

EVOLUTIONARY BIOLOGY

Comparative cranial morphology in living and extinct platypuses: Feeding behavior, electroreception, and loss of teeth

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The modern platypus, *Ornithorhynchus anatinus*, has an eye structure similar to aquatic mammals; however, platypuses also have a “sixth sense” associated with the bill electro- and mechanoreception that they use without opening their eyes underwater. We hypothesize that *Ornithorhynchus* and the Miocene taxon *Obdurodon* have different sensory capacities, which may have resulted from differences in foraging behavior. To estimate differences in foraging, sensory systems, and anatomical divergence between these monotremes, we compared their skull morphologies. Results indicate that the bill of *Obdurodon* is more dorsally deflected than that of *Ornithorhynchus*, suggesting a pelagic foraging behavior in *Obdurodon* compared to the bottom-feeding behavior in *Ornithorhynchus*. The infraorbital foramen of *Obdurodon*, through which the maxillary nerve passes sensory data from the bill to the brain, is relatively less developed than that of *Ornithorhynchus*. Whereas bill-focused sensory perception was likely shared among Mesozoic monotremes, the highly developed electrosensory system of *Ornithorhynchus* may represent an adaptation to foraging in cloudy water. Computed tomography imagery indicates that the enlarged infraorbital canal of *Ornithorhynchus* restricts the space available for maxillary tooth roots. Hence, loss of functional teeth in *Ornithorhynchus* may possibly have resulted from a shift in foraging behavior and coordinate elaboration of the electroreceptive sensory system. Well-developed electroreceptivity in monotremes is known at least as far back as the early Cretaceous; however, there are differences in the extent of elaboration of the feature among members of the ornithorhynchid lineage.

INTRODUCTION

Extant platypuses (*Ornithorhynchus anatinus*) forage at the bottom of streams with their eyes closed, using only electro- and mechanoreception (1–3). The Miocene monotreme *Obdurodon dicksoni* has a larger bill than *Or. anatinus* and a seemingly well-developed trigeminal nerve, similar to the extant platypus (4–6). Morphological similarities in bill structure between these species suggest that they may have filled similar ecological niches. However, there are also several notable morphological differences. For example, *Ornithorhynchus* has no teeth as adults in contrast to *Obdurodon*, which had fully functional cheek teeth. Many mammals have lost their teeth as a result of evolution, including echidnas, anteaters, and baleen whales, but none of these edentulous animals actually masticate their prey with their jaw moving (7). In contrast, the adult extant platypus still masticates its prey by using horny pads, located in the same position as the cheek teeth of *Obdurodon*, to crush items being consumed (2). Therefore, the loss of teeth in *Ornithorhynchus* is unlikely to be attributable to the lack of their necessity given that commutation of food remains an important component of feeding in the living animal. The cause of the loss of teeth is still unclear.

Or. anatinus swims under water with its eyes shut. However, its eyes show morphological similarities to those of other aquatic and semi-aquatic mammals, such that the lens is adapted to underwater vision with a steeply curved posterior surface in relation to the flatter anterior surface (8, 9). This at least raises the possibility that *Obdurodon* may have kept its

eyes open while foraging for food. However, the difference of sensory efficiency between *Ornithorhynchus* and *Obdurodon* is also still unclear.

The skull morphology of *Ob. dicksoni* has been examined in detail (4–6). However, there has been relatively little attention paid to comparing features that may relate specifically to differences in feeding behaviors and sensory efficiency with modern platypuses. Here, we report several skull differences between the two species that would appear to reflect differences in how these two species operated within their respective habitats, and a potentially correlated difference that may have led to loss of teeth in adult *Or. anatinus*.

RESULTS

Morphological measurements and angles of the skulls of *Ob. dicksoni* and *Or. anatinus* (Fig. 1) are shown in Table 1. Regression results suggest that all variables are significantly correlated to skull size ($P < 0.05$; Fig. 2). Because mainland and Tasmanian *Ornithorhynchus* were plotted along the same regression line, they were analyzed together (Fig. 2). Regression lines and corresponding prediction intervals for *Ornithorhynchus* and the plot of *Obdurodon* are shown in Fig. 2.

Obdurodon has a higher angle (a) and lower angle (b) than *Ornithorhynchus* (Table 1 and Fig. 1). When the effect of size is removed by allometric comparison, the result is not different (Fig. 2). Together, these results suggest that the bill of *Obdurodon* is deflected more dorsally relative to the basicranium (dorsal flexion of the face) than that of *Ornithorhynchus*, which exhibits ventral deflection (ventral flexion of the face).

Obdurodon is bigger than *Ornithorhynchus* in all skull measurements, but the proportions of the measurements are also different (Table 1). On the basis of the allometric comparison, the size of the infraorbital foramen for *Obdurodon* falls on the regression line of *Ornithorhynchus* (Fig. 2). In addition, in the regression of infraorbital foramen on the greatest length of the skull (GLS), *Obdurodon* plots below the lower

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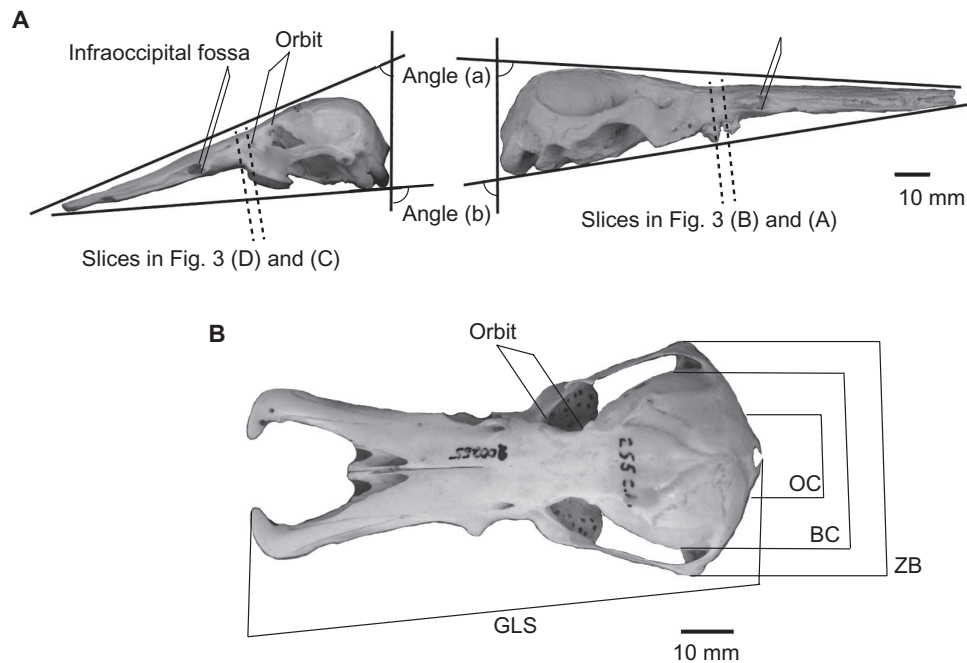


Fig. 1. Photographs showing measurements on the skulls of *Ornithorhynchus* in left lateral (A, left side) and dorsal (B) views, and *Obdurodon* in right lateral view (A, right side). GLS, greatest length of the skull; OC, occipital condyle; BC, braincase; ZB, zygomatic breadth.

Table 1. Skull measurements of *Obdurodon* and *Ornithorhynchus*.

Data are means \pm SD. *n*, number of specimens.

Measurements	<i>Obdurodon</i>	<i>Ornithorhynchus</i>	<i>n</i>
GLS	131.20	92.80 \pm 8.31	32
Angle (a)	87.06	69.15 \pm 3.43	25
Angle (b)	80.59	93.33 \pm 3.55	25
Infraorbital foramen	3.47	3.13 \pm 0.38	32
Braincase	35.86	32.18 \pm 2.19	32
Zygomatic breadth	50.63	42.20 \pm 3.98	32
Occipital breadth	27.45	23.76 \pm 2.36	32
Orbit	11.85	9.17 \pm 0.84	32
Geometric mean	25.41	21.02 \pm 1.87	32

prediction interval for *Ornithorhynchus* (Fig. 2). When geometric mean was used as the independent variable, the results indicated that the size of the infraorbital foramen was just smaller than the lower prediction interval for *Ornithorhynchus* (Fig. 2). In contrast, the orbit size of *Obdurodon* seems to be greater than the lower prediction interval (that is, within prediction intervals) for *Ornithorhynchus* when using GLS as an independent variable (Fig. 2). In addition, measures for *Obdurodon* are greater than or just on the higher prediction interval of *Ornithorhynchus* when geometric mean was used as an independent variable (Fig. 2). These results indicate that *Obdurodon* had a relatively smaller infraorbital foramen (and maxillary nerve) but an identical or a

larger orbit (and eye) than *Ornithorhynchus* in relation to size (for both GLS and geometric mean). Although the result above is based on intra-specific allometry of *Ornithorhynchus*, previous reports on the inter-specific allometry of the eye also support our finding of larger eyes in *Obdurodon* in relation to its skull size (fig. S1).

Cross-sectional images of *Obdurodon* and *Ornithorhynchus* indicate a narrower infraorbital canal in *Obdurodon*, compared to *Ornithorhynchus*, and further reveal the complete lack of space for what might otherwise have been normal mammalian tooth roots in the maxilla of *Ornithorhynchus* (Fig. 3).

DISCUSSION

Possible behavioral change over time in feeding strategies

Obdurodon exceeds the range of *Ornithorhynchus* in terms of cranial deflection (Fig. 2), indicating that the rostrum of the extinct taxon was more dorsally deflected with respect to the basicranium than that of *Ornithorhynchus* (Fig. 1). Interspecific and intraspecific differences in the cranial deflection with respect to the basicranium have been reported in other mammals [for example, in previous studies (10–17)]. Cranial deflection is relatively “plastic” in mammals. For example, investigations of canids have revealed significant intraspecific variation in this trait, which is determined by the physical relationships of the splanchnocranium and neurocranium to each other (11–17). However, Tasmanian and mainland *Ornithorhynchus*, which became isolated from each other around 0.7 to 0.94 million years ago (Ma) (18), are plotted along the same regression line (Fig. 2). Thus, there may be purifying selection for the trait; that is, the degree of cranial deflection is functionally important and maintained by natural selection in *Ornithorhynchus*. Therefore, the difference in the angle of cranial deflection between modern and fossil ornithorhynchids may reflect differences in behaviors, rather than being a product of neutral evolution.

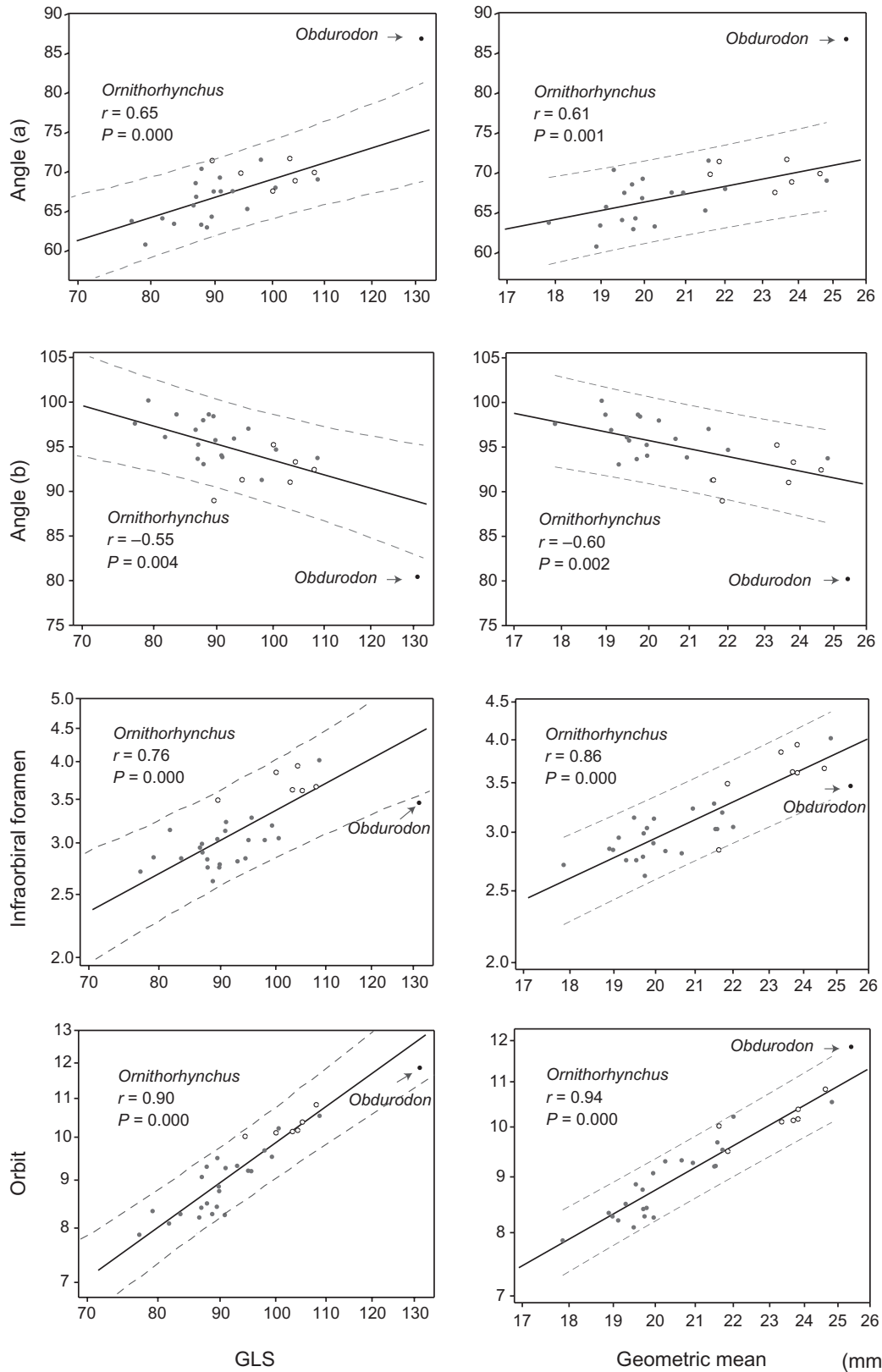


Fig. 2. Bivariate plots of skull measurements. Regression lines and 95% prediction intervals of the measurements and angles plotted by GLS and geometric mean in the *Ornithorhynchus* compared to *Obdurodon*. Scales are log-transformed for linear measurements. Mainland platypuses are shown as gray circles, whereas Tasmanian platypuses are shown as black open circles.

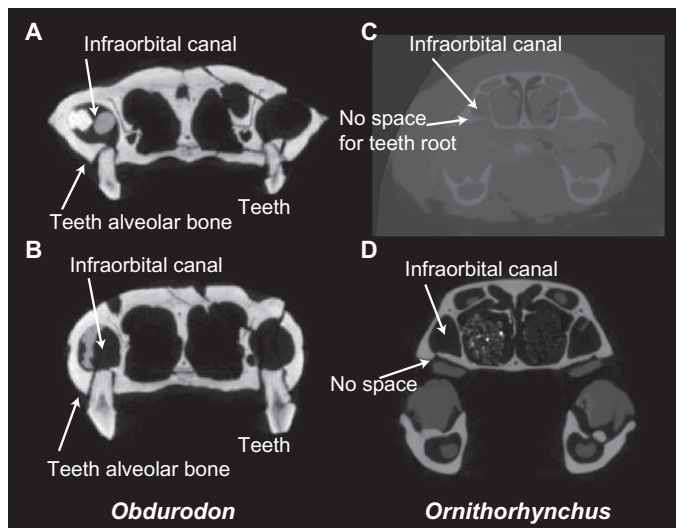


Fig. 3. CT slices along the anteroposterior axis of *Obdurodon* and *Ornithorhynchus* skulls at the tooth or horny pad position (see Fig. 1). (A and B) *Ob. dicksoni* (from Digimorph; Queensland Museum F20568). (C) *Or. anatinus* (YAMA M-1). (D) *Or. anatinus* (from Digimorph; American Museum of Natural History M200255).

In other mammals, interspecific differences in cranial deflection are often considered to reflect differences in sensory efficiency [such as width of visual field in lagomorphans (17) or vocalization in chiropterans (10)]. However, *Ornithorhynchus* depends less on vision and sound than do many mammals (2, 19–21), and sensory efficiency probably does not explain the ventrally deflected bill in the skull of *Ornithorhynchus*.

Another possible explanation for a ventrally deflected bill is feeding behavior. If the rostrum is deflected ventrally, it should optimize bottom feeding by aquatic mammals, as seen in, for example, dugongids feeding on sea grasses and fossil cetaceans on benthic prey (22). *Ornithorhynchus* is known to forage on the bottom of rivers and lakes (2). Therefore, the ventrally deflected bill of *Ornithorhynchus* likely represents an adaptation to this kind of foraging. In contrast, the more dorsally deflected bill of *Obdurodon* suggests that this taxon might not have been a bottom feeder but rather may have foraged in the water column (above the bottom).

Adaptive changes in sensory system

Allometric comparison of the skull measurements indicates that *Obdurodon* has a relatively larger orbit (and eyes) and a narrower infraorbital foramen (and maxillary nerve) than *Ornithorhynchus* (Fig. 2). A well-developed trigeminal nerve, including the maxillary nerve, is the most prominent anatomical feature responsible for relaying “bill sense” (electro- and mechanoreception) to the brain of the platypus (2, 3). Although *Obdurodon* had a bigger bill than *Ornithorhynchus* (7, 8), the trigeminal nerve should be a direct index of bill sensitivity. Therefore, our findings regarding the infraorbital foramen suggest that the bill of *Obdurodon* was less electro- or mechanoreceptive than that of *Ornithorhynchus*. The results regarding orbit size suggest that *Obdurodon* had greater visual acuity than *Ornithorhynchus*. It suggests that within the ornithorhynchid lineage, there was an evolutionary transition from dependence on vision to dependence on electro- and mechanoreception during foraging. This transition probably involved a concomitant reduction in eye size and expansion of the trigeminal nerve (Fig. 2).

One possible cause of the transition in dependence from eyes to electro- and mechanoreception may have been a change in foraging behavior as discussed above. Vision might have been effective for *Obdurodon* foraging in the water column. However, *Ornithorhynchus* forages on the stream bottom, where mud can be stirred up by the moving bill and subsequently cloud the field of vision. In such a situation, vision becomes less effective, and electro- and mechanoreception of the bill are more important. This behavioral difference may be responsible for the sensory transition from vision to bill sense.

Cause of tooth loss in *Ornithorhynchus*

The enlargement of the trigeminal nerve and infraorbital canal, immediately above the base of the maxillary cheek teeth in ornithorhynchids, could well have resulted in increasing space constraints to maintain tooth roots required to support cheek teeth. Our computed tomography (CT) slice images indicate that *Obdurodon* had tooth alveoli in the upper jaw (Fig. 3) (7, 8). In contrast, the extant *Ornithorhynchus* maxilla is very thin and unable to house tooth roots. This change in the maxilla, as well as increased dependence on electro- and mechanoreception in *Ornithorhynchus* associated with bottom foraging, correlates with hypertrophy of the infraorbital canal and the associated maxillary nerve (Fig. 3). *Ornithorhynchus* is unique among mammals that have lost their teeth in that it still masticates using horny pads, which do not require alveoli for support (Fig. 3). It should be mentioned that *Obdurodon* barely managed to sustain teeth because it had a substantially developed infraorbital canal, albeit slightly less developed than that of *Ornithorhynchus* (Figs. 2 and 3).

Well-developed trigeminal nerves and electroreception are found in monotremes at least as far back as the early Cretaceous (23, 24). However, there are differences in the extent of elaboration of these features within the group. Toothed monotremes, such as the species of *Obdurodon* that lived during the Miocene, may have had less-developed electroreceptive capacities than *Ornithorhynchus*. *Ornithorhynchus* is sometimes called a living fossil, yet this species is characterized by autapomorphies that distinguish it from its extinct relatives. The loss of teeth and extremely well-developed electroreceptivity in *Ornithorhynchus* may have emerged relatively recently.

MATERIALS AND METHODS

We examined 32 skulls of *Or. anatinus* in the mammalogy collections of the U.S. National Museum of Natural History (Washington, DC). We obtained comparative data about the skull of *Ob. dicksoni* from Digimorph (<http://digimorph.org>). The holotype, Queensland Museum F20568, is a skull from the middle Miocene Ringtail Site from the Riversleigh World Heritage Area in northwestern Queensland. Ringtail Site has been radiometrically dated at 13.56 ± 0.66 Ma (25). To compare the internal morphology of the infraorbital canal, we CT-imaged a fluid specimen (preserved in 50% ethanol) of *Or. anatinus* in the Department of Acupuncture and Moxibustion, Tokyo Ariake University of Medical and Health Sciences, Tokyo (YAMA M-1), using the TXS320-ACTIS industrial microfocus CT scanner (Tesco Corp.) at the National Museum of Nature and Sciences, Tokyo. Slice images were obtained from the three-dimensional (3D) data from Digimorph and the fluid specimen. We used ImageJ software (National Institutes of Health) for 3D image processing.

Caliper measurements (Fig. 1) were taken from skulls of *Or. anatinus* and a 3D-printed replica of the skull of *Ob. dicksoni* (using DMM.com service, Japan; acrylic plastic, 0.2-mm resolution). In addition, photographs were taken from the left side of the specimens of the two species,

and the two angles were measured (shown in Fig. 1) using ImageJ. The angles were determined on the basis of the intersections of the lateral and dorsoventral planes. The lateral plane was defined on the basis of how the specimen lays when placed on a flat surface. The dorsoventral plane was defined as the plane connecting the occipital condyle and the dorsal ridge of the foramen magnum, which determines the orientation of the cranium from the neck.

To eliminate the effect of size, allometric regressions were used to compare skull measurements for both species. We used the GLS and the geometric mean of all linear measurements as independent variables in this analysis. All statistical analyses were performed using Minitab 14 (Minitab Inc.).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/10/e1601329/DC1>

fig. S1. Relationship between body mass and orbit size (anteroposterior diameter) for *Ornithorhynchus* and *Obdurodon*.

Reference (26)

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