. Taphonomy of KK F1435

KK F1435 specimen is preserved in relative articulation from skull to tail, indicating portions of the skeleton remained connected by soft tissue when it settled on the seafloor. The skull is preserved in ventral view. The rostrum shows multiple fractures and many anterior teeth are dislodged. The premaxilla appears anterior to the dentary (an apparent overbite), but this offset is likely exaggerated or artificial owing to proximal shattering of the dentary from the dead-fall. A major fracture occurs ~ 20 cm from the rostral tip. The dentary is displaced proximally with substantial breaks near the posterior end of the dentary and through the pre-maxilla-nasal suture. Posterior to these breaks the skull is severely fractured with many fragments unidentifiable. The basisphenoid is detached and was recovered among scattered vertebrae and ribs ~ 1.5 m posterior to the skull (Figs. 2 and 3).

Bones of the neck are absent. The trunk region is highly scattered, many bearing bite marks or exhibiting crushing consistent with oral processing. This pattern does not extend to the tail, which, is partially articulated, with minor displacement caused by scavenging or currents (Fig. 3g).

The majority of the presacral region is missing, with only six partial ribs, a left scapular, left humerus, a semi-articulated left forefin, nine complete isolated dorsal vertebral centra (one with an articulated neural spine), six partial vertebrae and a section of crushed vertebral centra with some associated neural spines. A semi-articulated caudal vertebral section is preserved (belonging to the pre-flexural region), while only a few isolated vertebrae from the post-flexural region are preserved. Isolated phalanges pertaining to the other fins are scattered throughout the specimen (Fig. 3).

Several of the vertebral centra preserve bite marks along their fractured margins. These bite marks are conical and are more consistent with the type of damage expected from a pliosaur rather than the blade-like punctures typically associated with sharks. The counter parts of each of the following vertebral centra have not been discovered and were presumably consumed (Fig. 4).

Vertebral centra (v1) is 138 mm wide with an anteroposterior thickness of 47 mm (Fig. 4a–g). It is split mediolaterally with the cancellous bone preserving two buttressing puncture wounds on one side (labelled 1 and 2 in Fig. 4a–g) labelled (1 and 2) and several suspected bite marks on the other labelled (3). Puncture wound (1) is 5 mm from the edge of the lateral margin on the anterior surface and is 26 mm deep, angling ventrally. Puncture wound (2) may indicate oral processing, where the initial bite (1) encountered some resistance before shifting, potentially extending the bite; alternatively, both impressions represent two consecutive teeth. This is best visualised by the internal surface of the scan, where the marks appear conical (Fig. 3b, f and g). On the opposite side, subtle bite marks (3) line the broken margin (Fig. 4a–e).

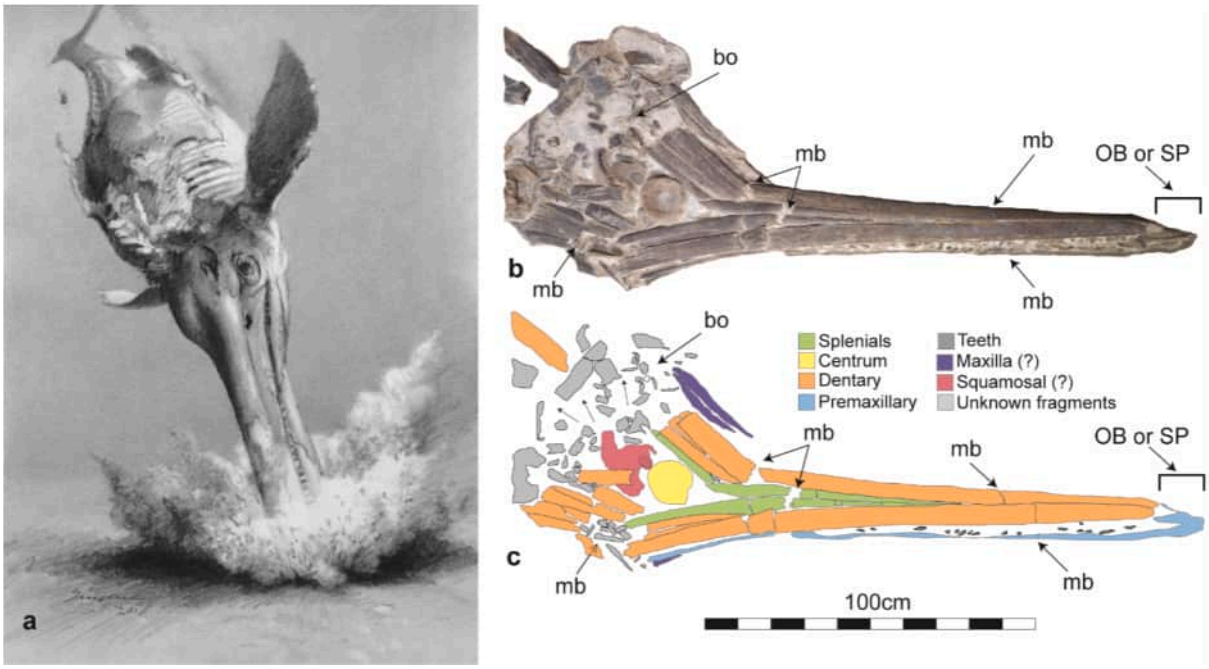

Fig. 2. Ichthyosaur dead–fall: photographs and schematic outlines showing skull breaks from impact damage. (a) Reconstruction sketch of the ichthyosaur during dead–fall impact on the seafloor. (b) Ventral–view photograph of KK F1435. (c) Schematic outline of broken bones, ventral view. Abbreviations: bo, blown-out; mb, major break; OB or SP overbite or shunted proximally.

Fig. 3. Three-dimensional mesh images of KK F1435 with bite marks and stomach content. (a) Near-complete skull; (b) Stomach content block; (c) articulated autopodium; (d) Basiosphenoid, seven dorsal vertebrae, an isolated neural spine, five partial ribs, left scapula, humerus, and ten isolated digits; (e) Two complete dorsal vertebral centra (one with articulated neural spine) and five partial dorsal vertebral centra that preserve bite marks (v1 and v3), one vertebral centra is shattered; (f) One complete dorsal vertebra, possibly six other shattered dorsal vertebrae along with portions of their neural spines, and one split vertebrae with a rib deformed against the fractured edge (v2); (g) Semi-articulated pre-flexural caudal vertebrae primarily consisting of mostly of pre-flexural vertebrae and a few scattered post-flexural vertebrae; (h) Silhouettes of the approximate *in situ* position of each block. Abbreviations: b, basisphenoid; f, femur; h, humerus, ip, ischiopubis; n, neural spine; p, phalanx; r, rib; s, scapula, sc stomach content; v1-v3 dorsal vertebral centra with tooth marks.

Vertebral centra (v2) is 148 mm tall and 60 mm anteroposteriorly wide (Fig. 4h–k). It is split dorsoventrally and bears a puncture wound (1) near the ventral margin (Fig. 3i–k), with the wound exhibiting a slight medial angle consistent with an anterior penetration. A rib is preserved ventral and adjacent to the dorsal margin of the fracture and is crushed and deformed against the broken vertebral margin (Fig. 4h).

Vertebral centra (v3) measures 132 mm wide with an anteroposterior thickness of 47 mm (Fig. 4ln). It is split mediolaterally with two puncture wounds near the central portion of the centrum. The wounds appear to have penetrated straight through from the anterior surface to the posterior side.

4.4. Stomach contents analysis

Four concretions were discovered in the same bedding plane as the scattered ichthyosaur specimen, ~0.5 m posterior to the skull. The mass preserving the suspected gut contents is a globular concretion with four rounded peaks, exposed on a flat bedding surface (Fig. 5a, b). Two bones slightly projected from these rounded peaks at discovery and were mechanically prepared prior to neutron-tomography scanning (Fig. 5c, d). One is a pterosaur dentary fragment preserving two complete alveoli and one partial alveolus plus a short portion of the medial ridge (Fig. 5c, h). The alveoli are slightly raised from the jaw line, elliptical with their long axes parasagittal and opening dorsolaterally onto a sloping shelf-like surface. Distinct sulci between alveoli, mark positions of opposing maxillary teeth. One end of the fragment is taller than wide, while the opposite end is approximately equal in height and width; the latter matches the morphology expected for the specimen's anterior end. The second bone is tentatively identified as the posterior end of the same pterosaur's dentary, showing a depression interpreted as the mandibular glenoid.

Neutron tomography recovered no additional pterosaur elements but did reveal several belemnites, isolated fish vertebrae and ribs, and shell fragments. These remains, including the pterosaur fragments, are oriented at irregular angles—often perpendicular to the expected horizontal alignment of the flat marine substrate. The soft-tissue package that housed the gut contents likely moved with the currents, entraining shells and grit from the seafloor (Fig. 5).

There is a chance the ichthyosaur fell onto the pterosaur remains or that currents swept the pterosaur fragments into the ichthyosaur assemblage; however, given the rarity of pterosaur remains and the fact the fragments occur in a concretion within the ichthyosaur assemblage – with belemnites preserved perpendicular to the bedding plane – we consider stomach contents the more likely hypothesis. The discovery of only two fragmentary elements does not preclude this interpretation: the ichthyosaur remains were widely scattered and the trunk region was

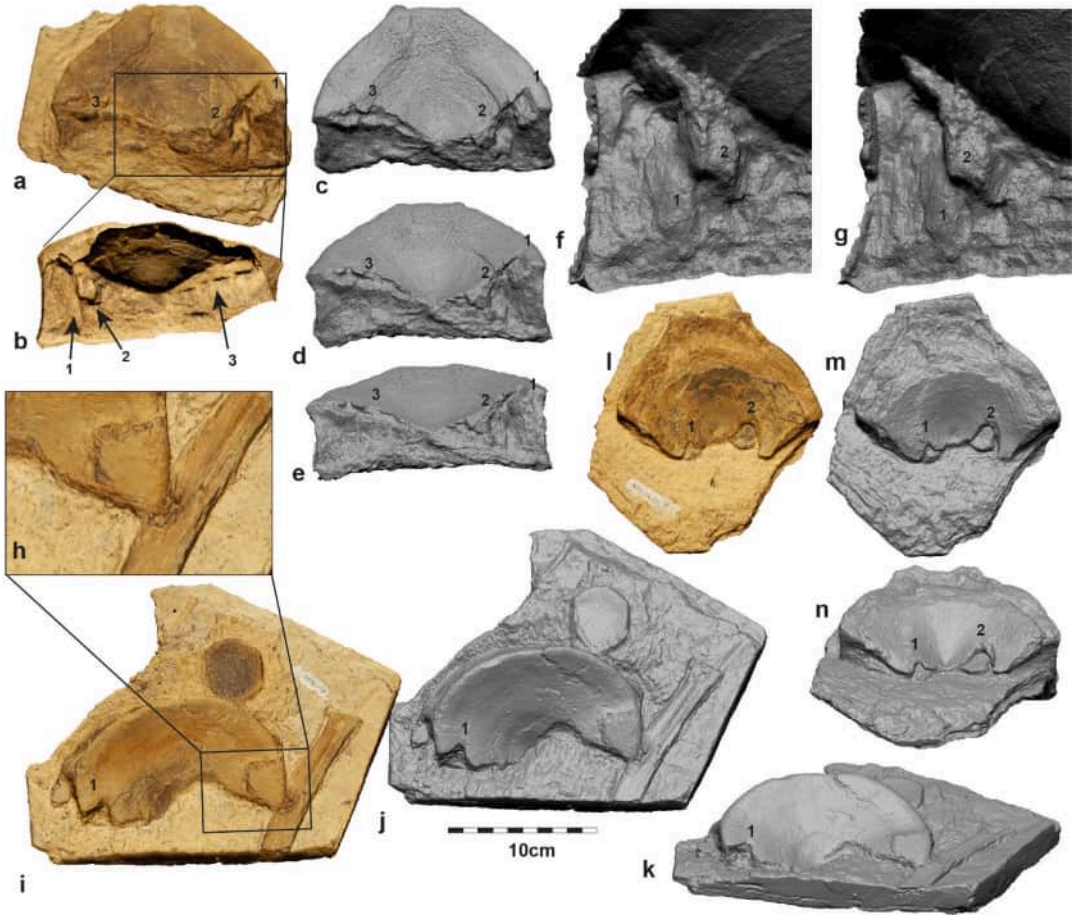

Fig. 4. Vertebral centra showing preserved bite marks. Each bite mark is numbered to link with different views. (a-g) Vertebral centrum 1. (a) with two puncture wounds on one side (1 and 2) and several on the other (3); (b) enlarged region of the internal surface of the vertebral centra shows the morphology of the marks; (c-e) anterior to medial views of the bite marks; (f-g) close-up internal views of the specimen displaying the two large bite marks; (h-k) Vertebral centrum 2. (h) close-up of deformed rib on the broken edge of vertebral centrum 2; (i) Vertebral centrum 2, with deformed rib on its broken dorsal surface; (j-k) Vertebral centrum 2 showing different angles of the bite marks; (l-n) Vertebral centrum 3, showing two bite marks near the centre of the vertebra. Note: the specific locations of vertebral centra are highlighted in Fig. 3.

clearly targeted by predators and scavengers, which could have removed or dispersed additional pterosaur material. There is no clear evidence of acid etching on the pterosaur fragments; however, absence of etching does not preclude consumption. A similar lack of acid etching was reported for the gut contents remains of another ichthyosaur (QM F16811), which preserved hatchling-sized turtles and a bird tibiotarsus (Kear et. al. 2003). Likewise, the fossilized gut contents of the Cretaceous crocodile *Confractosuchus sauroktonos* White et al., 2022 show little acid etching, despite extant crocodilians having extremely potent stomach acids. These observations suggest alternative explanations—such as death occurring soon after the last meal—may account for the preservation, a hypothesis previously prosed in both cases.

The dentary fragment preserving multiple alveoli, enabled taxonomic identification through detailed comparison with Australian pterosaur material. It shows close affinity to "Anhanguera-like" Australian taxa (notably *Thapunngaka shawi* Richards et al., 2021, 2024) and is near-identical to the dentary of an Ornithocheiroidae, gen. et. sp. indet. (QM F44423; Fletcher and Salisbury, 2010). Pairwise analysis indicated that the closest alignment was between alveoli 3–4, with QM F44423 being the closest match. A slight variation exists between KK F1435 and QM F44423 due to a groove between alveoli 3–4, which would have received an opposing tooth in KK F1435 but does not appear to be preserved in QM F44423 (Fig. 6).

5. Discussion

The taphonomy of KK F1435 is best explained as a sequence of predation or natural oral processing leading to death, subsequent carcass deadfall, and later consumption by predators and/or scavengers. Distinct bite marks preserved on three vertebral centra (Fig. 4) and the size of the punctures point to a large pliosaur as the most likely attacker; no other contemporaneous predators (e.g., sharks or other ichthyosaurs) possess teeth large enough to produce such marks. Many bones are crushed, split or partially missing in patterns consistent with consumption (Figs. 3 and 4), and surviving fragments indicate chunks of the carcass were torn off and crushed in the mouth prior to swallowing. This pattern—tearing, repositioning in the jaws, and crushing of bone—matches documented feeding behaviour of aquatic predators (Hocking et al., 2017) and is consistent with a predator hovering above the carcass while processing it, allowing partially processed vertebral fragments to resettle among the scattered remains.

Ventral preservation of the KK F1435 skull obscures most teeth. Comparative lateral skull material of *P.australis (*MV P231150, Toolebuc Fm., Boulia) illustrates a heterogeneous dental array: anterior teeth project forward, the next series are longer and slightly posteriorly inclined, mid-rostral teeth are robust and orthal, and the most caudal teeth are short, stout, and closely packed. These caudal teeth likely did not occlude between upper and lower jaws but instead interacted with soft tissues, potentially filtering water while retaining prey. Overall, the

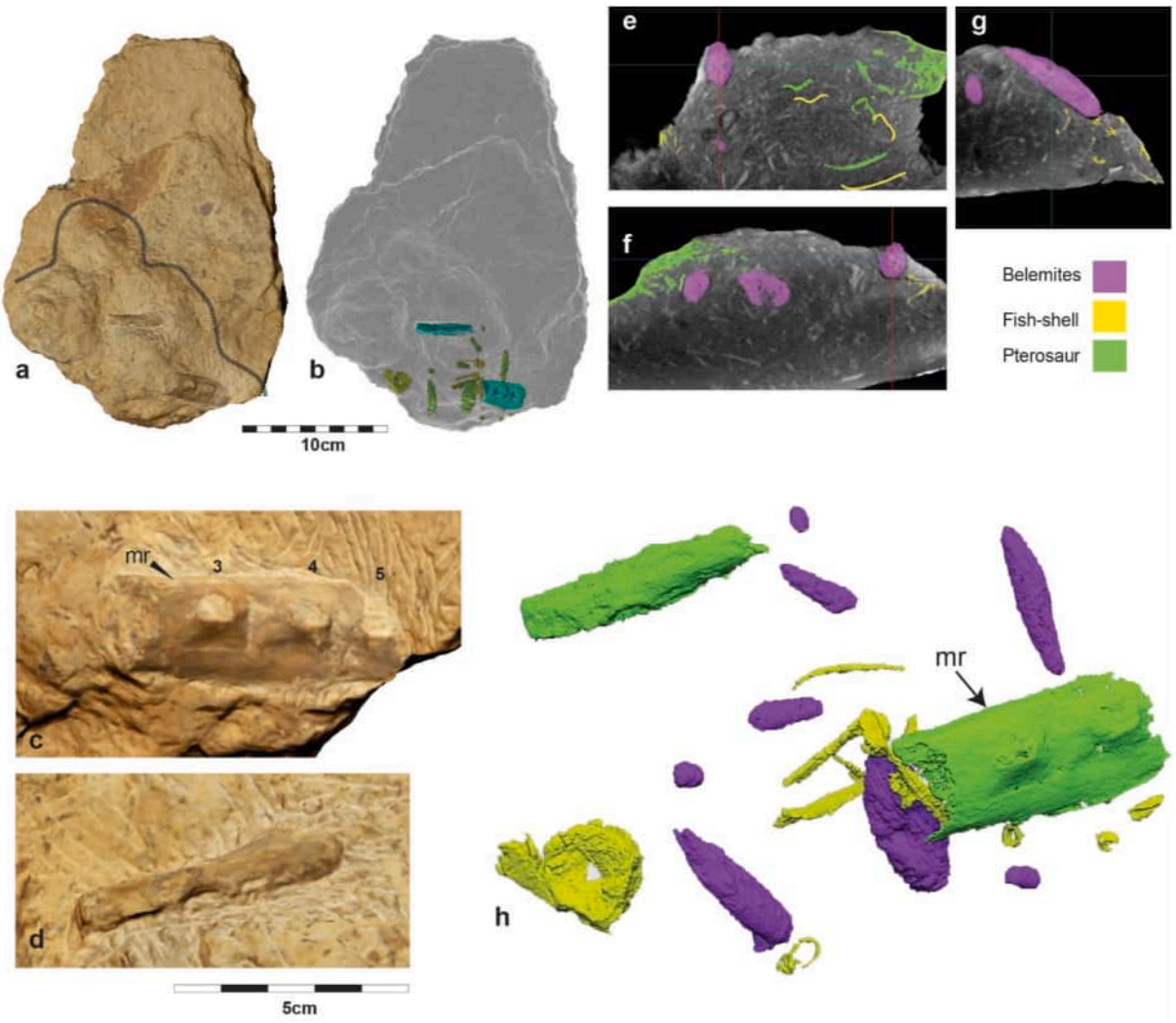

Fig. 5. The stomach content block. (a) Stomach content block with globular region highlighted and the two pterosaur bones exposed; (b) Stomach content block in transparency displaying pterosaur, shell fragments and belemnites; (c) *in situ* close-up of the pterosaur dentary fragment; (d) close-up digital renders of the pterosaur dentary fragment; (e) 3D render of possible proximal end of the pterosaur dentary of the quadrate-articular contact; (f-h) Neutron tomography scan images of the gut content including belemnites, fish, shell fragments and pterosaur; (i) 3D renders of the gut content. Abbreviations: mr, medial ridge.

dentition implies sequential functions—slash, grip, pierce, crush—and a filtering role, suggesting advanced oral processing and a potentially broad diet for *P.australis*. Historic observations (e.g., Kiprijanoff, 1881) and numerous platypterygine specimens show distal teeth that radiate anteriorly; taphonomic processes (deadfall of bloated carcasses, rostral splitting, tooth loss, rostral fractures, and posterior cranial trauma) commonly remove rostral tips and obscure this occlusal morphology in many specimens.

KK F1435 exhibits clear posterior cranial impact damage with shattered elements but no associated tooth marks. The basiosphenoid, was located 0.5 m posterior to the skull. It appears that when the rostrum struck the seafloor, the right side of the skull blew outward laterally, possibly dislodging the basiosphenoid. The premaxilla appears to overlap the dentary (an apparent overbite), but this apparent configuration may be taphonomic in the dentary impacted the seafloor first, fractured, and was forces proximally (Fig. 2).

We previously suggested the remains were likely still connected by soft tissue prior to settling on the sea floor. Given the specimen's condition, it is possible that much of the thoracic viscera and ribs were consumed, causing carcass deflation, and that additional osteological elements were consumed once the carcass reached the seafloor. Under such a scenario, anterior translocation of abdominal contents—as observed in KK F435—is not surprising.

Trophic interactions preserved in the fossil record are exceptionally rare but, when present, provide direct insights into ancient ecosystems. Multi-level interactions comparable to that documented here have been reported elsewhere (e.g., Kriwet et al., 2008; Smith and Scanferla, 2016), while notable two-level interactions include vertebrate predators with intact prey in their stomachs (e.g., Hu et al., 2005; White et al., 2022). Repeated predator–prey interactions have also been documented (e.g., Frey and Tischlinger, 2012).

Pliosaurs, as apex predators exceeding > 10 m in length with massive skulls and large teeth produced bite traces that are seldom preserved or recognised—likely because their feeding behaviour resulted in minimal discarding of skeletal elements. For example, a near-complete plesiosaur torso and a 70 cm turtle were found within *K.queenslandicus* body cavities (McHenry, 2009), indicating many prey skeletons were retained and thus not available for secondary fossilization with bite marks.

The preservation of KK F1435 is therefore exceptional: numerous crushed bones, bite marks and evidence of oral processing are present, including bite marks that dissect articular faces (Fig. 4). The bites fractured the vertebrae, with the corresponding halves not preserved and presumably consumed (Figs. 3 and 4). These taphonomic features support the hypothesis that pliosaur prey processing involved

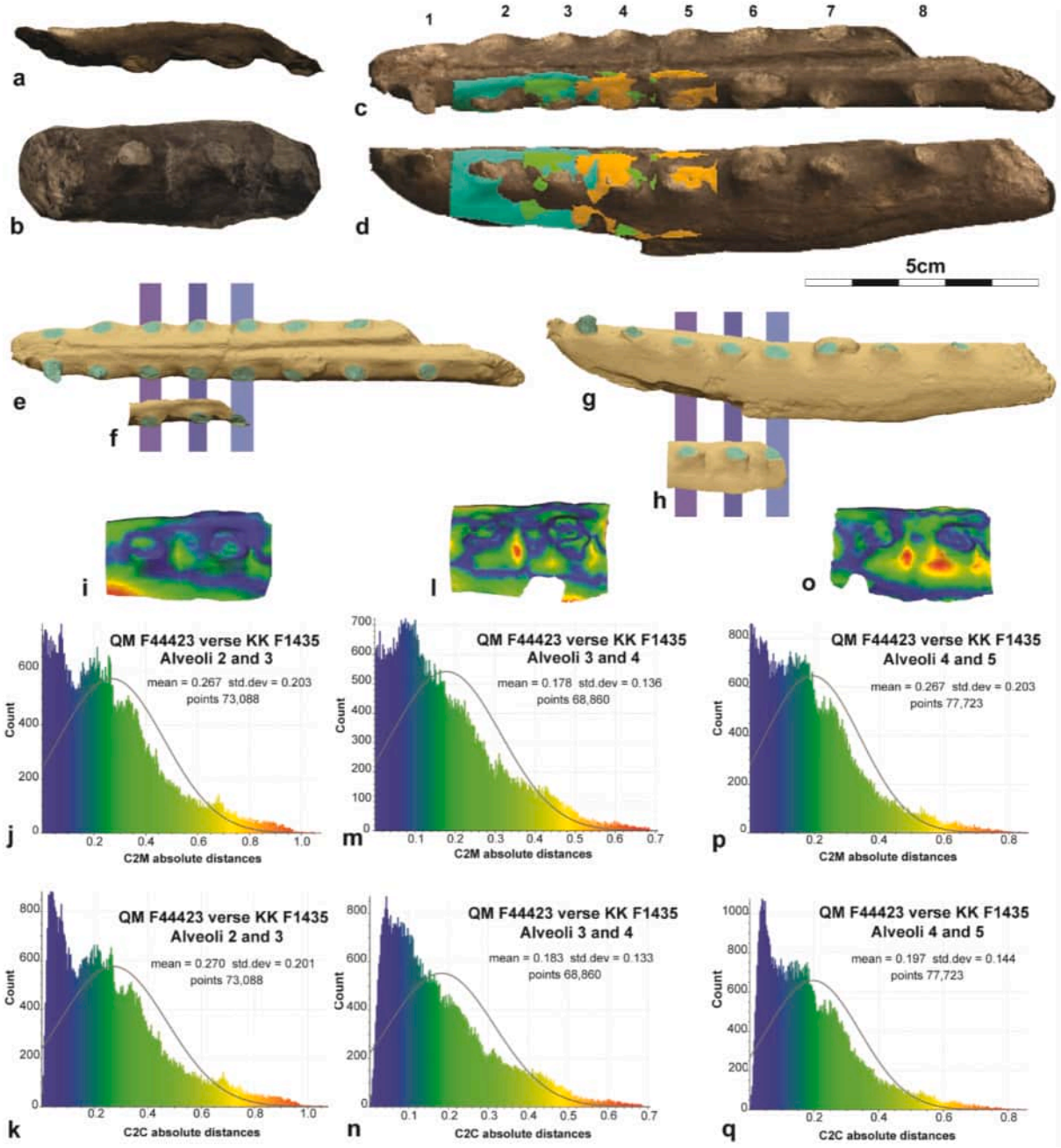

Fig. 6. Comparison of dentary fragments of alveoli 2 and 3, 3 and 4 and 4 and 5 from Ornithocheiridae indet. QM F44423 with KK F1435 (digested pterosaur) using pairwise analysis. KK F1435; (a) Occlusal view; (b) Labial view; QM F44423; (c) Occlusal view; (d) Labial view; (e) Occlusal view inter-alveolar alignment QM F44423; (f) Occlusal view inter-alveolar alignment KK F1435; (g) Labial view inter-alveolar alignment QM F44423; (h) Labial view inter-alveolar alignment; (i-k) Comparison of alveoli 2–3; (l-n) Comparison of alveoli 3–4; (o-q) Comparison of alveoli 4–5.

repositioning in the mouth by inertial bites followed by crushing bites from medial teeth—an analogy to crocodilian processing behaviour (Foffa et al., 2014; Cleuren and De Vree, 2000; White et al., 2022).

Previously described pliosaur bite marks range from deep elliptical depressions with small concentric fractures (Thulborn and Turner, 1993) to circular punctures (Jain et al., 2025). The bite marks in KK F1435, however, do not form complete elliptical depressions; instead, bones have split along the bite marks, and one vertebral centrum preserves conical-like marks on the fractured margin (Fig. 4a–g) indicating high-force crushing and fracture propagation rather than simple indentation.

Ichthyosaur diets are commonly reported to include fish and cephalopods (Pollard, 1968; Keller, 1976; Massare, 1987; Böttcher, 1989; Lomax, 2010; Druckenmiller et al., 2014; Dick, Schweigert and Maxwell, 2016). Direct evidence for *P.australis* likewise includes fish, cephalopods, turtles, birds and—presented here for the first time—pterosaurs as stomach contents. These records support the hypothesis that *Platypterygius* and perhaps other Cretaceous ichthyosaurs were opportunistic, feeders (Kear et al., 2003). Collectively, these discoveries provide a unique glimpse into the trophic interactions within this Early Cretaceous marine palaeoecosystem (Fig. 7).

6. Conclusion

The preservation of the *P.australis* KK F1435 provides a rare window into Toolebuc Formation trophic interactions. The fractured rostrum

Fig. 7. Life reconstruction of the probable trophic interactions identified with the specimen KK F1435 featuring *Platypterygius australis,* pterosaur (Ornithocheiroidae indet) and *Kronosaurus queenslandicus.* Artwork by Peter Trusler.

and blown-out skull appear to result from a post-mortem deadfall impact rather than bite damage. Several globular concretions occur among the remains; one contains pterosaur fragments. Given its position, morphology, and the perpendicular orientation of belemnites within the mass, we interpret the concretion as gut contents — potentially the animal's last meal. If so, this would be the first documented case of an ichthyosaur consuming a pterosaur and supports interpretations of opportunistic feeding in Early Cretaceous ichthyosaurs (Kear et al., 2003). The specimen also preserves one of the most extensive arrays of pliosaur bite marks reported. Together, these features record an exceptionally rare three-level trophic chain preserved in the fossil record.

CRediT authorship contribution statement

Matt Andrew White: Writing - Designed and wrote the manuscript, Writing – review & editing, Data curation, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Joseph John Bevitt:** Resources, Data curation. **Mackenzie Jordan Enchelmaier:** Writing – review & editing, Software, Resources, Data curation. **Kevin William Petersen:** Resources, Data curation. **Peter William Trusler:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Travel costs, time and monetary expenses towards this research was self-funded.

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Author contributions

MAW and PWT wrote the manuscript. KWP conducted the fieldwork and recovered the specimen. MAW and PWT created the figures. JJB scanned the concretion containing the pterosaur fragments and provided the data for 3D processing. MAW processed the 3D data. MJE surface scanned the *Platypterygius* vertebra centra with bite marks and the stomach content concretion creating three-dimensional images for figure generation. PWT created the life restoration artwork. PWT, MJE, JJB reviewed initial drafts of the manuscript.

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