Evidence for tactile feeding in pterosaurs: a sensitive tip to the beak of *Lonchodraco giganteus* (Pterosauria, Lonchodectidae) from the Upper Cretaceous of southern England

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ABSTRACT

The sense of touch is important for hunting and feeding in vertebrates, especially when visual cues are unreliable. Foramina in the jaws and face, associated with nerves and sensory organs, may provide information about feeding. Pterosaurs, many of which had large, well-developed eyes, are often assumed to have been visual feeders. Here, we show that the lonchodectid pterosaur *Lonchodraco giganteus* (Bowerbank, 1846) has clusters of circular foramina at the anterior mandibular symphysis (the odontoid) and on the lateral margins of the rostrum that indicate enhanced sensitivity of the rostrum tip. This pattern

implies tactile feeding. The foramina were likely occupied by Herbst corpuscles or similar integumentary sensory micro-organs (ISO). They presumably served a sensory function at the jaw tip to enhance food gathering. A similar morphology occurs in some avians that feed using tactile cues, including probe feeders such as kiwis, sandpipers, and ibises, tactile hunters such as spoonbills, and filter feeders such as ducks and flamingos. The beak morphology of *L. giganteus* does not closely resemble that of these birds, and thus its modus operandi for feeding remains speculative, however tactile feeding for fish or invertebrates in shallow water seems likely. Like birds, pterosaurs evolved a diverse range of feeding strategies.

Keywords: Pterosauria, Lonchodectidae, Mechanoreceptors, Palaeoecology, Upper Cretaceous.

1. Introduction

One of the most fundamental problems an animal faces is sensing its environment and detecting its food. Different strategies of food detection include vision, tactile (touch), auditory, olfaction and gustation. Each has advantages and disadvantages. Vision is effective at sensing the environment and prey at a distance, but it is less effective at night or low visibility conditions. Touch necessarily has a limited range and alerts prey, but functions in low light or low-visibility conditions where vision may be severely limited.

Diapsids, including birds, crocodilians, lizards and turtles, tend to have well-developed vision. Birds have especially well-developed vision, because safely navigating at high speeds

requires sensing the environment at a distance. However, some birds have elaborated other senses. Petrels have a well-developed sense of smell (Bonadonna and Bretagnolle, 2002; Bonadonna et al., 2003), while owls have excellent hearing (Volman, 1994) and oilbirds have rudimentary echolocation (Brinkløv et al., 2013). A number of birds, including kiwis, sandpipers, ibises and other probing birds, and dabblers such as ducks, appear to use tactile cues for foraging (Leitner and Roumy, 1974).

The extinct pterosaurs were a group of archosaurs that evolved flight independently from birds. Like birds, they would have needed excellent eyesight to sense their environment and take off, navigate, and land safely. Many pterosaurs had large eyes, suggesting excellent sight (Witton, 2013). Presumably, like birds, they would have relied heavily on vision while foraging. However, like birds it is possible that some pterosaurs may have elaborated other senses for use in contexts where vision is less effective.

Many birds, especially those that feed by probing, have numerous foramina distributed along their maxillae/premaxillae and dentaries and these may be concentrated into dense clusters at the tip of their beaks (Piersma et al., 1998; Nebel et al., 2005; Cunningham et al., 2007). These clusters of foramina are well developed in such groups as Scolopacidae (Snipes, Sandpipers, Godwits), Threskiornithidae (Ibis and Spoonbills) and the New Zealand Apterygidae (Kiwi spp.), forms that are phylogenetically widely separated (Cunningham et al., 2013). Although small foramina have been reported on the beaks of pterosaurs (Martill et al., 2020a, b), and loose concentrations of them are figured for a dsungaripterid (Chen et al., 2020) and some tapejarids (e.g. *Caiuajara dobruskii* Manzig et al., 2014; Martill et al., 2020b) dense concentrations of foramina at the tip resembling those of some avians has not previously been observed in the Pterosauria.

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66 Here we describe an example of a pterodactyloid pterosaur from the Late Cretaceous of
67 England with such a concentration, and we comment on the possible function of these
68 structures and on the palaeoecology of the pterosaur (Fig. 1).

69

70 2. Material and methods

71 The specimens described and figured here are accessioned in the collections of the
72 Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, United Kingdom,
73 specimen numbers prefixed **CAMSM**; Centro Paleontológico (CENPALEO) of the
74 Universidade do Contestado, Mafra, Santa Catarina, Brazil Museu Nacional, Universidade
75 Federal do Rio de Janeiro, Brazil, specimen numbers prefixed **CP.V**; Faculté des Sciences Ain
76 Chock (FSAC), Université Hassan II, Casablanca, Morocco, specimen numbers prefixed **FSAC**
77 **KK**; Magyar Természettudom anyi Múzeum, Budapest, Hungary, specimen numbers prefixed
78 **MTM**; Natural History Museum, London, specimen numbers prefixed **NHMUK**;
79 Palaeontology-Stratigraphy Museum, Babeş Bolyai University, Cluj-Napoca, Romania,
80 specimen numbers prefixed **PSMUBB**.

81

82 3. Results

83 3.1 Systematic palaeontology

84 Pterosauria Kaup, 1834

85 Pterodactyloidea Plieninger, 1901

86 Lonchodectidae Unwin, 2001

87 *Lonchodraco* Rodrigues and Kellner, 2013

88 *Lonchodraco giganteus* (Bowerbank, 1846)

89

90 *Lectotype*. Associated skeletal elements of anterior premaxilla and dentary with dentition,

91 NHMUK PV 39412. This material is part of the holotype specimen of *Pterodactylus giganteus*

92 Bowerbank, 1846 that also includes a partial left scapulocoracoid, a proximal humerus and

93 ulna and a piece of wing phalanx. The bones all remain on pieces of chalk matrix.

94 *Synonymy*. A complete synonymy of *Lonchodraco giganetus* can be found in Averianov

95 (2020).

96 *Type locality and horizon*. The specimen comes from a now abandoned Culand chalk pit at

97 Burham, Kent, southern England. According to some authors this locality exposes the

98 Middle Chalk, probably *lata* to *planus* zones, and is therefore of Late Cretaceous, Turonian

99 age (see Benton and Spencer, 1995). If this stratigraphic placement is correct, this would be

100 the youngest toothed pterosaur known. More likely, the specimen is from the Cenomanian

101 West Melbury Marly Chalk and Zig Zag Chalk formations of the lower Chalk Group (see

102 Bristow et al., 1997; Farrant and Aldiss, 2002).

103 3.2. *The premaxilla and rostrum*

104 These two elements of the skull lie in juxtaposition to each other as though the mouth was

105 slightly open. They are not quite in alignment with the midline of the mandibular symphysis

106 with the mandible being offset with respect to the midline of the premaxilla by

107 approximately 7 mm. The offset becomes greater more posteriorly, suggesting that had the

specimen been more complete the lower jaw would have been disarticulated at least partially at the quadrate/articular joint. Both elements represent only the tip of the rostrum extending anteriorly from the nasoantorbital fenestra, the anterior margin of which can be seen on the left lateral margin of the premaxilla/maxilla. The corresponding anterior margin of the nasoantorbital fenestra is not preserved as the bone from this region has flaked away, contra Rodrigues and Kellner (2013) who argued that it was not seen as the jaw represented a more anterior position.

3.2.1 Premaxilla

As preserved the premaxilla is 70 mm long and 29 mm wide at its most posterior point. It tapers anteriorly to a rounded, blunt rostral tip with a rounded dorsal margin. The dorsal surface is most likely the expression of a dorsal crest, as an anterior view reveals a slight constriction above the dental roots. There are 5 teeth preserved on the left side, but spaces for at least two more, while there are just 2 teeth on the right side, but with at least 14 estimated alveoli (chalk matrix conceals some of the alveoli) in total. The teeth are almost isodont and evenly spaced approximately 4 mm apart (Figs. 1-3). The posterior teeth appear to be somewhat smaller than the anterior most teeth (crown height 4 mm vs estimated 8 mm respectively). Conspicuous on the lateral margin are a series of small circular foramina forming a zone located just dorsal of the occlusal margin and anterior of tooth position 4 (Fig. 1-3).

3.2.2 Dentary

Only the anterior mandibular symphysis is present. The dentary is 63 mm long on the left side and 54 mm long on the right side of the specimen. On the right side of the specimen the lower jaw exposes the dental row and part of the occlusal surface which appears to be a

flat shelf. Lying below the dental border three teeth are present anteriorly with an additional six alveoli preserved more posteriorly. The left side of the dentary is less well preserved, with much of the outer surface bone having flaked away to reveal the internal structure and matrix infill. Ventrally there is a prominent median keel that deepens to some 12 mm below the jaw. It tapers with subparallel margins to a rounded ventral border (Figs. 1, 2). Anteriorly the dental margin rises to form a small bony plate that locates between the first tooth pair of the rostrum. This bony plate is perforate, with at least 7 foramina of approximately 0.5 mm diameter. The foramina are arranged in a circular series surrounding a central complex of smaller foramina that in places merge with adjacent foramina (Figs. 2, 3). Several other foramina are more randomly distributed toward the lateral margins of the dentary.

4. Comparative anatomy

4.1. Comparisons with other pterosaurs

Small foramina are present on the jaws of many pterosaurs across a wide range of clades, distributed across various parts of both the upper and lower jaws, including in basal clades such as the Rhaeticodactylidae (*Caviramus* Fröbisch and Fröbisch, 2006, fig. 2), and many clades within Pterodactyloidea. In examples of Azhdarchidae, elongate, slit-like foramina spaced evenly and arranged in slightly offset pairs along the occlusal surface have been described for *Alanqa saharica* (Ibrahim et al., 2010), while similar foramina are found on the lateral and occlusal margins of the Maastrichtian *Albadraco tharmisensis* (Solomon et al., 2020) and also on the curved mandible of the mid Cretaceous *Xericeps curvirostris* (Martill et al., 2018). Averianov (2010) noted such foramina on two specimens referred to the

azhdarchid *Azhdarcho lanciocolis*. In the Tapejaridae, smaller, but still elongate foramina have been figured for *Caiuajara dobruskii* where they are divided into two discrete areas either side of the midline of the occlusal surface of the premaxilla (Manzig et al., 2014 fig. 5a,b.), but other tapejarids have only a few foramina as in *Afrotapejara zouhrii* (Martill et al., 2020a), a single foramen as in a large *Tapejara wellnhoferi* (Wellnhofer and Kellner, 1991) or appear to lack such features altogether as in a juvenile *Tapejara wellnhoferi* (Eck et al., 2011). In the possible chaoyangopterid *Apatorhamphus gyrostega* elongate oval and slit-like foramina are present on the lateral margins of the rostrum and the occlusal surface (McPhee et al., 2020). The mandible of the enigmatic azhdarchid *Bakonydraco galaczi* has two rows of ten elongate oval foramina on the occlusal surface, one row either side of the midline (Ősi et al., 2005, fig. 2). The most posterior foramina are circular but they become oval anteriorly and those at the distal tip are slit-like. There are also a few foramina on the lateral margins of the mandible.

Recently an example of *Dsungaripterus weii* was figured in which the distal, edentulous part of the palate is perforated by numerous (at least nine on the right side) elongate slit-like foramina (Chen et al., 2020 fig. 4A). Slit-like foramina are also reported for Tapejaridae, Azhdarchidae and Thalassodromidae (Ibrahim et al., 2010; Martill et al., 2020a, b; Smith et al., submitted 2020). In Ornithocheiridae oval foramina are present either side of the median ridge of the palate of *Coloborhynchus sedgwicki* Owen, 1859 (see also Unwin, 2001), and round foramina are also conspicuous in ctenochasmatid *Platelorhynchus streptorophorodon* Howse and Milner, 1995.

4.2. Comparisons with other reptilian clades (excluding Aves)

Neurovascular canals on the jaws are found on a wide range of reptilian clades both extant and extinct. They are especially prominent on large theropod dinosaurs across a range of clades. For example, an extensive neurovascular network is present on the mandible and premaxilla of the piscivorous aquatic theropod *Spinosaurus aegyptiacus* (Dal Sasso, et al., 2005; Ibrahim, et al., 2014, 2020), on the macro predator *Daspletosaurus horneri* (Carr et al., 2017), and in the allosaurid *Neovanator salerii* (Barker et al., 2017). An extensive neurovascular system similar to that of *Spinosaurus* with external foramina on the premaxillaries is also present in the Jurassic pliosaur *Pliosaurus kevani* (Foffa et al., 2014).

In crocodilians they are widespread across all extant species as well as in fossil forms (Iordansky, 1973; Foffa et al., 2014), and are also present on the distal jaws of ichthyosaurs (Kear 2005) and mosasaurs (Álvarez–Herrera, et al., 2020). Clearly, the a sensory neurovascular system in reptile jaws is very widespread and likely plesiomorphic for Reptilia.

4.3 Neurovascular foramina in Aves

Neurovascular foramina are widespread in the jaws of Aves, but are especially well developed in Spheniscidae and Scolopacidae, among others (Ksepka et al., 2012; Cunningham et al., 2013). There is an extensive body of research into the form and function of bill-tip micro-organs in birds, especially chickens, and ducks and geese (Gottschaldt and Lausmann 1974; Leitner and Roumy, 1974; Gentle and Breward, 1975; Soliman and Madkour, 2017). At least four types of sensory mirco-organ occur in the tips of bird beaks: Herbst corpuscles, Merkel receptors, Ruffini corpuscles and Grandry corpuscles and are identifiable by histological analysis and, to a lesser degree by their distribution on the beak (Soliman and Makdour, 2017) with Herbst and Grandry corpuscles tending to dominate the

beak tip. In ducks and geese, Grandry corpuscles are velocity sensors while Herbst corpuscles are highly sensitive pressure sensors (Piersma et al., 1998), especially in probe feeders (Cunningham et al., 2013). Both are linked to the central nervous system via the trigeminal nerves. Neurovascular foramina are especially well developed in the bills of penguins, including some of the most basal forms from the Paleogene (Ksepka et al., 2012).

4.4 Neurovascular foramina in mammals

Several extant mammal species also possess extensive neurovascular canals on their jaws. Notably the echidna monotremes (*Zaglossus* and *Tachyglossus*) have slit-like neural foramina on their elongate rostra (Augee et al., 2006) that, at least superficially, resemble those of azhdarchid pterosaurs. In the case of the long-beaked echidna, *Zaglossus bruijnii* both electroreception and mechanoreception occurs in the distal 20 mm of the rostrum (Manger et al., 1997). Foramina for electroreception occur on the jaws of some cetaceans (Czech-Damal, 2011) but may be restricted to the soft tissues, with the trigeminal nerve emerging more posteriorly on the skull.

4.5. Biology of mechanoreceptors

Mechanoreceptors in the jaws of tetrapods are the beginning of the somatosensory pathway that projects via the trigeminal nerve system (Cunningham et al., 2013). On leaving the brain, the trigeminal nerve divides into three branches, namely ramus mandibularis, ramus ophthalmicus and ramus maxillaris (Romer 1956). R. mandibularis and r. maxillaris pass through the skull and emerge beneath the dermis through a series of small, often slit-

like foramina. Usually the microorgans responsible for mechanoreception are located within the dermis overlying the bony skeleton, rather than within the foramina themselves. However, enlarged foramina may form the locus of the mechanoreceptor, as in the Kiwi *Apteryx* spp. (Cunningham et al., 2007).

5. Discussion

Sensory organs in the tips of tetrapod skulls perform a wide range of functions. These include light sensing and magnetoreception (Pinzon-Rodrigues et al., 2018) (pineals and true eyes), pressure sensing, (Soliman and Madkour, 2017), chemo sensing (olfaction and gustation), infra-red heat sensing in snakes (Gracheva et al., 2010), touch and vibration detection (tactile star faced mole: Crish et al., 2003), and are mainly involved in detection and manipulation of prey. However, many of these receptors are embedded within the dermis or larger vacuities in the skull and may not leave traces in the cranial skeleton. Where the craniofacial nerves travel through the interior of bones, as in the case of mandibularis, maxillaris and ophthalmic nerves in avians, their arrival at the exterior, by necessity leaves a foramen where the nerve or nerve branches exit the bone. The nature of these foramina depends on the size of the nerve (or other vessel), whether or not it accommodates a mechanoreceptor, and the angle of exit from the bone, producing either circular or elongate oval foramina depending on exit angle. The phylogenetic bracket allows us to assume that any of these senses could have been significant for prey detection and manipulation in pterosaurs.

Modern birds, which are both the closest living relatives of Pterosauria, and perhaps close functional analogues as well, can help shed light on how the morphology of these foramina

is correlated with feeding ecology. Well-developed foramina are seen in a number of different clades and functional contexts. First, densely packed foramina are seen in birds that use the beak for probing, such as kiwi, sandpipers, and ibises (Cunningham et al., 2013). Second, dense foramina are seen in birds that engage in dabbling or filter-feeding, such as ducks, geese, and flamingos (Leitner and Roumy, 1974). Third, numerous foramina are seen in some herbivores, such as the extinct flightless duck *Thambetochen*, moa, and dodo birds (Olson and Wetmore, 1976; Hume et al., 2006; Ashwell and Scofield, 2007; Worthy and Scofield, 2012).

In wading birds that feed by probing with elongate, slender, straight and sometimes gently curved bills, dense concentrations of foramina at the beak tips house Herbst's corpuscles (and perhaps other integumentary sensory micro-organs [ISOs] *sensu* Brazaitis, 1987) and may occur on both the mandible and premaxilla (Piersma, et al., 1998; Cunningham et al., 2007; Cunningham et al., 2013). According to Piersma et al., (1998) the corpuscles detect slight changes in fluid pressure in pore waters of the sediment, where fluid flow is disrupted by objects within the sediment. Thus, Herbst corpuscles are mechanoreceptors rather than chemo or electro-potential receptors, as had previously been thought (Soliman and Makdour, 2017). Although probable mechanoreceptors are reported for pterosaurs (Chatterjee et al., 2013), discrete clusters concentrated at the beak tips have not previously been described.

In pterosaurs, foramina, likely to accommodate the nerves for mechanoreception in the jaws, occur widely within the group. However, dense concentrations of foramina, as seen in some avians, have not previously been reported for Pterosauria. Several pterosaurs have been noted to possess organised patterns of their foramina, however, no pterosaur exhibits

268 a concentration at the anterior tip as seen in *Lonchodraco*. In the tapejarid *Caiuajara*
 269 *dobruskii* (Manzig et al., 2014) foramina are clustered in two elongate, parallel fields on the
 270 occlusal surface of the palate (Martill et al., 2020b, fig. 8b) (Fig. 4B). In *Afrotapejara zouhrii*
 271 (Martill et al., 2020a, fig. 5c), they are arranged in off-set pairs on the occlusal surface of the
 272 rostrum, as also seen in *Bakonydraco* (Fig. 4A). The spoon-billed pterosaur *Plateleorhynchus*
 273 exhibits two rows of foramina that parallel the jaw margins and appear to produce a near
 274 circular sensory array at the jaw 'spatula' (Howse and Milner, 1995) (Fig. 5I, J). In some
 275 azhdarchoids, foramina form a single row on the lateral margins of the jaws (e.g. *Alanqa*
 276 *saharica*, Ibrahim et al., 2010) (see Fig. 5A,B) and in the tapejarid *Afrotapejara*, which has
 277 two rows arranged in off-set pairs on the occlusal surface (Fig. 5C,D). In other azhdarchoids
 278 both lateral and occlusal foramina are arranged in two off-set rows (e.g. *Albadraco*
 279 *tharmisensis*, Solomon et al., 2020) (Fig. 4C, D). Rostral foramina have also been reported in
 280 the dsungaripterid *Dsungaripterus weii* (Chen et al., 2020) (Fig. 4E). In the ornithocheirid
 281 *Coloborhynchus sedgwicki* foramina are arranged in single, off-set rows either side of a
 282 median ridge on the occlusal surface of the premaxilla/maxilla (Fig. 5G, H).

283 In *Lonchodraco*, the first pterosaur reported with a concentration of foramina at the jaw
 284 tips, the foramina are arranged in a radial pattern around a central eminence of the anterior
 285 mandibular margin, with an array of foramina distributed laterally along the mandibular
 286 margin, and the premaxillary margin (Figs. 2, 3, 6). Located so far anteriorly it is likely that
 287 these are involved with either tactile or 'remote touch' perception of prey. *Lonchodraco* is a
 288 poorly known pterosaur (the holotype is the only specimen), therefore there are few
 289 features on which to interpret its palaeoecology. It has a dentition of small, well-spaced
 290 conical teeth of more or less equal size in both jaws (Rodrigues and Kellner, 2013;
 291 Averianov, 2020), and the lower jaw is only slightly smaller than the upper. Likely it was

longirostrine, and like other members of Lonchodectidae, had a dorso-ventrally compressed cross-sectional jaw outline.

Comparisons made with birds suggest that a high density of foramina on the jaws occurs in several contexts. These are probe feeding in sediments, tactile foraging for small prey in water, dabbling and filter-feeding, and herbivory. The relatively broad tips of the jaws in *Lonchodraco* probably rule out probing. The relatively large, conical teeth exclude either filter-feeding or herbivory. Instead, the relatively small, closely spaced teeth and the small size of the animal suggest it fed on small animals, perhaps including small fish and crustaceans, which were acquired using tactile foraging, probably in water or saturated substrates.

Tactile foraging also implies that the prey were acquired in conditions where vision would be less useful. Such conditions might include foraging at dusk or at night. Alternatively, tactile foraging might be useful in turbid, cloudy water where visibility was poor. Until exceptionally preserved soft tissues are discovered however, it is unlikely that the true function of these foramina can be established.

6. Conclusions

Foramina for nerves that innervate the mechanoreceptor systems are widespread in the jaws of Pterosauria. In many taxa they are well-spaced, and arranged in rows or pairs of rows. Concentrated patches of foramina representing localised hypersensitivity are rare in pterosaurs, being found on the occlusal surface of some Tapejaridae, and on the anterior margins of the jaws of the lonchodectid *Lonchodraco giganteus*. Such a concentration at the

tip of *Lonchodraco* appears unique for Pterosauria, and might be comparable to the situation seen in some probe feeding birds such as Scolopacidae, and pursuit piscivores such as Sphenicidae. However, the rostrum of *Lonchodraco* resembles neither of these bird groups. The foramina in *Lonchodraco* most likely housed mechanoreceptors such as Herbst' corpuscles, and were responsible for prey detection and/or manipulation.

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Figure captions

Fig 1. Holotype rostrum and mandible of *Lonchodraco giganteus* (Bowerbank, 1846) (NHMUK 39412) in a, left lateral and b, right lateral views. Scale bar = 10 mm.

Fig. 2. *Lonchodraco giganteus* (NHMUK 39412). Two views of anterior rostrum and mandible. a, view showing anterior margin of mandible with small, triangular symphyseal process; b, anterior view of rostrum showing the rounded termination of the beak and the fine perforations of the dental borders. Black arrows indicate symphyseal process/odontoid. Scale bar = 10 mm.

Fig. 3. Detailed images of the jaw tips of *Lonchodraco giganteus* (Bowerbank, 1846) (NHMUK 39412). A, rostrum in anterior view; B, odontoid process with perforations arranged in circular cluster; C, line drawing of sensory pits in black on odontoid process seen in B; D, anterior portion of premaxilla shown in right lateral view; E, detail of anterior rostrum seen on D; F, anterior mandible in ventral view. Red arrows highlight sensory foramina. Scale bars = 10 mm.

Fig. 4. Examples of neurovascular pattern distribution in Pterosauria. A, symmetrical parallel single-file rows on occlusal surface of mandible, *Bakonydraco galaczi* MTM Gyn/3 (Ösi et al., 2005, fig. 2B); B, symmetrical parallel multiple rows on premaxilla, *Caiuajara dobrusckii* CP.V 1449, (Manzig et al., 2014 fig. 5A); C-D, two rows of paired foramina on lateral and occlusal surfaces of mandible and rostrum (only rostrum figured here), *Albadraco tharmisensis* (PSMUBB V651a, Solomon et al., 2020 fig.2 A2, B2); E, elongate foramina distributed seemingly randomly on all surfaces of premaxilla (seen here in right lateral aspect), *Dsungaripterus weii* IVPP V 26256 (Chen et al., 2020, fig. 4A). Not drawn to scale.

Fig. 5. Examples of foramina in other pterosaur jaws. A-D, specimen referred to cf. *Alanqa saharica* FSAC-KK 4002 in right lateral (A, B), occlusal (C, D) views. E-H, holotype rostrum of *Coloborhynchus sedgwicki* (Owen, 1859) CAMSM B 54422 in right lateral (E, F) and occlusal (G, H) views. I-J, holotype premaxilla and maxilla of *Plateleorhynchus streptophorodon* NHMUK PV R 11957 in occlusal view. (I, J, after Howse and Milner, 1995). All scale bars = 20 mm.

Fig. 6. Hypothetical restoration of the jaw tips of *Lonchodraco giganteus* based on holotype specimen NHMUK PV R 11957.

Figure 1

Figure 3

Figure 4

Figure 5

Figure 6

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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT Author Statement

David M. Martill: Conceptualisation, Methodology, Investigation, Writing - original draft. **Roy E. Smith:** Investigation, Writing - original draft. **Nicholas Longrich:** Investigation, Writing - original draft. **James Brown:** Methodology, Investigation, Writing - original draft.