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Predation of the Early Cretaceous (Late Albian) pachycormiform, *Australopachycormus hurleyi* Kear, in Queensland's Eromanga Basin

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ABSTRACT

Additional remains of the marine pachycormiform fish, *Australopachycormus hurleyi* Kear, 2007, have been located in collections of the Queensland Museum from the Early Cretaceous (Late Albian) Toolebuc Formation of the Eromanga Basin, near Boulia in central western Queensland. The specimens significantly extend knowledge of the neurocranium, especially relating to the morphology of the orbital area, maxilla and mandible. The additional specimens show evidence of predation, with one possibly also having been regurgitated in a partially digested state. □ *Australopachycormus hurleyi*; neopterygian; pachycormiform; Early Cretaceous (Late Albian); Eromanga Basin; Toolebuc Formation.

Investigation of collections of fossil actinopterygian fishes in the Queensland Museum, both in Brisbane and in its material loaned to the Stonehouse Museum in Boulia, central western Queensland, has revealed the presence of two additional neurocranial specimens of the pachycormiform, *Australopachycormus hurleyi*, Kear, 2007. These not only provide additional morphological detail to that outlined in Kear (2007) but also exhibit details of preservation that help interpret their taphonomy. Currently known material of *A. hurleyi*, including the holotype, QMF52641, has mostly come from the marine Toolebuc Formation of Early Cretaceous (Late Albian) age, from the poorly exposed western rim of the Eromanga Basin near Boulia, within the Great Artesian Superbasin, defined by Jell *et al.* (2013). Only an isolated rostrodermethmoid has been identified by Wretman and Kear

(2013) from near Richmond in the north of the Basin, also from the Toolebuc Formation.

The Toolebuc Formation is a thin, organic rich unit, generally 20–45 m thick, that includes coquinitic limestone and shales (including oil and kerigenous shales). Cook *et al.* (2013) indicate that the Formation was deposited in a layered epeiric sea, with dysoxic to anoxic benthic conditions. Henderson (2004) showed that the Formation contained shell beds in response to benthic oxygen fluctuations during a maximum deepening event. Many of the fossil vertebrates from near Boulia have been collected as isolated neurocrania or partial skeletons in calcareous concretions that have been concentrated and exposed on the soil surface by physical factors, with little or no evidence of lateral transport. This is the case with the current specimens. However, in recent

years, more complete skeletons particularly of large reptiles have been found.

Preparation of the specimens involved mechanical and acetic acid techniques.

Abbreviations

bc	brain case
cfct	compression fracture
cdk	coronoid tusk
co	coronoid
den	dentary
dt	dentary teeth
dpal	dermopalatine
ecp	ectopterygoid
fr	frontal
ga	gill arch element
gr	gill rakers
ha	hyoid arch element
hm	hyomandibular
le	lateral ethmoid
mx	maxilla
pmx	premaxilla
pa	parietal
par	parasphenoid
pro-op	prootic-opisthotic
qu	quadrate
rdr	rostromethmoid
sc pl	sclerotic plate
sph-pts-obs	sphenotic-pterosphenoid orbitosphenoid
ve	vertebral arch

CLASS ACTINOPTERYGII

SUBCLASS NEOPTERYGII

ORDER PACHYCORMIFORMES

Australopachycormus hurleyi Kear, 2007 (Figs 1–4)

Australopachycormus hurleyi Kear, 2007: 1033–8.

Material Examined. QMF52641, holotype (see Kear 2007). QMF49220, an incomplete skull and a plaster cast of the specimen before preparation. The specimen is from 'Lorna Downs' Station (at 23° 22.127' S and 140° 11.858' E) near Boulia, CWQ. QMF10913, a partial

acetic acid prepared neurocranium and a coloured fibre glass cast of the specimen prior to acetic acid preparation. The specimen was collected 15 miles (ca. 24 km) north of 'Springvale' Station, NE of Boulia, CWQ.

Age and Formation. From the marine Toolebuc Formation of Early Cretaceous (Late Albian) age.

Description. The following descriptive notes augment the original description of *Australopachycormus hurleyi* by Kear (2007). Measurements for the specimens are presented in the Appendix.

The cranial roof is obtusely angular across the dermopterotic-parietal area, becoming broadly convex across the back of the orbits and narrowing to a more tightly dorsally convex cross section anteriorly; no fronto-parietal boss appears present; the anterodorsal neurocranial surface slopes posteriorly at a low angle to the horizontal, then bends slightly dorsally above the brain case. The posterior of the neurocranium has suffered bone loss in QMF10913 (Fig. 1A–D) making it difficult to identify most individual elements of the brain case. The brain case appears to have been almost fully ossified. Posteriorly, only dorsolateral surface bone remains. The lateral margin of the dermopterotic is damaged by conical, compaction fracturing and compression into the post-temporal fossa. The dermosphenotic forms much of the dorsal margin of the orbit and is attenuated anteriorly. The hyomandibular facet exhibits local, dorsal compressed fracturing into the base of the post-temporal fossa. Other isolated, circular, pressure fractures are also evident on the parasphenoid. The posterior portion of the anterior semi-circular canal is exposed in dorsal view. Laterally, the subtemporal fossa is insignificant.

The orbit is best preserved in QMF10913 (Fig. 1A) but neurocranial elements within the orbit are mostly fractured and somewhat displaced on the right side. Very eroded and often fractured elements are exposed on the right side of QMF49220. The eye was large (see Appendix) and was supported by two, heavy sclerotic plates joined dorsally and ventrally, with each expanded mesially and transversely; the

Australopachycormus hurleyi Kear

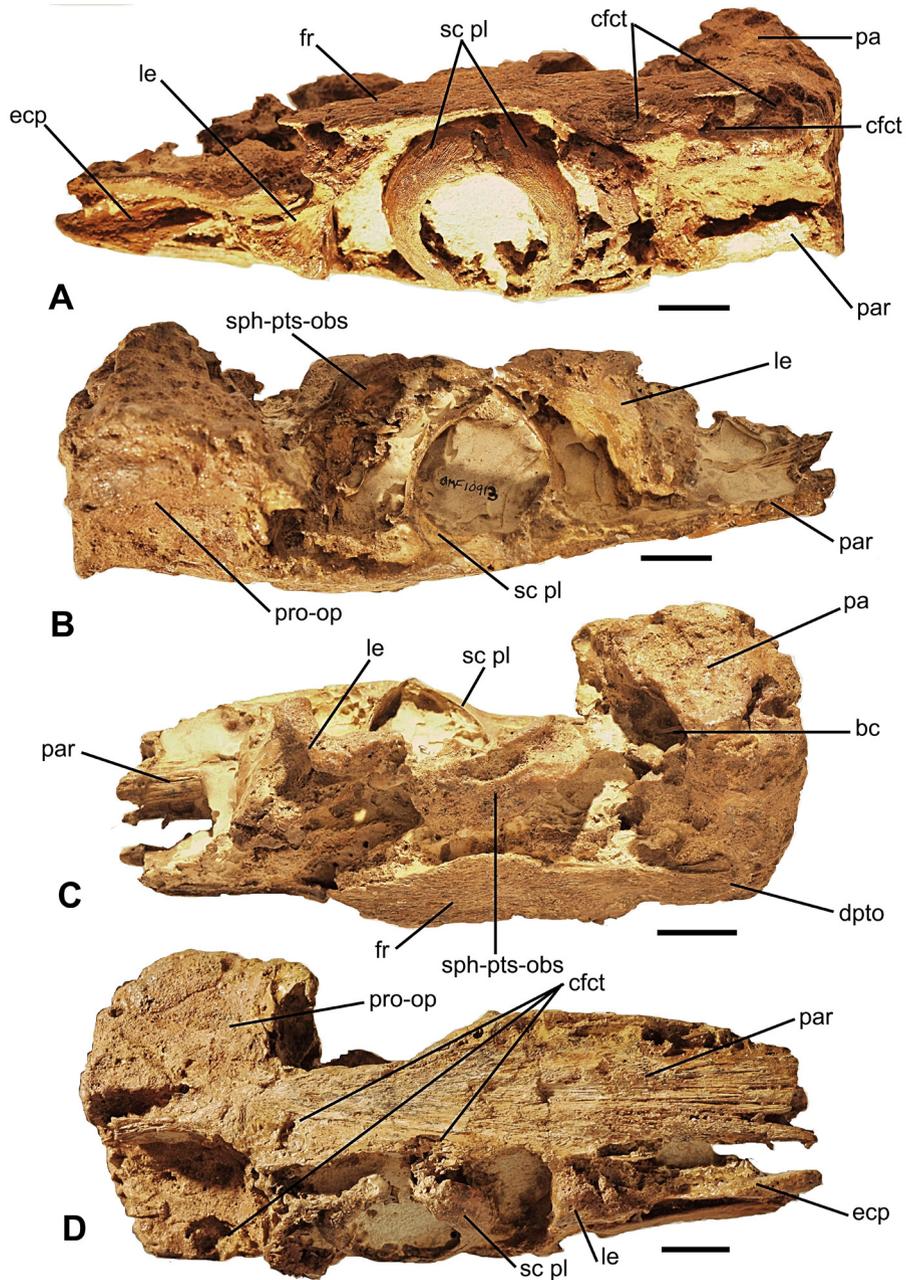


FIG. 1. *Australopachycormus hurleyi* Kear, 2007, specimen QMF10913; **A**, left lateral view of partial skull showing conical compression fractures along and below dermopterotic margin and large sclerotic plates; **B**, right lateral view showing displaced lateral ethmoid, united sphenotic-pterosphenoid- orbitosphenoid and lack of defined junctions in braincase; **C**, dorsal view showing enlarged parietals and displaced but little corrosion of lateral ethmoid and united sphenotic-pterosphenoid-orbitosphenoid and arched dorsal surface of parasphenoid; and **D**, ventral view showing broad parasphenoid with several conical compression fractures. Scale bar = 1 cm.

plates are gently convex externally and gently concave internally. The surface of each plate is ornamented over the outer moiety by very fine, reticulating ridges, especially ventrally.

The lateral ethmoid is large and complex in QMF10913 (Fig. 4A) but is corroded in QMF49220 (Fig. 4B). The anterior is poorly preserved in both specimens examined. The posterior surface is curved, smooth and expanded medially, forming the anterior border of the orbit; it expands dorsally and curves posteriorly to broadly support the back of the rostrodermethmoid and dorsal margin of the frontal; its dorsolateral surface is rugose in QMF10913, possibly to support the front of the supraorbital immediately above a large scooped opening that is believed to be the nasal opening. The lateral ethmoid is expanded medially to meet its counterpart from the other side and is excavated transversely into a large, posteromedially orientated, trough-like, olfactory capsule that is penetrated by variable small foramina; it medially appears to have met the anterior of the orbitosphenoid and presumably carried the passage for the olfactory nerves; the bone extended anterolaterally to be overlain by a posterodorsal plate of the ectopterygoid and dorsally by the rostrodermethmoid. Laterally, the anterodorsal surface supports a partial element believed to be part of the nasal, lying outside the ectopterygoid, while its anteroventral surface supports the upper margin of the maxilla.

The rostrodermethmoid is largely lacking in the specimens. That above the parasphenoid in QMF10913 exhibits two large, anteriorly directed cavities. These were not associated with paramedial teeth, replicating similar structures in the holotype in which paramedial teeth are also represented below them. A near complete rostrodermethmoid from near Richmond, North Central Queensland, identified as *A. hurleyi*, was illustrated by Wretman and Kear (2013).

The sphenotic, pterosphenoid and orbitosphenoid are strongly united and contribute the bulk of the dorsomedial wall of the orbit but junctions of the three elements are difficult to define. However, the sphenotic appears to be a small bone with a curved dorsolateral rim

above a smoothly concave outer surface that is overlain ventrally by the upper margin of the pterosphenoid. The pterosphenoid is small, penetrated anteriorly by a large optic fenestra. A foramen for the trochlear nerve penetrates the bone above the optic fenestra. Internally, the pterosphenoid contributes to the base of the braincase. The orbitosphenoid appears to be the largest of the bones. It internally contributes to the anterior of the cranial cavity and externally provides the smoothly concave upper wall of the orbit; it is separated from the sphenotic by a shallow, broad, oblique groove and appears as a raised, overhanging rim posteriorly with its broadened upper surface loosely underlying and supporting the frontal. The bone appears to contribute to the margin of the large opening for the olfactory tract. The basisphenoid is poorly preserved. The anterior of the prootic is fractured and difficult to interpret.

The parasphenoid is imperfectly preserved in QMF10913, extending anteriorly to beyond two tapering cavities that appear too far back to represent sockets of the paramedial teeth. These cavities are large and sub-ovate and are anteriorly directed with slight divergence. The parasphenoid is broad and ventrally flattened by significant bone loss (but arched in the holotype). Compression fracturing of the right lateral margin suggests tooth damage during predation. Posterior to the back of the orbit, the parasphenoid steps up slightly and curves slightly dorsally (again exhibiting an indication of predator tooth damage) while narrowing and twisting to lie along the sides and base of the basi-exoccipital; it is linked laterally to the prootic by poorly defined ascending processes. Anterodorsally, the parasphenoid surface above the twin cavities is markedly convex and is densely ridged longitudinally.

Remains of a broad, thin, sheet-like ectopterygoid are present in both referred specimens. This is angled anteroventrally inside the premaxilla and terminates in a swollen base that narrows posteriorly and ventrally parallels the parasphenoid margin. Fragmentary anterior remains of an elongated, thin, possible endopterygoid are present external to the parasphenoid in QMF49220. Fragmentary evidence for possible

right dermopalatines are present in QMF49220. The bones are reduced to a fine splint posteriorly and support a single series of very small, blade-like teeth, reducing in size posteriorly.

Remains of the jaws are preserved in QMF49220. Although eroded and with loss of surface enamel from the teeth, sufficient of the premaxilla and its teeth is present to show its great similarity with that in the holotype, QMF52641 (see Kear 2007). The left maxilla is reasonably well represented and is elongated (reduced to a long point covered by the premaxilla anteriorly in the holotype), deepening along its exposed length before deepening slightly posteriorly (Fig. 3). It is slightly convex laterally and is spooned dorsally to abut and be supported by the anteroventral base of the lateral ethmoid. The bone broadens dorsomedially where it carries a shallow dorsal groove, more defined posteriorly by a dorsolateral flange, apparently to accommodate at least one infraorbital and a supramaxilla. A single row of very small marginal teeth is present, distributed evenly along the bone but absent posteriorly. The teeth are blade-like and spearhead pointed and are slightly angled medially.

Both sides of the lower jaw are preserved with external bone loss in QMF49220 with the left side (seen in Fig. 3) better preserved than the right (Fig. 2). The extreme anterior of the mandible is lacking but the remaining part is clearly similar to that in the holotype. The tooth-bearing dorsal margin is shared by both the coronoid and dentary. The posterolateral end of the mandible is formed by a relatively elongate angular that reaches anteriorly to below the middle of the orbit and extends well behind the level of the groove for the supramaxilla. It deepens and thickens posteriorly and sweeps posterodorsally to form the rounded posterior margin of the lower jaw. Mesially, the posterior of the articular of the right side in QMF49220 appears deep, articulating with the quadrate. A retroarticular is present in a corroded state. The anterior, coronoid part of the dorsal margin of the left mandible is elevated as part of a swollen coronoid plate for a distance of some 50 mm and bears a single, very large, deeply socketed tusk, ovate in section, as well as

three much smaller teeth anteriorly. The tusk crown has lost its enamel; the smaller teeth had a spearhead shaped crown. Posterior to the large tusk, the elevated part of the coronoid is edentate, as is the remainder of the bone except for very fine denticles along the dorsomedial margin, posterior to the diastema. Most of the mandibular marginal teeth are borne on the dentary. Thus the main mandibular teeth as a whole appear only to be a single row. The dentary teeth are of similar size and structure to those anterior to the coronoid tusk. Where seen on the right side of QMF49220, they are very deeply socketed, slightly more than twice as deeply rooted as the crown is exposed. At least 16 dentary teeth are present.

A partial natural mould of the hyomandibular is present on the left side of QMF49220 and is very similar morphologically to that in the holotype but has been rotated posteriorly at about 90° to its original position. Gill arches are incomplete but are largely represented on the right side. Gill rakers are short and relatively robust. One element on the left side is elongated. The left hyoid arch is displaced and the elements are rotated but are too broken and corroded for description.

Taphonomy. Preservation of QMF49220 of *A. hurleyi*, differs markedly from that in the holotype, QMF52641, in which much of the rostrodermethmoid and bones behind the front of the orbit are almost completely missing (Kear 2006). It appears that the spine tip in the holotype was lost before fossilisation (or was not collected) probably sank and, because of its weight, partially embedded itself nose-first into the surface sediment. The body of the fish collapsed after death and decay and subsequent loss of the bulk of the back of the skull of the holotype, possibly by water movement, would then have left the preserved part of the skull to be covered and fossilised with the bones immediately anterior to the orbit broken and partially splayed outwards. Isolated pachycormid rostrodermethmoids, including that identified as *A. hurleyi*, are known from near Richmond, NCQ, in the Eromanga Basin (Wretman & Kear 2013) suggesting their loss could occur during predation, fossilisation or collection. Presence

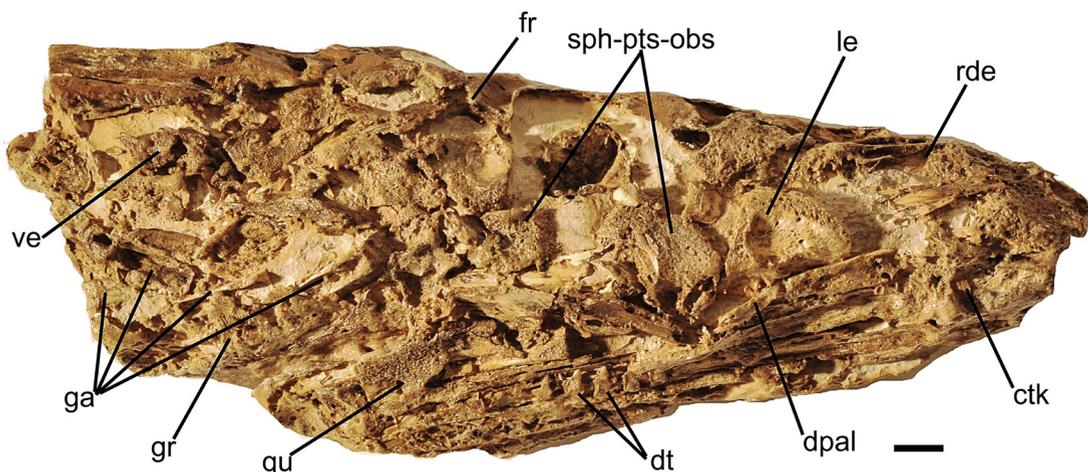


FIG. 2. *Australopachycormus hurleyi* Kear, 2007, specimen QMF49220, oblique view of roof and right side of neurocranium (with some matrix remaining) showing obliquely crushed but compressed mass of broken, disassociated and acid corroded bones; deep, external folds in opercular area associated with possible toughened skin; and almost complete loss of surface bones. Scale bar = 1 cm.

of the holotype's separated hyomandibular, however, precludes a suggestion that loss of posterior skull elements occurred during predation and scavenging was unlikely (see below).

Neurocrania in Eromanga actinopterygians such as the aspidorhynchid *Richmondichthys* (Bartholomai 2004) and the pachyrhizodontid, *Pachyrhizodus marathonsensis* Etheridge Jnr., 1905 (see Bartholomai 2012) were generally preserved as isolated heads (and rare bodies) with one side retaining most of the more delicate dermal bones intact and with little displacement. The other side of the neurocranium (or body) usually suffered loss of surface bones. Schafer (1972) noted that drifting carcasses lose limbs and skulls while drifting and parts can be embedded at different places. It is suggested that the more complete and better preserved side of these fish was that pressed into the surface sediments while the other side was subjected to winnowing and the possibility of scavenger activities before final burial and fossilisation. QMF10913 has the left side elements much more completely preserved, suggesting this was the surface initially buried in the bottom sediments.

Although the left side of the skull in QMF49220 has more complete elements than the remainder of the specimen, the crushing, breaking and disarticulation of the cranial bones within the general skull envelope in QMF49220 is inconsistent with usual sedimentary compaction and fossilisation of Toolebuc fish neurocrania. The bones of the left side show breaks and the outer surfaces that are partially corroded by what appears to be acid etching while in the gut of an animal, conditions that must have been applied before burial. Everhart (2003) similarly records that the surface of bone has the characteristic appearance of being etched by stomach acids, which gives the bone a 'spongy' appearance, clearly distinct from fresh bone and similar to the preservation of bone in QMF49220 (Fig. 2). The mandible in this specimen is broken medially, with the two parts bent apart, with the posterior compressed into a more confined space medial to an unbroken and less robust maxilla (Fig. 3). Similarly, the bones of the hyoid arch are broken and are partially rotated upwards reducing the depth of the skull. Originally near-vertical bones in the head, such as the hyomandibular, have been rotated through 90° and pushed posteriorly,

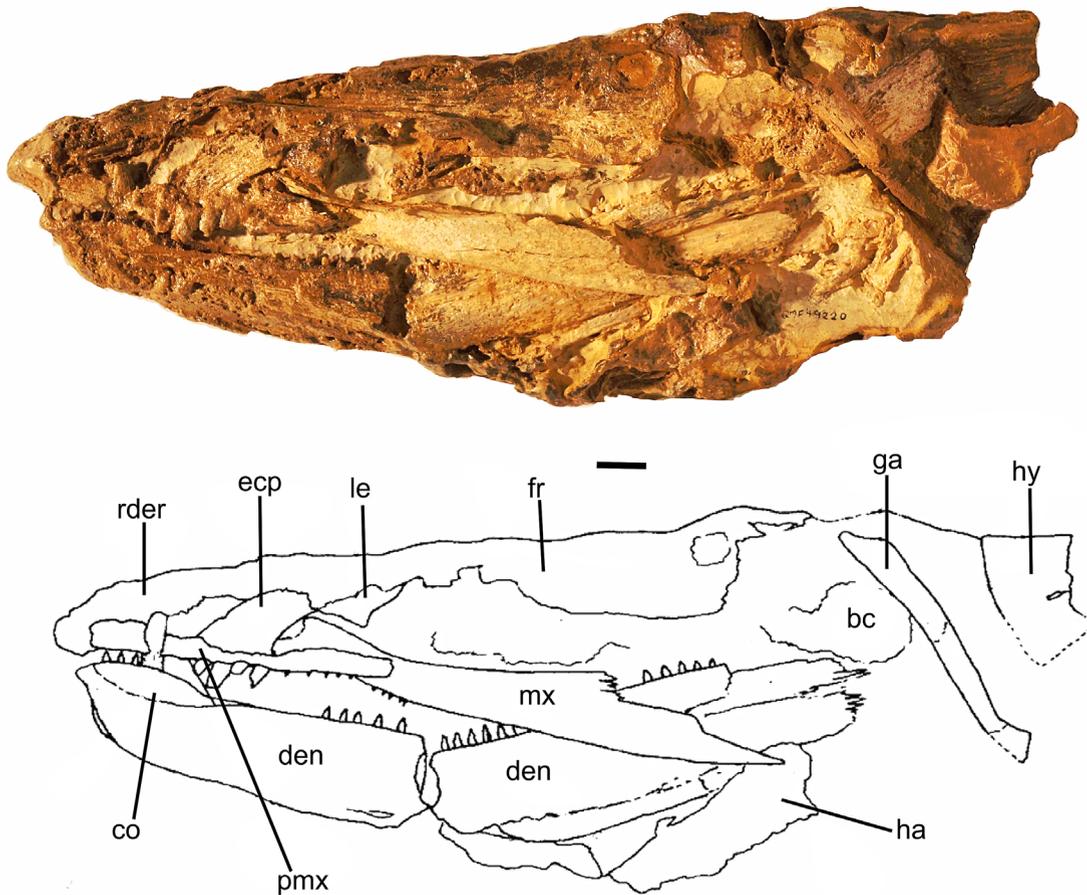


FIG. 3. *Australopachycormus hurleyi* Kear, 2007, specimen QMF49220; left lateral view of skull with some matrix remaining, showing compacted and broken elements and reduced surface corrosion of most bones, together with interpretative drawing showing major bones, including broken mandible inside maxilla, displaced and broken hyoid arch and rotated hyomandibular. Scale bar = 1cm.

again consistent with muscular crushing and compaction of the remains. The majority of the internal bones are preserved as a broken but usually disassociated mash of large and small corroded bony fragments, separated from one another by matrix but contained within a consolidated, compressed and elongated, 'sausage-shaped' mass. Enamel on the larger left coronary and premaxillary teeth has been corroded but this has not usually occurred with regard to the smaller teeth present. Enameloid loss on isolated teeth from the Upper Cretaceous Carlyle Shale of Kansas, USA, was considered a possible result of animal digestion by Shimada

(1997). Dentary and coronoid teeth and bones in QMF49220 shows varying degrees of loss or degradation that are interpreted, herein, as the result of digestive acid etching.

The united sphenotic, pterosphenoid and orbitosphenoid, an unusually robust element in QMF10913, has been broken in two in QMF49220 and the parts separated. Remains of the four epibranchials of the right side in this specimen, however, are not greatly disarticulated and gill rakers are only slightly moved where they are preserved. The upper half of the posterior of the right lateral ethmoid has been lost by

etching (Fig. 4B, cf Fig. 4A). Nearly all bones on the outside of the right side of the skull have been lost. The specimen, has darkened areas at the surface that may represent remains of a toughened skin that incorporate degenerated remnants of dermal bones, a conclusion supported by deep longitudinal surface folds around internal elements, especially below and above the opercular series, consistent with strong muscular crushing. What remains of the frontals is also covered by possible folded, toughened skin. It is considered possible that initial containment in this way was probably responsible for maintaining the mass of broken, partially digested and disassociated neurocranial bones together as a unit, immediately prior to possible regurgitation.

QMF10913 has some features suggesting predation but evidence for possible ingestion of the skull is much less convincing than that for QMF49220. Bones of the right hand side, especially those around the orbit, were disarticulated and moved medially and much of the rostrum has been lost. Dermal bone above the left orbit and otic region is still present and does not appear to be strongly corroded. The sclerotic plates (Fig. 1A) and the lateral ethmoids (Fig. 4A for right lateral ethmoid) are virtually unaffected by acid corrosion posteriorly, as is the brain case as originally present in the cast of QMF10913. Extensive surface shedding of bone is associated with the parasphenoid and the right side of the head, consistent with the left side being, in part, buried in sediment and with the right side winnowed before burial and vertically compressed during sediment compaction. No acid etching is evident on dislocated bones medially surrounding the right orbit. Two circular compression fractures are present along the edge of the left dermopterotic, 2.2 cm apart. These oppose a single, similar fracture in the hyomandibular facet and into the post-temporal fossa, midway below the upper fractures, damage that could only occur after tooth slippage up the hyomandibular surface or after dislocation of the articulating head of that bone. Possible, widely-spaced, circular compression fractures (depressions) are also evident in the parasphenoid, anterior and posterior to the ascending wing and

are interpreted as bite marks. The shape of the bite marks suggests that they were caused by conical, somewhat circular teeth.

Numerous large, pelagic, predatory animals co-existed with *A. hurleyi* in the epeiric sea of the Eromanga Basin in the area along its central western rim. Collections made over many years by the late Mr Richard (Dick) Suter, of the Stonehouse Museum, Boulia, record more than 150 specimens of large ichthyosaurs (*Platypterygius*) together with rare plesiosaurs and pliosaurs, including the massive, *Kronosaurus* (Suter, pers. comm.). The degeneration of the skull remains of QMF49220 are not conducive to interpretation by abrasion of gastroliths, although rare plesiosaur skeletons from the area are frequently preserved with them intact (Suter, pers. comm.). Sharks also coexisted with *A. hurleyi*, along with large pelagic actinopterygians such as *Pachyrhizodus* (see Bartholomai 2012) and the ca. 3 m. *Cooyoo*, revised by Lees & Bartholomai (1987) but their teeth could not have been responsible for the circular, widely separated fracturing present in QMF10913.

Ichthyosaurs are statistically the most common of the large reptilian predators in the Toolebuc Formation near Boulia and they had conically-shaped circular teeth. Teeth in the much larger but rarely encountered *Kronosaurus* (also recorded in the Queensland Museum collections) are also conical but are much larger and more separated in adult specimens. Plesiosaur remains are also rare in the Boulia collection. It is thus considered more likely that *P. australis* (reviewed by Zammit 2010), was the predator associated with the additional *A. hurleyi* skulls described herein. Pollard (1968) reported on ichthyosaur gastric contents which were found associated with skeletal remains from the Early Jurassic of Lyme Regis, UK and concluded that they mainly preyed on dibranchiate cephalopods and fish. However, Ball (2002), recorded that in the vomit of predators (thought to be from *ichthyosaurs*) prey were swallowed whole and the soft tissues in the gut digested, and with hard residues, such as belemnites, regurgitated. Pelagic invertebrate food sources existed in the western part of the Eromanga Basin but are relatively rarely found as fossils compared

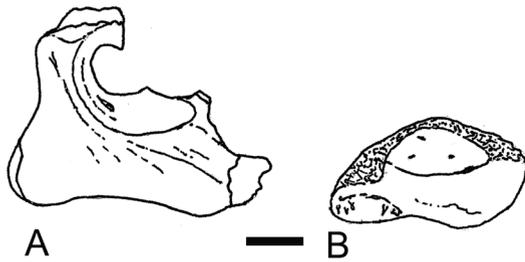


FIG. 4. *Australopachycormus hurleyi* Kear, 2007, drawings of right lateral ethmoids to show possible corrosion. **A**, lateral view of well preserved, undistorted ethmoid from QMF10913; **B**, lateral view showing remaining base of the ethmoid from QMF49220, interpreted as the result of corrosion. Scale bar = 1 cm.

with the invertebrate fossil record in the northern part of the Basin (see Cook *et al.* 2013). Food availability may have forced the reptilian fauna of the Toolebuc Formation and Allaru Mudstone to rely more heavily on other vertebrates in the west of the Basin.

Involvement of larger benthic scavengers generally appears unlikely in the reduction and modification of the skulls of *A. hurleyi* or in complete removal of missing individual elements. The fluctuating dysoxic to anoxic bottom waters that prevailed during deposition of the Toolebuc Formation suggest that such conditions would have precluded the general presence of large benthic scavengers. Monospecific benthic communities of the bivalve *Inoceramus* existed within the fluctuating palaeoenvironment (Henderson 2004), suggesting that larger benthic scavengers could exist where more oxygenated and probably isolated microhabitats were present. The scavenging isopod, *Brunnaega*, has been shown by Wilson *et al.* (2011) to be associated with remains of the fossil actinopterygian, *Pachyrhizodus marathonsensis* (Etheridge Jr. 1905) from the Toolebuc Formation on 'Canary' Station, near Boulia, in the same general part of the Eromanga Basin as that from which *A. hurleyi* has mostly been recorded. The crushing, breaking and disarticulation of the cranial bones within the general skull envelope, especially in QMF49220, is not able to be attributed to small invertebrate scavenging.

The fact that *Australopachycormus* was also a middle-sized predator would not preclude it from being the prey of larger animals. The nature of the preservation discussed above for QMF49220 suggests that this skull was ingested, subjected to digestive stomach acid and compressed before and during digestion by muscular action, and later regurgitated. Regurgitated fossilised remains were termed 'speiballen' by Schafer (1972), a term usually applied to indigestible stomach contents preserved in mass after regurgitation, including hard parts of small prey, such as belemnites. QMF49220 was not collected in association with other regurgitated and indigestible stomach contents nor was it combined with stomach contents preserved in situ where deposited, nor fossilised within the remains of the predator involved.

The presence of the skull of a single, large fish does not fit comfortably with Schafer's suggested diagnosis for regurgitated remains. Regardless, the characters displayed in QMF49220 indicate that predation, digestion and regurgitation were most likely involved in the history of this particular skull prior to fossilisation. The specimen would most likely have been part of a carcass swallowed whole or in large chunks. No puncturing by teeth of the external bones of the head of this specimen is evident, suggesting that the rather large head of *A. hurleyi* was swallowed without a significant bite by the predator.

CONCLUSIONS

Additional detail has been provided on the morphology of the skull of the pachycormid, *Australopachycormus hurleyi* Kear, 2007, based on new material collected from the marine Toolebuc Formation of Early Cretaceous (Late Albian) age from near Boulia in central western Queensland, Australia. This augments the description of the species provided by Kear (2007) and that in Wretman & Kear (2013) especially regarding the upper and lower jaws and the orbital region. The new information supports Kear's (2007) conclusions regarding a sister-taxon relationship with the Late Cretaceous, Northern Hemisphere *Protosphyraena*. Although

interpreted as a pelagic predator, it has been shown that *A. hurleyi* was itself prey to larger animals and, at least in one instance, (that of QMF49220) was believed to have been regurgitated after partial digestion, probably by one of the co-existing marine reptiles in the epeiric sea of the Eromanga Basin of central Queensland. Bite damage by an animal like the ichthyosaur, *Platypterygius australis*, on a second specimen of *A. hurleyi* suggests that this ichthyosaur was most likely the predator involved and supports the conclusion that it was also the predator most likely involved with both pachycormids studied in the current work.

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Appendix

<i>Australopachycormus hurleyi</i> Kear, 2007 (QMF49220)	<i>Australopachycormus hurleyi</i> Kear, 2007 (QMF10913)
Total length of preserved elements . . . 322.0 mm	Length of orbit 65.0 mm
Length of preserved neurocranial elements 227.0 mm	Length of sclerotic plates (external) . . . 46.5 mm
Posterior depth of preserved skull (including mandible) 110.0 mm	Internal opening within sclerotics 29.7 mm
Length of mandible 235.0 mm	Posterior neurocranial breadth 93.0 mm
Depth of mandible (mid-mandible) . . . 32.2 mm	Neurocranial breadth across dermosphenotics 93.0 mm
Depth of mandible (below coronoid fang) 27.4 mm	Posterior cranial depth 66.9 mm
Minimum length of crown of large coronoid fang 18.0 mm	
Width of crown base of large coronoid fang 5.3 mm	
Length of exposed crown of anterior coronoid teeth 3.6 mm	
Maximum exposed length of crown of dentary teeth 4.5 mm	
Total length of dentary tooth (including root) 10.5 mm	
Length of premaxilla 87.6 mm	
Width of largest premaxillary tooth . . . 5.5 mm	
Maximum length of posterior premaxillary tooth crowns 1.2 mm	
Maximum length of maxilla 135.0 mm	
Maximum depth of maxilla 20.6 mm	
Anterior depth of maxilla 10.3 mm	
Length of exposed crown of maxillary teeth 1.2 mm	
Length of exposed crown of largest dermopalatine tooth 4.4 mm	
Estimated breadth of neurocranial roof across dermosphenotics 100.0 mm	
Breadth across front of rostrodermethmoids (as preserved) 39.2 mm	