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New information about the skull and dentary of the Miocene platypus *Obdurodon dicksoni*, and a discussion of ornithorhynchid relationships

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A reconstruction of the skull, dentary and dentition of the middle Miocene ornithorhynchid *Obdurodon dicksoni* has been made possible by acquisition of nearly complete cranial and dental material. Access to new anatomical work on the living platypus, *Ornithorhynchus anatinus*, and the present comparative study of the cranial foramina of *Ob. dicksoni* and *Or. anatinus* have provided new insights into the evolution of the ornithorhynchid skull. The hypertrophied bill in *Ob. dicksoni* is seen here as possibly apomorphic, although evidence from ontogenetic studies of *Or. anatinus* suggests that the basic form of the bill in *Ob. dicksoni* (where the rostral crura meet at the midline) may be ancestral to the form of the bill in *Or. anatinus* (where the rostral crura meet at the midline in the embryonic platypus but diverge in the adult). Differences in the relative positions of cranial structures, and in the relationships of certain cranial foramina, indicate that the cranium may have become secondarily shortened in *Or. anatinus*, possibly evolving from a more elongate skull type such as that of *Ob. dicksoni*. The plesiomorphic dentary of *Ob. dicksoni*, with well-developed coronoid and angular processes, contrasts with the dentary of *Or. anatinus*, in which the processes are almost vestigial, as well as with the dentary of the late Oligocene, congeneric *Ob. insignis*, in which the angular process appears to be reduced (the coronoid process is missing). In this regard the dentary of *Ob. insignis* seems to be morphologically closer to *Or. anatinus* than is the dentary of the younger *Ob. dicksoni*. Phylogenetic conclusions differ from previous analyses in viewing the northern Australian *Ob. dicksoni* as possibly derived in possessing a hypertrophied bill and dorsoventrally flattened skull and dentary, perhaps being a specialized branch of the *Obdurodon* line rather than ancestral to species of *Ornithorhynchus*. The presence of functional teeth and the robust, flattened skull and dentary in *Ob. dicksoni* argue for differences in diet and lifestyle between this extinct ornithorhynchid and the living *Ornithorhynchus*.

Keywords: *Obdurodon*; *Ornithorhynchus*; platypus; Monotremata; Riversleigh; Miocene

1. INTRODUCTION

The platypus family, Ornithorhynchidae, is one of four in the order Monotremata, the egg-laying mammals that are today restricted to the Australo-Papuan region. Monotremes are considered to be the most primitive of living mammals because of the retention of 'reptilian' characteristics such as oviparity and a therapsid-like shoulder girdle that have been lost in marsupial and placental mammals.

From the time of their discovery in Australia, by Europeans two centuries ago, until 1995, only two monotreme families had been recognized: the semi-aquatic Ornithorhynchidae (the platypus-like monotremes), and the terrestrial Tachyglossidae (the ant-, termite- and worm-eating echidnas). The Early Cretaceous monotreme *Steropodon galmani*, recovered as a lower jaw fragment with three molars *in situ* from opal-bearing deposits at Lightning Ridge in New South Wales, Australia, had been included within Ornithorhynchidae when first described because its molar teeth are strikingly similar to the lower molars of known ornithorhynchids (Archer *et al.* 1985). However, in order to reconcile *Steropodon*'s great age (approximately 110 million years (Ma) old) with evidence from molecular studies indicating divergence dates between Ornithorhynchidae and Tachyglossidae that possibly postdate the Cretaceous (the latest Cretaceous at the earliest (Westerman & Edwards 1992)), *Steropodon* was placed in its own family, Steropodontidae (Flannery *et al.* 1995), rather than accept a significantly paraphyletic Ornithorhynchidae. The decision to remove *Steropodon* from Ornithorhynchidae was taken in a paper describing *Kollikodon ritchiei* (Flannery *et al.* 1995), an extraordinarily derived, new monotreme with bunodont molars from the same Lightning Ridge locality that produced *Steropodon galmani*. The addition of Steropodontidae and Kollikodontidae brings the number of known families within Monotremata to four.

The earliest undoubted ornithorhynchid, *Monotrematum sudamericanum*, is known from late Early Palaeocene deposits of Patagonia, Argentina (Pascual *et al.* 1992). The oldest Australian ornithorhynchid, *Obdurodon insignis*, comes from the late Oligocene central Australian Etadunna Formation and was the first pre-Pleistocene ornithorhynchid found, identified by comparison with *Ornithorhynchus anatinus*, which retains vestigial molar teeth in the juvenile (Woodburne & Tedford 1975). A second, undescribed *Obdurodon* species has been recovered from the Mammalon Hill locality of the Etadunna Formation. *Obdurodon dicksoni*, from early and middle Miocene limestone deposits at Riversleigh, Queensland, Australia, is by far the most complete fossil ornithorhynchid known. Beautifully preserved cranial material as well as isolated molars and premolars have been recovered. The Pliocene ornithorhynchid record is minuscule, with only a limb element of an *Ornithorhynchus* species recovered (Rich 1991). Pleistocene *Ornithorhynchus* material, much of it found in conjunction with archaeological sites, appears to be identical to that of the living species *Or. anatinus* (Archer *et al.* 1978; Marshall 1992; Davis 1996).

The amphibious ornithorhynchids have been considered to be the more plesiomorphic living monotreme family because of their more generalized dietary niche and longer list of plesiomorphic features (e.g. formation of the secondary lateral wall of the braincase and contents of the cavum epiptericum (Zeller 1989*b*), and certain features of the middle ear such as the lack of a cochlear aqueduct in *Or. anatinus* (Zeller 1993)). The palaeontological record supports this placement; whereas, the ornithorhynchid fossil record stretches back to the early Palaeocene (Pascual *et al.* 1992), the first tachyglossid does not appear in the fossil record until possibly the middle Miocene (Griffiths *et al.* 1991; Archer *et al.* 1995).

This study presents a reconstruction of the skull, dentary and dentition of *Ob. dicksoni*, the only pre-Pleistocene ornithorhynchid for which the skull is known. The skull, previously described by Archer *et al.* (1992, 1993), was found with all premolars present but all molars absent. It provides our best look at a relatively plesiomorphic ornithorhynchid as well as a functional ornithorhynchid dentition. The present work describes and identifies cranial foramina in the skull and compares these with the foramina in *Or. anatinus*. Features of the soft anatomy that can be inferred from the fossil skull are discussed.

Skull nomenclature is primarily that of Zeller (1989*a*). Dental terminology is that of Archer *et al.* (1993).

2. MATERIALS AND METHODS

The *Ob. dicksoni* holotype (QM F20568) is an almost complete skull with both left and right first and second premolars in place. The major damage is to the cranial roof where a narrow oblique section of the skull is missing. The basicranium sustains slight damage on the left side but is essentially complete. The left lateral side of the rostrum and parts of the palate are incomplete. No os paradoxum, ectopterygoids or tympanic bones (fragile, loosely attached structures in *Or. anatinus*) have been preserved.

The skull was recovered from freshwater carbonate deposits from Ringtail Site, Ray's Amphitheatre, Gag Plateau, Riversleigh World Heritage property. Ringtail Site is low in the System C sequence interpreted by Archer *et al.* (1995) to be middle Miocene in age. Because molars were absent from the skull, isolated molars from the same site (QM F18973, QM F16888, QM F18985 and QM F23994) were used to complete the reconstruction. Two dentary fragments (also edentulous) have been recovered: a section of a left dentary that includes the anterior part of the molar tooth bed with alveoli for a six-rooted M/1 (QM F18977 from Neville's Garden Site, System B sequence; early Miocene *fide* Archer *et al.* (1995)); and a more posterior fragment (also of a left dentary) that includes the posterior part of the tooth bed with alveoli for a five-rooted M/2 and single-rooted M/3 (QM F18981 from Quentin's Quarry, System C). The second fragment preserves most of the coronoid process, mylohyoid process, angular process and ascending ramus of the dentary.

(a) ***Referred specimens***

QM F18978 from Neville's Garden (System B); QM F30249, F30716 and 30717 from Dirk's Towers (System B); QM F18976, F18979, F18980, F18982, F18983, F18986, F18987, F18988, F18989, F20755 and F23722 from Ringtail Site (System C); QM F18974, F18975 and F18977 from Quentin's Quarry (System C); QM F18984 from Bob's Boulders Site (System C).

Congeneric comparisons were made with late Oligocene (Woodburne *et al.* 1993) *Ob. insignis* material from central Australia (QM F11627, left dentary fragment; SAM P18087, lower left molar (holotype)). Comparisons with fossil *Ornithorhynchus* were made from Pleistocene *Or. anatinus* (QM F707, edentulous left dentary fragment). Comparisons with modern *Or. anatinus* involved a juvenile skull and mandible from Queensland (QM J23753); a series of juvenile and adult skulls from Victoria (C5569, C25089, C25093 and C26491); and an os paradoxum from New South Wales (AM M26638).

(b) ***Abbreviations***

AM M, modern mammal collection, Australian Museum, Sydney; C, Museum of Victoria, Melbourne; QM F, fossil collection of the Queensland Museum, Brisbane; QM J, recent mammal collection of the Queensland Museum, Brisbane; SAM P, palaeontological collections of the South Australian Museum, Adelaide.

3. RESULTS

Because general descriptions of the *Ob. dicksoni* skull appear in Archer *et al.* (1992, 1993), the present work focuses on detailed descriptions of features pertinent to the reconstruction presented herein and to the cranial foramina, which are described here for the first time. The reconstructed skull and dentary of *Ob. dicksoni* (figure 1*a–c*) are compared with those of an adult male *Or. anatinus* (figure 2*a–c*).

To review Archer *et al.* (1992, 1993), the main features distinguishing *Ob. dicksoni* from *Or. anatinus* include: a hypertrophied rostrum in *Ob. dicksoni* that is both wider and longer than the rostrum in *Or. anatinus*; lack of fusion of the component rostral bones in *Ob. dicksoni*, clearly showing the septomaxillae separate from and overlying the premaxillae and contrasting with the relatively well-fused rostrum in adult *Or. anatinus*; a remarkably flat skull table in *Ob. dicksoni* with no downward deflection of the rostrum as in *Or. anatinus*; expanded zygoma on the skull and well-developed angular and coronoid processes on the dentary in *Ob. dicksoni* for robust jaw adductor musculature; an ovoid, enclosed interseptomaxillary fenestra (a narial interspace through which the dorsal nostrils open) in *Ob. dicksoni*, a space which is open and V-shaped in *Or. anatinus*; prominent anterolateral maxillary processes

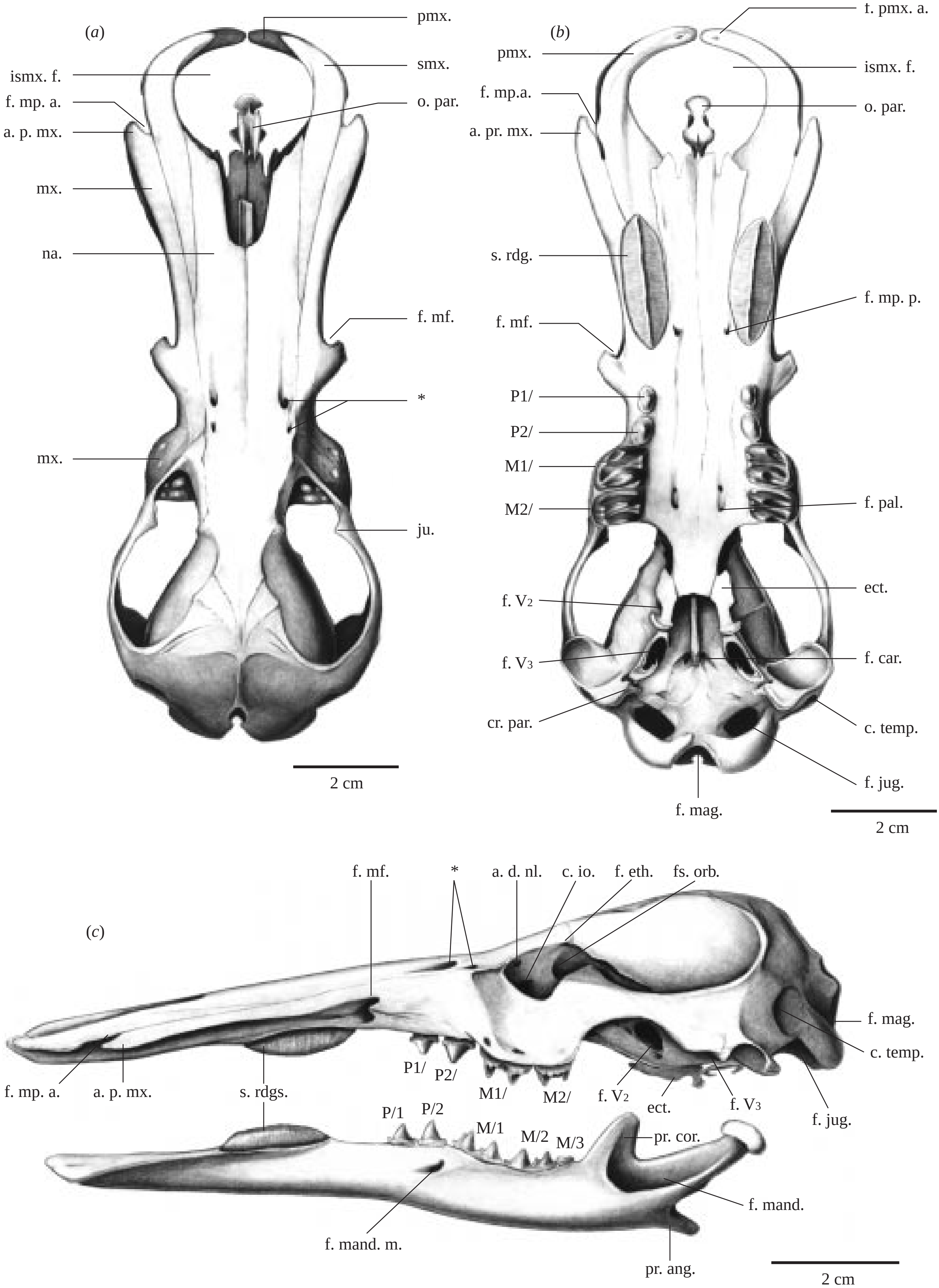

Figure 1. Reconstruction of the skull and dentary of *Obdurodon dicksoni*. Based on QM F20568 (holotype), and QM F18977 and QM F18981 (dentary fragments). (*a*) Dorsal view, (*b*) ventral view and (*c*) lateral view. For abbreviations, see table 1.

Table 1. *Abbreviations for figures 1*a–c *and 2*a–c

a. d. nl.	aditus ductus nasolacrimalis
a. p. mx.	anterior process of maxillare
c. io.	canalis infraorbitalis
c. temp.	canalis temporalis
cr. par.	crista parotica
ect.	ectopterygoid
f. V_2	foramen for V_2
f. V_3	foramen for V_3
f. car.	foramen caroticum
f. ethm.	foramen ethmoideum
f. jug.	foramen jugulare
f. mag.	foramen magnum
f. mand.	fossa mandibularis
f. mand. m.	foramen mandibulare medium
f. mf.	foramen maxillofaciale
f. mp. a.	foramen maxillopalatinum anterius
f. mp. p.	foramen maxillopalatinum posterius
f. pal.	foramen palatinum
f. pmx. a.	foramen premaxillare anterius
f. sph.	foramen sphenopalatinum
fs. orb.	fissura orbitonasalis
ju.	jugale
k. d. pd(s).	keratinized dental pad(s)
ismx. f.	interseptomaxillary fenestra
mx.	maxillare
na.	nasale
o. par.	os paradoxum
pmx.	praemaxillare
pr. ang.	processus angularis
pr. cor	processus coronoideus
smx.	septomaxillare
s. rdgs.	secateuring ridges

formed by extensions of the maxillae in *Ob. dicksoni* (processes that are absent in *Or. anatinus*); and well-developed, functional teeth (albeit with shallow roots) in *Ob. dicksoni*, in contrast to the keratinous pads that take the place of true teeth in the adult *Or. anatinus*.

With only a single *Ob. dicksoni* skull, it cannot be said with certainty where within the size range for the species this skull falls. However, because some of the teeth in the sample are larger than ones that would have fit into the alveoli of this skull, this specimen would not have been at the top end of the size range for the species (assuming for the present that all Riversleigh material represents a single taxon (Archer *et al*. 1992, 1993)).

(a) ***Dorsal view*** (***figure 1*a**)

The left premaxilla, septomaxilla, lateral aspect of the rostrum, anterior section of the zygomatic arch and the missing diagonal section of the skull roof have been restored in the illustration of the skull.

The os paradoxum, the median dumb-bell-shaped bone anterior to the vomer and maxilla and flanked by the rostral prongs of the premaxillae in *Or. anatinus* (figure 2*a*), has been reconstructed for *Ob. dicksoni* because the construction of the snout is basically similar in both ornithorhynchids. The origin of this interesting bony element, known to date only in *Or. anatinus*, is not known. Hypotheses have variously suggested that it is homologous with the prenasal of the pig (Turner 1885); that it is the fused rudiment of the 'reptilian' anterior vomer or prevomer (Wilson 1894; Broom 1932); or that it a vestige of the palatal processes of the premaxillae (Parrington & Westoll 1940). Zeller (1989*a*) could not positively identify this bone as either a prevomer or as part of the premaxillae but he does believe that it is a very specialized feature in *Or. anatinus* and is not a 'reptilian' retention. Its scroll-like posterodorsal flanges support the medial part of Jacobson's cartilage housing the vomeronasal, or Jacobson's, organ in *Or. anatinus* (Symington 1891).

The bones of the rostrum in this adult skull are comparatively unfused, allowing for examination of the sandwiching of component bones that form the rostrum. The right premaxilla and septomaxilla are complete showing that the shorter septomaxilla terminates lateral to the underlying premaxilla, which meets its opposite at the midline. This contrasts with the rostrum in adult *Or. anatinus* where the premaxilla and septomaxilla are fused together in the adult and the resulting prongs of bone do not meet at the midline. However, in foetal *Or. anatinus*, illustrated by Zeller (1989*a*), the premaxillae are fused ventrally and the septomaxillae, overlying the premaxillae and separated from them by the developing marginal cartilage, terminate lateral to the midline (in part to accommodate the os carunculae) as they do in *Ob. dicksoni*.

The septomaxilla in monotremes has been recognized by some authors as being homologous with the septomaxilla in 'reptiles', therapsids and some early mammals such as Docodonta (e.g. Watson 1916; de Beer 1937; Goodrich 1958; Kermack & Kielan-Jaworowska 1971; Kuhn 1971; Zeller 1989*a*; Archer *et al*. 1992, 1993), but has been misidentified as the premaxilla (e.g. van Bemmelen 1901; Wilson 1901; Kesteven & Furst 1929). Recent studies have confirmed that a septomaxilla is retained in monotremes and in some edentates among living mammals (Zeller *et al*. 1993). The huge, discrete septomaxilla in *Ob. dicksoni* clearly illustrates the unequivocal delineation of this splint-like bone from the premaxilla in an adult monotreme. The septomaxilla, comparatively large in both *Ob. dicksoni* and in *Or. anatinus*, is especially well developed in *Ob. dicksoni* because of the hypertrophy of the snout. This bone helps to support and retain the marginal cartilage sandwiched in between the septomaxillae and maxillae dorsally, and the premaxillae and maxillae ventrally, in *Or. anatinus*, and would have done so in *Ob. dicksoni* (Archer *et al*. 1992, 1993).

The widened area on the dorsolateral surface of the maxilla dorsal to the insertion of M1/ in *Ob. dicksoni* is quite thin, and it appears as if the shallow roots of the molars breached the bone in life; this condition is not seen in *Or. anatinus* skulls examined. Posteriorly the molar alveoli open ventral to the eye socket. In *Or. anatinus*, fenestrations occur in the approximate positions of the missing molar alveoli.

The cranial bones in *Ob. dicksoni* are well fused (unlike the bones of the rostrum), a feature also seen in multituberculates (Kermack & Kielan-Jaworowska 1971). The *Ob. dicksoni* skull shows moderately developed temporal muscle scars (for Mm. temporalis, trapezius anterior, rhomboideus and pterygoideus (Schulmann 1906)), that are also evident on *Or. anatinus* (figure 2*a*). Development of these scars is related to age and sex in *Or. anatinus*, being much more evident and elaborate in adult males

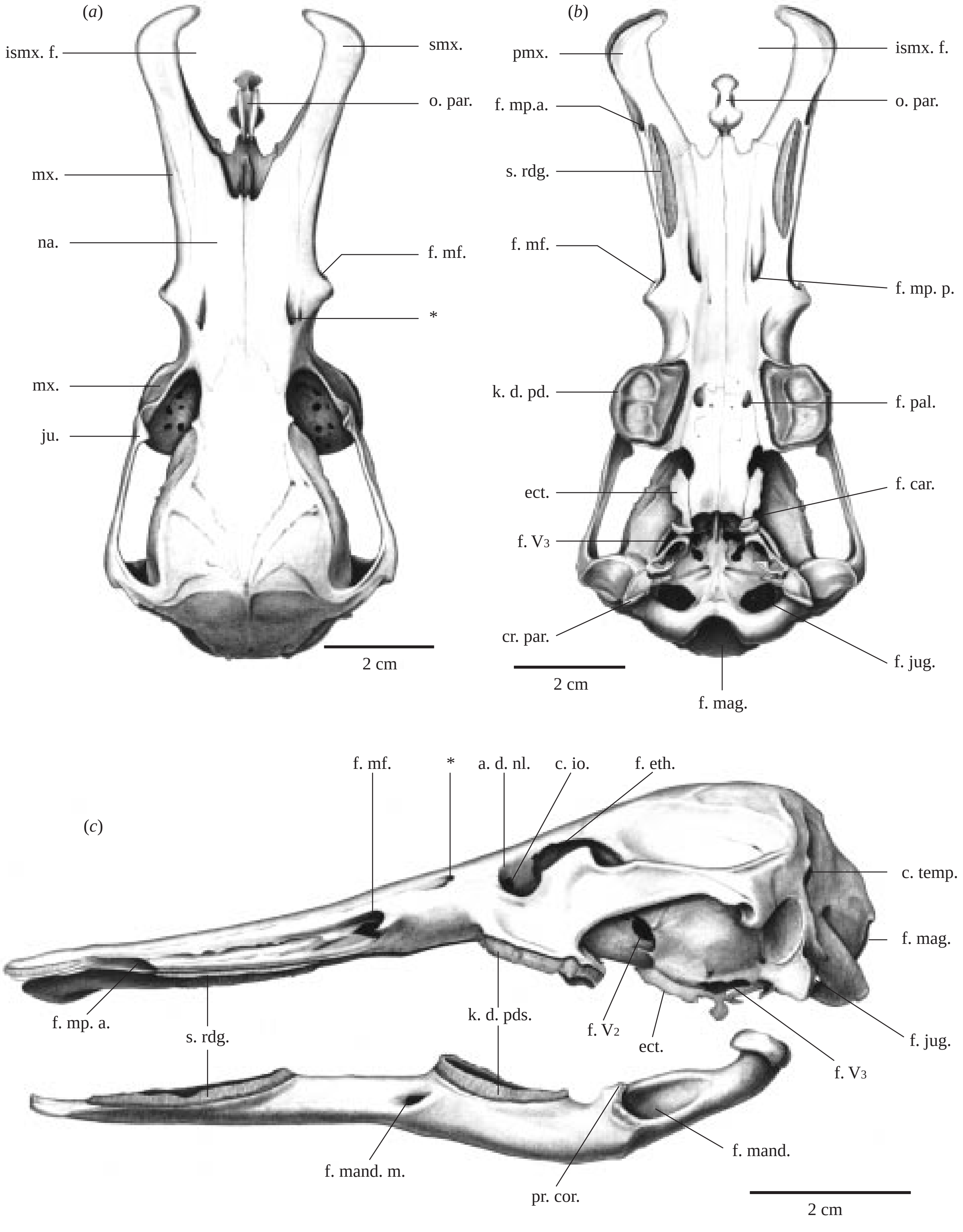

Figure 2. The skull and dentary of *Ornithorhynchus anatinus* (skull and dentary, C25089 with supplemental information from C25093 and C26491; os paradoxum, M26638). (*a*) Dorsal view, (*b*) ventral view and (*c*) lateral view. For abbreviations, see table 1.

and better developed in *Or. anatinus* than in tachyglossids, which have a reduced masticatory apparatus. Because the jaw musculature was more robust in *Ob. dicksoni* (a necessary corollate of a more functional dentition as evidenced by a more well-developed mandible and wider zygoma), it might be assumed that muscle scars would be prominent in larger/male *Ob. dicksoni*.

The small, triangular jugal, reconstructed on the left side, angles medially in *Ob. dicksoni* as in *Or. anatinus*, but there is no shallow notch along the dorsal margin of the zygoma posterior to the jugal, in contrast to the situation in *Or. anatinus*. Fusion has obscured any indication of sutures. The jugal (erroneously reported as absent in Monotremata (Kermack & Kielan-Jaworowska 1971), but which is absent only in tachyglossids (Griffiths 1978)), is reduced in the two ornithorhynchids compared here.

(b) *Ventral view (figure 1*b)

Ventrally, the rostrum and palate in *Ob. dicksoni* exhibit a complex lamination of the maxillae and premaxillae. Neither side of the central palatal region is complete in this specimen (the right side being more intact than the left).

The palate has deep embrasures anteriorly in approximately the same position that longitudinal epithelial ridges occur in *Or. anatinus* (the anterior horny plates of Poulton (1889)) (figure 2*b*). These ridges are formed from thickenings in the oral epithelium of the stratum corneum and are penetrated by long, thin papillae that create an irregular surface along the plates (Poulton 1889). They function as grasping and holding devices in the absence of anterior dentition, aiding in securing and manipulating prey and growing throughout the life of the animal to combat wear caused by grit and sand ingested during feeding (Poulton 1889). A small sulcus indicates the presence of these ridges in *Or. anatinus*. In *Ob. dicksoni* these pits are exceptionally deep, presumably for greatly enlarged epithelial ridges of the same type (Archer *et al.* 1993), and such epithelial ridges have been reconstructed here.

The ectopterygoids and ectotympanics have been reconstructed here as they appear in *Or. anatinus*. Although the function of the ectopterygoids in *Or. anatinus* is not known, Griffiths (1978) suggests that they offer resistance to upward movements of the posterior part of the tongue and could aid in transferring food from the cheek pouches to the oral cavity. Ectopterygoids (incorrectly identified as alisphenoids (Kesteven & Furst 1929)) are retained in all living monotremes (although morphologically dissimilar in the two families (Griffiths 1978)), and are also present in multituberculates and possibly in docodonts, although absent in therians (Kermack & Kielan-Jaworowska 1971). They may represent remnants of 'reptilian' pterygoids (Goodrich 1958). Facets on the palatines for the ectopterygoids are comparatively large and broad in *Ob. dicksoni* and, although they have been reconstructed as they appear in *Or. anatinus*, the ectopterygoids may have been more robust in *Ob. dicksoni*.

The monotreme ear region is plesiomorphic in that it is open ventrally, with no osseous floor for the epitympanic recess, although there is a slight overhang in tachyglossids formed by the ectopterygoid. Absence of an osseous floor is also a feature of several plesiomorphic marsupials including some borhyaenids and several Tiupampian didelphimorphians. In some features, particularly the tight connection between the ectotympanic and malleus, the tympanic region of monotremes resembles that of therapsids (Zeller 1993) and multituberculates (Meng & Wyss 1995). The horseshoe-shaped ectotympanic in *Or. anatinus* is morphologically similar to the angular bone (from which it was derived) of some Mesozoic synapsids (Zeller 1993) and the multituberculate *Lambdopsalis bulla* (Meng & Wyss 1995). The horizontal orientation of the ectotympanic in all living monotremes is a derived condition related to enlargement of the cranial cavity; the ectotympanic of *Lambdopsalis bulla* is similarly oriented, a feature regarded by Meng & Wyss (1995) to be a possible synapomorphy linking the two groups.

The basisphenoid forms a prominent crest in *Ob. dicksoni*, extending well beyond the posterior margin of the palate. It is a thick ridge of bone slightly bulbous at its caudal end, in contrast to the thin plate of bone that forms this crest in *Or. anatinus*. The orientation of the glenoid fossa is much more oblique in *Ob. dicksoni* than in *Or. anatinus*, where the fossae are oriented nearly perpendicular to the long axis of the skull. The posteromedial border of the fossa forms a lip in *Ob. dicksoni*, whereas in *Or. anatinus* there is little indication of a discrete termination of the fossa. This may reflect a tighter jaw articulation in *Ob. dicksoni* as occlusion of the triangular blades of the molars would have necessitated a more vertical or vertical oblique masticatory stroke. This contrasts with a more transverse stroke in *Or. anatinus* where the wide, flat, keratinous pads may move back and forth against each other in a more horizontal plane.

The most fundamental difference between *Ob. dicksoni* and *Or. anatinus* is the presence of rooted premolars and molars, apparently functional throughout life, in *Ob. dicksoni*. Teeth are absent in adult *Or. anatinus* (figure 2*b*), although juveniles retain vestigial molars until about one month after leaving the burrow (Griffiths 1978). Dental terminology used here is that of Archer *et al.* (1993) adapted from Every (1972, 1974) (table 2). This thegotic terminology is used rather than that developed for tribosphenic mammalian teeth both because monotreme molar cusps may not be homologous to those of tribosphenic mammals (Archer *et al.* 1992, 1993), and because this terminology emphasizes function rather than homology.

The upper molar row depicted (figure 1*b*), was drawn using left teeth (LM/1 = QM F16888 and LM/2 = QM F18973) and reversed to create the right molar row. Molars chosen from among paratypes from Ringtail Site have been sized to fit and 'reinserted' into the molar alveoli.

The adult dental formula for *Ob. dicksoni* is apparently P1-2/1-2; M1-2-/1-3 (the upper dentition has been mislabelled as P3-4/ and M1-3/ in Archer *et al.* (1993)). This differs from the postcanine dental formula established for *Or. anatinus* (Green 1937) in having only two, rather than three, upper molars. An abrupt change in tooth morphology distinguishes the unicusped premolariform teeth from the wide molariform teeth, a monotreme characteristic evident in the earliest taxa known, *Steropodon galmani* and *Kollikodon ritchiei* (Archer *et al.* 1985; Flannery *et al.* 1995). Although questions remain about the identity of the premolariform teeth (Luckett & Zeller 1989;

Table 2. *Abbreviated table of thegotic terms relevant to dental structure in ornithorhynchids*

(Adapted from Archer *et al.* (1993).)

structure	upper dentition	lower dentition
crest(s) or loph(s)	drepanon(s)	drepanid(s)
cusp(s)	akis(es)	akid(s)
paracone(s); paraconid(s)	parakis(es)	parakid(s)
a blade subtended by two akises	diakidrepanon(s)	diakidrepanid(s)
two blades sharing an akis, creating a V-shaped blade system	triakididrepanon(s)	triakididrepanid(s)

Archer *et al.* 1993), we have interpreted the premolariform teeth to be premolars and molariform teeth to be molars.

The upper premolars are single crowned, with a primary akis (presumably the parakis) and well-developed, rugose basal cingula on both teeth except beneath the lingual base of the parakises. P1/ is smaller than P2/. The first premolar is double rooted, whereas the second premolar appears to have three roots (a small accessory root evident from the lingual side), a feature that could cause problems with its identification as a premolar. The premolariform morphology and contrast in size and shape with the molar teeth, however, suggest that the multiple-rooted condition is autapomorphic (Archer *et al.* 1993; but see Luckett & Zeller 1989).

Ornithorhynchid molars are distinguished by triakididrepanons (three-cusped, two-blade structures) with the junctions of the blades lingual on the upper jaw and buccal on the lower jaw. This apparently autapomorphic dental morphology, with a reversed system of triangular blades, 'mimics with two teeth the function of four tribosphenid molars' (Archer *et al.* 1993). M1/ is square in shape, with both anterior and posterior triakididrepanon blade systems; lingual and buccal cuspules are present; and a wide occluding basin is present between the triakididrepanons. The anterior cingulum is small but the posterior cingulum is quite well developed. M2/ is wider than long, with a large triakididrepanon anteriorly and a smaller triakididrepanon posteriorly. Lingual and buccal cuspules are likewise present. The anterior cingulum is well developed (although the posterior cingulum is not), and together with the posterior cingulum of the M1/ it forms a large interdental basin not unlike that formed between the triakididrepanons of M1/ (Archer *et al.* 1993).

The molars have multiple, shallow roots (less than one-third the height of the crowns (Archer *et al.* 1993)) that may have been only loosely held in the alveoli in life, a condition most certainly responsible for the lack of molar teeth not only in the skull but also in the edentulous dentary fragments recovered. Many of the Riversleigh molars have lost or damaged roots (as do both of the upper molars—QM F16888 and QM F18973—used in this reconstruction) or are enamel caps. The roots may have been buttressed by supportive gum tissue in life in order to maintain stability. The skull has alveoli for a six-rooted M1/ and four-rooted M2/.

(c) *Lateral view* (*figure 1c*)

It is in the lateral view that the comparative robustness of the *Ob. dicksoni* skull is most obvious. The relatively unreduced dentary with well-developed coronoid and angular processes correlates with the heavier skull and contrasts with the more gracile form of *Or. anatinus* (figure 2*c*).

Noted by Archer *et al.* (1992, 1993), the flattened nature of the skull and dentary differs from the skull of *Or. anatinus*, where the rostrum is ventrally deflected from the basicranium and the dentary angles cranially in a comparatively sharp fashion, making the profile in *Or. anatinus* comparatively deeper than the profile in *Ob. dicksoni*.

A deep groove between the lamination of the septomaxilla and maxilla dorsally and that of the premaxilla and maxilla ventrally for the insertion of the marginal cartilage runs anteroposteriorly from the anterior tip of the rostrum to the f. maxillofaciale. In proportion, the depth of this groove quite exceeds that in *Or. anatinus*, an indication that the marginal cartilage was much more well developed in *Ob. dicksoni* than in *Or. anatinus* (Archer *et al.* 1992, 1993).

The zygomatic arch is robust; the arch is especially deep ventral to the eye socket and dorsal to the ear region in comparison to *Or. anatinus* (figure 2*c*). There appears to be no evidence of a lacrimal in *Ob. dicksoni*, which is absent from both living monotreme families (Watson 1916; de Beer 1937; Zeller 1989*a*; contra Kesteven & Furst 1929).

The two dentary fragments, both of the left side, provide complementary information. The more anterior fragment, extending from just in front of the origin of the molar tooth bed and terminating posterior to the alveoli for M/1, retains the alveoli for M/1 and a remnant of the mandibular foramen. The alveolar pattern indicates that M/1 had six roots, as does the holotype, a left M/1, of *Ob. insignis* (none of the M/1s recovered from Riversleigh have complete sets of roots). The more posterior fragment (described in Archer *et al.* (1993)), missing the body of the dentary anterior to the alveoli for M/2 as well as the proximal part of the ascending ramus (including the articular condyle), preserves the alveoli for a five-rooted M/2 and a single-rooted M/3. All alveoli open into the lumen of the dentary.

Before the discovery of the posterior jaw fragment assigned to *Ob. dicksoni*, the extent of development of the coronoid and angular processes in extinct ornithorhynchids was not known. The fragile, plate-like coronoid process has been lost on the jaw fragment recovered for *Ob. insignis*, the only other pre-Pleistocene ornithorhynchid jaw fragment known, and is also missing from the *Steropodon galmani* jaw fragment.

In *Ob. dicksoni* the coronoid process is well developed, reflecting the need for a wide area of attachment for the strong temporalis muscles that would have been present in the Riversleigh taxon. There is a fairly long, medially inflected angular process in *Ob. dicksoni* (broken at the tip in this specimen), which contrasts with the dentary of *Or. anatinus*, where this process is either absent or much reduced. It appears to contrast as well with the dentary of *Ob. insignis*, where the angular process, although also broken at the tip, appears more reduced than in *Ob. dicksoni*. The *Ob. dicksoni* dentary possesses a well-developed internal 'mylohyoid' process (broken just past the origin), confirmation that this process in ornithorhynchids does not represent a vestige of the coronoid process. The ascending ramus of the jaw curves smoothly upward to the condylar region in *Ob. dicksoni*, rather than exhibiting an angled bend as the ramus does in both *Ob. insignis* and *Or. anatinus*; this would correlate with the flattening of the skull base and lack of a deflected bill in *Ob. dicksoni*.

As in the upper dentition, there is a sharp change in morphology in the lower dentition from premolariform to molariform teeth. The single-cusped lower (presumptive) premolars (found as isolated teeth and not yet described) both have only two roots (Archer *et al.* 1993). P/1 is long and narrow, whereas P/2 is shorter and wider (Archer *et al.* 1993). The basal cingulid is complete in P/1 but incomplete lingually in P/2 (Archer *et al.* 1993).

Except for its larger size, the M/1 of *Ob. dicksoni* is nearly identical to the M/1 of *Ob. insignis*, originally interpreted as an upper-right second molar (Woodburne & Tedford 1975). The anterior blade is a diakidrepanid and the posterior blade is a triakididrepanid. As with the corresponding upper molar, the posterior cingulum is well developed, as is the anterior cingulum of M/2, creating an occlusal basin for the posterior triakididrepanon of the M1/ (Archer *et al.* 1993). No M/2 has been found among Riversleigh molars to date, so our reconstruction relies on extrapolation from the morphology of the M/2 of *Steropodon galmani* and the worn M/2 recovered for *Ob. insignis*. Both anterior and posterior halves of M/2 apparently had well-developed triakididrepanid blade systems (Archer *et al.* 1993).

The posterior-most alveolus in both the *Ob. dicksoni* and *Ob. insignis* dentaries indicates that a single-rooted, extremely reduced M/3 was present. Such a vestigial tooth could be expected from an animal that had already lost any trace of a third molar from the upper toothrow. Two undescribed Riversleigh teeth that appear to be M/3s have been recovered from Ringtail Site. The M/3 would have played only a minor functional role in the occlusion of the upper and lower molar rows.

(d) ***Foramina***

The extensive network of cutaneous nerves that innervate the electro- and mechanoreceptors of the upper and lower bill in *Or. anatinus* are the ophthalmic (V_1), maxillary (V_2) and mandibular (V_3) branches of the sensory part of the trigeminal nerve (Manger 1994). Edgeworth (1935) describes the trigeminal nucleus as single, a feature shared with Dipnoi, Holocephali, Plagiostomi, Ganoidei and Amphibia, although he declines to call this plesiomorphic. These branches exit through 14 large, distinct foramina on the skull and dentary, a remarkably high number of trigeminal foramina within Mammalia (Huber 1930). The foramen innervating the dermal dorsal shield (the asterisk (*) of Zeller (1989*a*)) and the foramen for V_2 in *Or. anatinus* are larger than those of any other mammal, highlighting the extreme specialization of the platypus bill (Zeller 1988).

In therian mammals, the trigeminal system innervates the region around the vibrissae, the acquisition of vibrissae being considered a synapomorphy of therian mammals (Huber 1930). The elaboration of the electrical sense, however, may be a monotreme synapomorphy (Manger 1994). The trigeminal system, interestingly, is enlarged in some semi-aquatic placental mammals such as *Micropotamogale* to innervate the well-developed vibrissae important in underwater navigation (Stephan & Kuhn (1982), cited in Zeller (1988)).

The unique arrangement of the rostral foramina for the trigeminal nerve in monotremes differs fundamentally from the arrangement of these foramina in marsupials and placentals (Huber 1930). The placement of the rostral foramina is essentially the same in all living monotremes (Huber 1930). Although there are marked differences between the two families in the arrangement of the foramina of the braincase, the course of the cranial nerves relative to the vestiges of the primary wall of the braincase are also the same in both families (Zeller 1989*b*).

There have been many arguments over the homologies of the cranial foramina in monotremes (see table 3). Zeller (1989*a*) refrains from using terminology that implies homology if there is doubt or error (e.g. the controversy over the homology of the 'foramen ovale'), preferring to define the foramen in question by its contents. The present account follows Zeller in this decision. In addition, Huber (1930) cites the misinterpretation of the anterior rostral foramina as vestigial alveoli for incisors and canines by Abel (1922) and Weber (1927).

The structure and placement of the cranial foramina in *Ob. dicksoni* are basically similar in position to the matching foramina in *Or. anatinus*. Therefore, it is assumed here that the innervation and vasculature would be essentially the same for both taxa.

(i) *Cranial foramina*

In *Ob. dicksoni* there is a small foramen on the ventral surface of the premaxilla close to the midline where the distal ends of the premaxillae meet. This foramen is not present in post-foetal *Or. anatinus* and is not seen in the foetal *Or. anatinus* modelled in Zeller (1989*a*). It resembles a small foramen in the anterior premaxilla in *Morganucodon* (Kermack *et al.* 1981) and the tritylodont *Oligokyphus* (Kühne 1956), which, according to Kühne, is also present in *Thrinaxodon liorhinus* and *Gomphognathus* cf. *mastacus*. We call this foramen in *Ob. dicksoni* the foramen premaxillare anterius.

The foramen maxillopalatinum anterius carries the branches of V supplying the anterolateral aspect of the bill in *Or. anatinus* (Manger 1994). In *Ob. dicksoni* this foramen appears as a notch bounded by the premaxilla ventromedially, the anterolateral process of the maxilla laterally and the septomaxilla dorsomedially. In *Or. anatinus*, where these large anterolateral maxillary processes do not develop, the anterior maxillopalatine foramen is a slit-like canal formed by the premaxilla medially and the maxilla laterally, terminating anteriorly at the anterolateral junction of the septomaxilla and maxilla. A similar foramen through the septomaxilla near the junction of the premaxillary–maxillary suture is seen in both *Sinoconodon* (Crompton & Luo 1993) and in the Upper Permian gorgonopsid *Dixeya quadrata* (Kermack & Kermack 1984). Because the maxilla forms a greater part of the dorsal surface of the bill in *Ob. dicksoni*, this foramen more closely resembles the septomaxillary foramen in these earlier taxa than does the foramen in *Or. anatinus*.

Table 3. *Table of synonyms for the major foramina of the skull and dentary in* Ornithorhynchus anatinus *and* Obdurodon dicksoni

(The terminology used by van Bemmelen (1901), Kesteven & Furst (1929), Jollie (1962), and Zeller (1989*a*, 1993) refers to foramina in *Or. anatinus*. Terminology of Archer *et al.* (1993) refers to foramina in *Ob. dicksoni*. The dorsal foramina for egress of the ethmoid nerve are of uncertain homology and thus are identified by an asterisk as in Zeller (1989*a*))

foramina	synonyms	reference
foramen maxillopalatinum anterius	foramen infraorbitale anterius	van Bemmelen (1901), Kesteven & Furst (1929)
	infraorbital canal	Jollie (1962)
	foramen maxillopalatinum anterius	Zeller (1989*a*)
	infraorbital foramen	Archer *et al.* (1993)
foramen maxillopalatinum posterius	foramen infraorbitale inferius	van Bemmelen (1901), Kesteven & Furst (1929)
	infraorbital canal	Jollie (1962)
	foramen maxillopalatinum posterius	Zeller (1989*a*)
	infraorbital foramen	Archer *et al.* (1993)
foramen palatinum	foramen palatinum	van Bemmelen (1901), Kesteven & Furst (1929), Zeller (1989*a*)
	anterior palatine foramen	Jollie (1962)
	greater palatine foramen	Archer *et al.* (1993)
foramen maxillofaciale	foramen infraorbitale laterale	van Bemmelen (1901)
	foramen infraorbitale	Kesteven & Furst (1929)
	infraorbital canal	Jollie (1962)
	foramen maxillofaciale	Zeller (1989*a*)
	infraorbital foramen	Archer *et al.* (1993)
*	foramen supraorbitale	van Bemmelen (1901)
	foramen opthalmicum superius	Kesteven & Furst (1929)
	infraorbital canal	Jollie (1962)
	*	Zeller (1989*a*)
	infraorbital foramen	Archer *et al.* (1993)
aditus ductus nasolacrimalis	foramen lacrymale	van Bemmelen (1901)
	foramen lachrymale	Kesteven & Furst (1929)
	lacrimal canal	Jollie (1962)
	aditus ductus nasolacrimalis	Zeller (1989*a*)
canalis infraorbitalis	foramen infraorbitale	van Bemmelen (1901)
	foramen infraorbitale posterius	Kesteven & Furst (1929)
	canalis infraorbitalis	Zeller (1989*a*)
	infraorbital canal	Archer *et al.* (1993)
foramen ethmoideum	foramen ethmoideum (pro nervo ophthalmico)	van Bemmelen (1901)
	ethmoid foramen	Jollie (1962)
fissura orbitonasalis	fenestra spheno-ethmoidea	van Bemmelen (1901)
	fenestra ethmoidalis	Kesteven & Furst (1929)
	orbital fissure—f. rotundum	Jollie (1962)
	fissura orbitonasalis	Zeller (1989*a*)
foramen sphenopalatinum	foramen spheno-palatinum	van Bemmelen (1901)
	foramen palatinum posterius	Kesteven & Furst (1929)
	sphenopalatine foramen	Jollie (1962)
	foramen sphenopalatinum	Zeller (1989*a*)
	spenopalatine foramen	Archer *et al.* (1993)
foramen for II, III, IV, V_1 *& VI*	foramen spheno-orbitale + opticum	van Bemmelen (1901)
	foramen sphenopticum	Kesteven & Furst (1929)
	optic foramen	Jollie (1962)
	foramen for II, III, IV, V1 & VI	Zeller (1989*a*)
	sphenorbital foramen	Archer *et al.* (1993)
foramen for V_2	foramen rotundum	van Bemmelen (1901), Kesteven & Furst (1929), Jollie (1962)
	foramen for V_2	Zeller (1989*a*)
	foramen pseudorotundum	Archer *et al.* (1993)
foramen for V_3	foramen ovale (Ram. III trigemini)	van Bemmelen (1901)
	foramen ovale	Kesteven & Furst (1929), Jollie (1962)
	foramen for V_3	Zeller (1989*a*)
	foramen pseudovale	Archer *et al.* (1993)

(*Cont.*)

Table 3. (*Cont.*)

foramina	synonyms	reference
foramen caroticum	foramen caroticum externum	van Bemmelen (1901)
	foramen arteriae carotis internae	Kesteven & Furst (1929)
	carotid canal	Jollie (1962)
	foramen caroticum	Zeller (1989*a*)
	internal carotid canal	Archer *et al*. (1993)
foramen vasculare externum medium	foramen vasculare externum medium	van Bemmelen (1901)
foramen vasculare externus laterale	foramen vasculare externum laterale, foramen vasculosum externa	Archer *et al*. (1993)
foramen jugulare	fenestra occipitalis (For, vagi + For. jugulare + For. praecondyloideum)	van Bemmelen (1901)
	foramen jugulare	Kesteven & Furst (1929), Zeller (1993)
	foramen for IX, X, XI & XII	Zeller (1989*a*)
	jugular foramen	Jollie (1962), Archer *et al*. (1993)
foramen magnum	foramen magnum	van Bemmelen (1901)
	foramen occipitale magnum	Zeller (1993)
canalis temporalis	canalis temporalis	van Bemmelen (1901), Zeller (1989*a*)
	temporal canal (post-temporal fenestra)	Jollie (1962)
	posterior temporal canal	Archer *et al*. (1993)
foramen mandibulare medium	foramen mandibulare mediu	Zeller (1989*a*)
fossa mandibularis	fossa mandibularis	Zeller (1989*a*)

The foramen maxillopalatinum posterius, a foramen on the palate through the maxilla, is much smaller and more anterior in relation to the posterolateral maxillary process in *Ob. dicksoni* than it is in *Or. anatinus*. In *Or. anatinus* it carries the numerous fibres of the middle superior alveolar nerve (V_2), which extend to the anterior margin of the bill (along with fibres of the external nasal nerve, V_1) (Manger 1994). Two paired foramina through the maxilla anterior to the palatine foramen occur in *Oligokyphus* (Kühne 1956).

The large foramen maxillofaciale in *Ob. dicksoni*, transporting the nerves to the lateral aspect of the bill posterior to the f. maxillopalatinum anterius, opens between the dorsal and ventral laminae of the maxilla. Its posterior border is formed by the anterior margin of the projecting posterolateral maxillary process as in *Or. anatinus*.

The foramen palatinum, a bilateral foramen in *Ob. dicksoni* with a smaller auxiliary foramen anterior to it, runs through the palatine just anterior to the posterior border of the toothbed. This position is substantially more posterior to that in *Or. anatinus*, where the single foramen is just posterior to the anterior limit of the toothbed. In both taxa the foramen is just cranial to the maxillo-palatine suture, although the suture lines in *Ob. dicksoni* are very faint.

The foramen sphenopalatinum apparently runs through the palatine posterior to the infraorbital canal in *Ob. dicksoni*, with a much more posterior course in this taxon both in relation to the palatine foramen and to the molar toothbed than in *Or. anatinus* (where it appears to share an opening with the palatine foramen).

In *Or. anatinus* a large canal for the n. ethmoidalis, a branch of V_1, pierces the nasal poseteromedial to the f. maxillofaciale (Zeller 1989*a*; Manger 1994). It is not homologous to any foramen in therians, probably being best identified with the 'vascular foramen' of Simpson (1937, cited in Zeller 1989*a*) as seen in the rostrums of multituberculates and possibly of *Morganucodon* (Zeller 1989*a*). This foramen has a long phylogenetic history, being present in theriodonts and lacertilians as well as the mammals discussed above; however, it is absent in therians (Zeller 1989*a*). This foramen is unusually large in *Or. anatinus* because of the thickness of the fibres of the r. lateralis of the n. ethmoidalis that travel through the large canalis nervus ethmoidalis (Zeller 1989*a*). Two foramina in the nasal posterior to the maxillary processes are present on the right side of this specimen of *Ob. dicksoni* (identified by an asterisk, *), the anterior foramen being the larger. The left side of this specimen is damaged, and as there can be either one or two foramina through the nasal in *Or. anatinus*, the number could be variable in *Ob. dicksoni* as well (although the reconstruction depicts them as bilaterally symmetrical). The fibres of the ethmoid nerve passing through these foramina innervate the dorsal shield of the bill and the posteromedial section of the skin of the upper bill in *Or. anatinus* (Manger 1994), and the presence of these foramina in *Ob. dicksoni* indicates that a dermal dorsal shield may have been present in this taxon as well.

The bones through which the foramina of the braincase pass are difficult to identify in *Ob. dicksoni* because of the extent of fusion. Nevertheless, relative positions and orientations provide a basis for comparison with *Or. anatinus*.

The aditus canalis ductus nasolacrimalis, or tear duct, appears to be a small slit posterodorsal to the angle of the orbit in *Ob. dicksoni*; the frontal/maxillary suture is just visible posteriorly. The nasolacrimal duct opens more dorsally in *Ob. dicksoni* than it does in *Or. anatinus*.

The infraorbital canal in *Or. anatinus* is proportionately larger than in any other mammal (Zeller 1988), and is even larger in relative terms in *Ob. dicksoni*. It runs rostrally through the maxilla carrying a large branch of V_2 (the superior alveolar nerve) to the bill in *Or. anatinus*, which branches at the maxillofacial foramen (Manger 1994). In *Ob. dicksoni* the bulk of the nerve fibres presumably would have exited through this latter large foramen while the remainder would have continued anteriorly to exit through the anterior maxillopalatine foramen, as in *Or. anatinus*.

The fissura orbitonasalis opening into the supracribrous recess anterior to the cranial cavity (de Beer 1937) appears to be similar in position to the orbitonasal fissure in *Or. anatinus*, running through the frontal bone dorsal to the f. sphenopalatinum and ventral to the orbital process.

The foramen in the side wall of the braincase for exit of the optic (II), oculomotor (III), trochlear (IV), V_1 and abducens (VI) nerves in adult *Or. anatinus* is a large, discrete foramen bordered by the pila praeoptica and the lamina obturans (Zeller 1989*a*). In young *Or. anatinus*, this opening is confluent with the foramen for V_2 but a strut of bone forms to separate these foramina in the adult (Kesteven & Furst 1929). This foramen in monotremes apparently is not homologous with the f. opticum and f. spheno-orbitale in therians (see table 3), both because the aperture for the ganglia are on different planes in both groups and because the relations with the bones differ (Zeller 1989*a*) The f. opticum of placentals opens between the pila praeoptica and pila metoptica (the p. metoptica being absent in monotremes although the pila antotica is present) and the f. sphenorbitale opens between the pila metoptica and alisphenoid (Zeller 1989*a*). The foramen for II–VI differs in *Tachyglossus aculeatus*, with an auxiliary foramen pseudosphenoorbitale, but the trochlear nerve (IV) leaves the cavum epiptericum through the f. prooticum in both monotremes, indicating that the primary wall of the braincase is homologous and synapomorphic for the two (Zeller 1989*b*). The foramen for II–VI in *Ob. dicksoni* resembles that of *Or. anatinus* but, between fusion and breakage of the cranium in this section, the identification of the component bones and understanding of the structure is difficult.

According to Zeller (1989*a*), the foramen for the exit of the maxillary branch of the trigeminal nerve (V_2) from the cavum epiptericum, called the foramen rotundum or the f. pseudorotundum in monotremes (see table 3), is homologous with neither the f. rotundum nor the f. pseudorotundum because of the aberrant conditions in both monotreme families. In *Or. anatinus* the exit for V_2 is bordered by the lamina obturans, alisphenoid and basisphenoid (Zeller 1989*a*). Zeller (1989*a*) sees the extent of variation in the relations of this foramen in therians as evidence that an f. rotundum was not present in the common ancestor of recent therians (and thus not in an ancestor shared with monotremes) and that separate derivations of an f. rotundum occurred independently within different therian lineages. The foramen for V_2 is a large ovoid foramina in *Ob. dicksoni* with two auxiliary foramina anterodorsal to the foramen (the posterior one being larger), a condition not seen in *Or. anatinus* skulls examined.

There has also been controversy over the terminology of the foramen for exit of the mandibular branch of the trigeminal, V_3, called by most authors the foramen ovale in monotremes (table 3). It is not homologous with either the f. ovale (through the alisphenoid) or the f. pseudovale (between the alisphenoid and petrosal) in therians (Zeller 1989*a*; but see Griffiths 1978), and is not identically formed in the two living monotreme families (Griffiths 1978; Zeller 1989*a*). It appears that in therians, a completely closed f. ovale through the alisphenoid is a derived condition and independently arrived at many times, and as such is not a homologous structure. In addition, it appears that a branching of V_3 prior to the aperture (as in *Or. anatinus*) negates the homology of the foramen. In *Or. anatinus* this huge foramen is bordered by the alisphenoid, the lamina obturans, the petrosal and the basisphenoid (Zeller 1989*a*). In *T. aculeatus* this foramen is bordered by the ectopterygoid and lamina obturans and is more rostral in position (Zeller 1989*a*). Fusion in this region of the *Ob. dicksoni* skull makes delineating the borders of the foramen impossible, but in position this foramen is more caudal in relation to the posterior margin of the palatine in *Ob. dicksoni* than in *Or. anatinus*. The lamina obturans forms an enlarged rim on its lateral border.

The foramen caroticum for passage of the internal carotid artery is a small bilateral foramen lateral to the posterior base of the basisphenoid crest and posterior to the caudal margin of the palate in *Ob. dicksoni*. The foramina open into the cranium anteromedially and are more posterior in relation to the foramen for V_3 in *Ob. dicksoni* than they are in *Or. anatinus*.

The 'foramen lacerum anterius' of van Bemmelen (1901) is a variably developed opening or series of perforations on the roof of the sulcus posterior to the f. caroticum and leading from it in *Or. anatinus*, but these openings are absent in *Ob. dicksoni*. According to Zeller (1989*a*), the naming of these as separate foramina is incorrect because bone is resorbed on both sides of the base of the skull, with a sulcus caroticus formed from the caudal part of the f. caroticum. The bony roof of the sulcus is solid in *Ob. dicksoni*, perhaps owing to the overall robustness of the cranial bone. Zeller suggests that degeneration of bone in *Or. anatinus* may be related to its aquatic lifestyle as a similar phenomenon occurs in sea lions (Stark (1967), cited in Zeller (1989*a*)); its absence in *Ob. dicksoni* may indicate that the Riversleigh animal was less specialized in this regard.

The fenestra vestibuli (the foramen for the footplate of the stapes, a circular footplate in monotremes, which is plesiomorphic for Mammalia) lies in the floor of the periotic (petrosal), posterolateral to the foramen for V_3. In both ornithorhynchids it is partly overhung by a shelf of bone formed by the crista parotica and the tympanohyal process. This foramen is slightly more posterior and closer to the tympanohyal process in *Ob. dicksoni* than it is in *Or. anatinus*.

Foramina for VII and VIII, best seen from the interior of the skull, are similarly placed in both ornithorhynchids but are difficult to see clearly in *Ob. dicksoni*.

The foramen jugulare for the glossopharyngeal (IX), vagus (X), accessory (XI) and hypoglossal (XII) nerves is enormous in both ornithorhynchids and is more obliquely angled in *Ob. dicksoni* than in *Or. anatinus* owing to the longer skull base and greater occipital slope in *Ob. dicksoni*.

The sizeable foramen magnum in *Ob. dicksoni*, for passage of the lower end of the medulla oblongata and other structures, has a dorsal notch that in *Or. anatinus* is the remnant of a deep embayment in the chondrocranium accommodating the projecting median lobe of the cerebellum (de Beer 1937). This notch is covered in young *Or. anatinus* by a membrane separating the median lobe from the ligamentum nuchae (Gregory 1947). The shape of this arched foramen is variable in *Or. anatinus*, and the foramen in *Ob. dicksoni* appears to be within this range of variation. It is more posterior in position in *Ob. dicksoni*, because of the greater occipital slope and more elongate cranium. The opening is more dorsal (thus slightly more horizontally directed), reflecting the flatter skull and presumably more horizontal body alignment in *Ob. dicksoni*.

Of particular interest in monotremes is the presence of the canalis temporalis (post-temporal canal), believed to be the remnant of the well-developed post-temporal fenestra or fossa in the 'reptilian' skull (Goodrich 1958). The post-temporal canal, relatively small in monotremes compared with earlier 'reptilian' forms, links the temporal fossa with the region dorsal to the ear capsule (Romer 1956). Running between the petrosal and squamosal, it occurs in stem 'reptiles' such as *Seymouria* (Romer 1956) through the earliest mammals including multituberculates (Kermack & Kielan-Jaworowska 1971). This canal, however, is absent in other living mammals (de Beer 1962).

In *Or. anatinus* the post-temporal canal is variously a canal or slit for the passage of the arteria diploëtica magna and a slip of the M. temporalis between the squamosal and auditory capsule (periotic), running laterally along the sidewall of the braincase (Rougier *et al.* 1992). The dorsal and lateral walls are formed by the squamosal, and the foramen runs anteriorly to open over the lamina obturans. Component bones cannot be distinguished in *Ob. dicksoni*, although relationships appear to be approximately the same as in *Or. anatinus*. In *Ob. dicksoni* the posterodorsal margin of the foramen is at a right angle to the cranial vault, whereas in *Or. anatinus* the margin angles ventrally. The canal is further from the glenoid fossa in *Ob. dicksoni* than in *Or. anatinus*, and the lateral margin does not follow the contours of the fossa as it does in *Or. anatinus*. The post-temporal canal appears to be proportionately large in *Ob. dicksoni*, but this opening varies widely in size and development in *Or. anatinus*.

(ii) *Mandibular foramina*

The mandible in ornithorhynchids is exceptionally well innervated by the mandibular branch of the trigeminal nerve (the inferior alveolar nerve), which gives off several branches, the largest of these exiting from the foramen mandibulare medium (Manger 1994). Laterally, only the barest indication of the f. mandibulare medium is preserved in the *Ob. dicksoni* anterior dentary fragment; it is just a notch-like remnant at the posterodorsal margin along the line of breakage of the fragment. This notch, just anteroventral to the anterior limit of the toothbed, appears to be roughly similar in position (perhaps slightly more anterior) and in configuration to this foramen in *Or. anatinus*, although its position is variable in the platypus.

The fossa mandibularis of the posterior dentary fragment is a uniformly rounded basin forming a deep, elongate trough that tapers smoothly up the ascending ramus. The lateral face of the dentary fragment has a section missing that would have included the anterior margin of the fossa; therefore, the reconstruction borrows information from the similar dentary of *Ob. insignis*. Because of this breakage it is not possible to ascertain whether or not the anterior margin of the lip rounded over the fossa as it does in *Ob. insignis*, or whether there were protuberances for attachment of the m. temporalis atop a well-developed prominence as there is in *Or. anatinus*. However, because the mandibular fossa is similar in other respects to the *Ob. insignis* dentary, and because the coronoid process for the temporalis is well developed in *Ob. dicksoni*, the assumption is made at present for the purpose of the reconstruction that no prominences or muscle attachments were present dorsolateral to the mandibular fossa in *Ob. dicksoni*.

There is a foramen that passes between the buccal and lingual sides of the dentary in both *Ob. dicksoni* and in some *Or. anatinus* (the masseteric canal is infilled in the *Ob. insignis* dentary and the presence or absence of this foramen at this stage cannot be determined). In *Ob. dicksoni* the dorsal margin is preserved although the ventral margin has been broken. The foramen opens just posteroventral to the single alveolus for M/3 and is anteroventral to the origin of the mylohyoid process. In *Or. anatinus* the foramen is posteroventral to where the alveolus for M/3 would have been, as in *Ob. dicksoni*, but the origin of the mylohyoid process is much more posterior in *Or. anatinus* than it is in *Ob. dicksoni* and the relationship between this foramen and the origin of the mylohyoid process is correspondingly more distant. An analogous but much larger foramen, the masseteric foramen, passes between both sides of the dentary in kangaroos (Macropodoidea). A much smaller foramen in phalangeridan possums (e.g. pseudocheirids) also passes transversely through the dentary in this region. However, in neither case is there evidence that these are homologous with the foramen in monotremes.

4. DISCUSSION OF THE DIFFERENCES IN CRANIAL MORPHOLOGY SEPARATING *OB. DICKSONI* FROM *OR. ANATINUS*

The similarities in skull form between the Miocene *Ob. dicksoni* and the living *Or. anatinus* are striking despite the fact that the two are approximately 15 Ma apart. Clearly, by at least the middle Miocene, the basic pattern—flattened skull with prominent, splayed bill—had been attained (Archer *et al*. 1993). Because of the similarities between the molar teeth of all ornithorhynchids, it is likely that members of the family shared at least a general skull morphology with a wide bill being a definitive feature.

Postcranial material for *Ob. dicksoni* has not yet been recovered from any of the Riversleigh sites (although an ilial fragment has been assigned to *Ob. insignis* (Archer *et al*. 1978)). However, both by inference from the platypus-like cranial morphology of *Ob. dicksoni*, and by the fact that much of the postcranial anatomy of *Or. anatinus* appears either plesiomorphic (in particular, the shoulder girdle) or specialized for aquatic life (e.g. the dorsoventrally flattened body form), it seems reasonable to assume that the body plan of *Ob. dicksoni* would have been similar.

(a) *Development of the bill in ornithorhynchids*

The bill in *Or. anatinus* is used both as a sense organ and as a tool for breaking the ground when burrowing (Burrell 1927). The hypersensitivity of the bill and the presence of mechano-, or touch, receptors in the bill have been known since the late 1800s (Poulton 1889). Electroreceptors, however, which are unique among mammals to monotremes and which are apparently able to detect small electromyogenic impulses given off by certain aquatic prey such as freshwater shrimp (Taylor *et al.* 1992), were not detected until 1986 (Scheich *et al.* 1986).

Huber (1930) believes that the platypus bill, as a navigational instrument, within its environment is superior to a rostrum with vibrissae. Although Huber's observations were made before knowledge of electroreceptive ability in *Or. anatinus*, he cites its extraordinary 'oral sense' as an important factor in the evolution of the ornithorhynchid neopallium.

Dorsal and ventral dermal extensions that continue the skin of the bill over the front of the face and throat (also called frontal shields) augment the sensory surface area of the bill. These immobile dermal shields (absent from the simpler beak of the echidnas) were first thought to protect the eyes from mud and debris when burrowing or foraging along muddy stream beds (Bennett (1860) and Oldfield Thomas (1888) cited in Burrell (1927)), but they actually emarginate just in front of the eye and would, therefore, be relatively inefficient as protective devices. It is probable that at least the dorsal dermal shield was present in *Ob. dicksoni*, because the foramina on the dorsum of the skull (*) are similar in position to those that supply the dorsal shield in *Or. anatinus*. It is unclear whether there was a ventral shield in *Ob. dicksoni*, although it is probable that one was present.

The contours of the bill in *Or. anatinus* are formed by an extensive cartilaginous plate, the cartilago marginalis, that fills the interseptomaxillary space (through which the dorsal nostrils open) and continues well beyond the bony limits of the rostrum. Only a remnant of the marginal cartilage is present during ontogeny in *T. aculeatus* (Wilson 1901). The marginal cartilage may be homologous with the anterior end of the palatal process, which would be an unusual instance of the reversion of bone to cartilage (Edgeworth 1935). A well-developed (possibly hypertrophied) marginal cartilage in *Ob. dicksoni* (indicated by the comparatively deep insertional area along the lateral aspect of the bill) and an exceptionally wide, flared bill (exaggerated in *Ob. dicksoni* by anterolateral maxillary processes absent in *Or. anatinus*), suggest that the bill in *Ob. dicksoni* was an important and highly sensory structure.

The rostral crura meet at the midline of this adult specimen of *Obdurodon dicksoni*, whereas the rostral crura diverge as bony prongs in adult *Or. anatinus* (Archer *et al.* 1992, 1993). However, Zeller (1989*a*) illustrates a foetal *Or. anatinus* in which the rostral crura meet at the midline as they do in *Ob. dicksoni*. The shape of the interseptomaxillary fenestra in foetal *Or. anatinus* also resembles the more ovoid shape of this fenestra in *Ob. dicksoni*, a consequence of the crura meeting at the midline. The ovoid shape contrasts with the V-shape of the fenestra in adult *Or. anatinus*. This ontogenetic evidence suggests that an *Obdurodon*-type bill, with the crura meeting at the midline, may have been ancestral to the bill form seen in *Or. anatinus*.

Reduction and osteological fusion appear to be entrenched monotreme features as all living monotremes exhibit these characteristics to some extent. Reduction and streamlining of the bill form is especially noticeable in *Or. anatinus* when compared to the form of the bill in *Ob. dicksoni*; the anterior maxillary processes have apparently been lost and the bill form has become more linear in *Or. anatinus*. The comparative lack of fusion of the rostral bones of *Ob. dicksoni* contrasts with the condition in living monotremes where, in adults, rostral suture lines are often difficult to see. The tendency towards fusion (particularly in the cranium), probably present in a common monotreme ancestor, seems either to have reversed itself at least in the rostral bones of *Ob. dicksoni* or to have evolved to the degree seen in the bills of all modern monotremes independently, given that the tendency towards fusion had established itself in the common ancestor.

Until discovery of the *Ob. dicksoni* skull, there were few clues as to the origin of the ornithorhynchid bill; reduction and fusion in the rostrum of *Or. anatinus* obscured traces of its ancestry. The structure of the rostrum in *Ob. dicksoni* and placement of rostral foramina (e.g. the foramina through the premaxilla and septomaxilla, which appear to be similar to foramina in some Mesozoic mammals and therapsids such as *Oligokyphus*, but which are missing in therian mammals), indicates that ornithorhynchids have retained these as plesiomorphic features. Taking these observations one step further, it is not inconceivable that the distinctive ornithorhynchid bill shape may have derived from a rostrum such as that of *Oligokyphus* in which the incisive foramina fused to form a single opening through the premaxillae; enlargement of such an arrangement may have resulted in a bill form like that of *Ob. dicksoni* (and thus of monotremes) in which this ovoid space bounded anteriorly by the conjoined premaxillae became progressively enlarged.

Development of a wide, flattened bill distinguishes ornithorhynchids from tachyglossids; the extent of bill development in fossil monotremes, therefore, is of great interest. *Steropodon* and *Kollikodon* both possess large mandibular canals, presumably for the innervation of a sensitive bill. The presence of both mechano- and electroreceptors in the bills of *T. aculeatus* (Gregory *et al.* 1989) and of *Zaglossus bruijnii* (Manger *et al.* 1997), suggests that they were present in a common ancestor and possibly that these senses were also present in *Steropodon* and *Kollikodon*.

Hypertrophy of the bill in *Ob. dicksoni* was surprising because ornithorhynchids were assumed to have gradually elaborated the snout from the more generalized form of a common monotreme ancestor (Murray 1984). Evidence for extensive innervation of the rostrum in *Ob. dicksoni* comes from the presence of the numerous large foramina along the bill with the same relative placement as the foramina in *Or. anatinus*.

Arguing against derivation of the bill of *Or. anatinus* from that of *Ob. dicksoni* is parsimony. The late Oligocene *Ob. insignis* possesses what appears to be a relatively small bill, *Ob. dicksoni* from the early Miocene possesses a hypertrophied bill, whereas the modern *Or. anatinus* possesses a much-reduced bill. If *Ob. insignis* gave rise to *Ob. dicksoni* which gave rise to *Or. anatinus*, the bill first enlarged and then reduced. Alternatively, some another species within the genus with a less hypertrophied snout gave rise to the genus *Ornithorhynchus*. The extent of hypertrophy of the bill of *Ob. dicksoni* may then represent a derived condition.

(b) *Comparisons involving the crania and dentaries*

Possibly correlated with reduction of the bill in *Or. anatinus* is shortening of the cranium in this species. The cranium appears more elongate in *Ob. dicksoni* and less so in *Or. anatinus*, an observation supported by quantification of morphological features and relative positions of the cranial foramina. The maxillary toothbed in *Or. anatinus* extends posteriorly, which may be a correlate to shortening of the cranium. Differences in cranial shapes are reflected in the relative positions of the cranial foramina, with many foramina closer together or closer to certain cranial structures in *Or. anatinus* than in *Ob. dicksoni*.

Flattening of both the skull and dentary in *Ob. dicksoni* represents an extreme in monotreme skull morphology, a group already noted for the unusual flatness of the skull (Owen 1868). In *Ob. dicksoni* the rostrum is not downturned, the foramen magnum is slightly more dorsal (indicating a more horizontal body alignment) and the dentary is not sharply angled. These are features that suggest a difference in lifestyle. *Ob. dicksoni*, with a flatter skull and body form, possibly foraged higher in the water column or perhaps even at the surface rather than in the benthic substrate where the modern platypus finds most of its food. It may have taken insects from the water's surface, a behaviour occasionally observed in the living platypus (Grant 1995). The downwardly deflected bill in *Or. anatinus* may reflect its habit of shovelling through benthic debris in search of aquatic invertebrate prey.

A trend towards reduction can be seen in the evolution of the dentary. In respect of morphology, the dentary of *Ob. dicksoni* resembles other mammals in having well-developed coronoid and angular processes. The dentary of *Or. anatinus* exhibits reduction of the angular and coronoid processes. The masticatory stroke would have become progressively less vertical (with reduction in height and subsequent loss of the high-crowned, interlocking molars) and progressively more horizontal. The masticatory musculature was correspondingly reduced as evidenced by the flat zygoma of *Or. anatinus* as well as by loss of major muscle attachment sites, in particular the coronoid process. Dentary reduction appears then to reflect overall reduction in skull morphology in *Or. anatinus*.

Few confident conclusions can be reached about differences between dentary structure in *Ob. insignis* and *Ob. dicksoni* because of breakage. However, although the tip of the angular process in this *Ob. insignis* specimen is broken, it appears to have been more reduced in the Oligocene ornithorhynchid (thus resembling more closely the angular process of *Or. anatinus*, where it is either reduced or absent). In addition, the *Ob. insignis* dentary does not curve gently upward as does the *Ob. dicksoni* dentary, but instead angles upward more sharply, as in *Or. anatinus*. Lack of an obvious angle in the *Ob. dicksoni* dentary corresponds to the flatness of the skull in this taxon, additional evidence that this skull conformation may be a derived rather than a plesiomorphic condition.

(c) *Dental evolution in ornithorhynchids*

Three correlated trends in dental evolution leading to and within the ornithorhynchid line can be seen: (i) elaboration and multiplication of the transverse shearing blades; (ii) progressive reduction of the roots of the molars; and (iii) increased role of the oral epithelium in dental function through production of horny pads.

The combination of wide, multiple-rooted molars with dual triakididrepanon blade systems is unique among mammals. Archer *et al.* (1985, 1992, 1993), Kielan-Jaworowska *et al.* (1987), Jenkins (1990), Kielan-Jaworowska (1992) and Flannery *et al.* (1995), have variously compared monotreme dentitions to those of tribosphenic mammals, pretribosphenic therians such as the advanced eupantothere *Peramus*, and mesungulatid dryolestoids. The possibility that monotremes might be related to Early Cretaceous eupantotheres such as *Vincelestes* was challenged by an analysis of *Vincelestes*, which revealed fundamental differences in the formation of the sidewall of the braincase (Rougier *et al.* 1992). Recovery of more fossil material, particularly the missing upper molars of *Steropodon galmani*, would be invaluable to the debate.

Although *Ob. dicksoni* apparently retained functional teeth throughout life, the molar roots are much shallower than those of *S. galmani*, which also had a much deeper jaw. As the molars widened and the jaw became less deep, the number of molar roots increased to four to six in the anterior two molars of species of *Obdurodon*. The shallowness of the roots and the ease of loss of molars from both skull and dentary fragments suggest that molars may have been fairly loosely held in the alveolar cavities by periodontal fibres. Hardened or built-up gum tissue may have helped to buttress the teeth in *Ob. dicksoni* or hold them more securely in their alveoli. This intermediate condition could have been a precursor to the evolution of horny epithelial pads as alternatives to functional teeth in *Or. anatinus*.

Elaboration of palatal epithelium occurs in all living monotremes. Tongues in both families have spines of keratinized tissue that work against the palate to assist further mastication (Griffiths 1978). Epithelial ridges on the palate in *Or. anatinus* aid in securing and dissecting prey in the absence of an anterior dentition. The possible presence of comparatively huge epithelial ridges as well as interlocking triangular blades on the teeth suggest that *Ob. dicksoni* may have fed on larger prey than *Or. anatinus*, perhaps small vertebrates such as frogs or snakes.

5. RELATIONSHIPS WITHIN MONOTREMATA

Phylogenetic affinities of monotremes are uncertain despite a significant increase in understanding about early mammals (e.g. Lillegraven & Krusat 1991; Krebs 1991; Rougier *et al.* 1992; Crompton & Luo 1993; Hu *et al.* 1997). Recent reviews of monotremes have tentatively linked them to early therians (Jenkins 1990; Kielan-Jaworowska 1992), dryolestoids (Bonaparte 1990; Archer *et al.* 1993), and multituberculates (Wible & Hopson 1993; Meng & Wyss 1995; but see Miao 1993). Results of molecular studies vary greatly, some suggesting a close relationship to marsupials (Janke *et al.* 1997; Kirsch & Mayer, this issue) with a revival of Gregory's (1947) Marsupionta, whereas others suggest that monotremes are genetically distant from therian mammals (e.g. Westerman & Edwards 1992; Retief *et al.* 1993).

On the basis of molar morphology, there appear to be four clades among monotremes: (i) kollikodontids with four bunodont molars; (ii) steropodontids with three molars, triakididrepanon blade systems and deep tooth roots; (iii) ornithorhynchids with three (or four) elaborated triakididrepanons and shorter but more numerous molar roots; and (iv) tachyglossids with complete loss of teeth. Among forms with high-crowned teeth, all share wide, rectangular molars with double V-shaped blade systems that have apparently converged on tribosphenid dental morphology (Archer *et al.* 1993). Because this unique pattern in toothed monotremes persists over a period of more than 110 Ma, it is the most striking example of dental conservatism known among mammals.

Steropodon galmani was included within Ornithorhynchidae when first described because it shared many features with the Oligo-Miocene species of *Obdurodon* (i.e. the distinctive double triakididrepanon blade systems, a diakidrepanon on the anterior half of the first lower molar and an enlarged mandibular canal) and because the mandibular canal suggested that a bill was present (Archer *et al.* 1985). Exclusion of *S. galmani* from Ornithorhynchidae was prompted by molecular studies (e.g. Westerman & Edwards 1992; Retief *et al.* 1993; Messer *et al.* 1995) that agree to a family split between Ornithorhynchidae and Tachyglossidae either near the Cretaceous–Tertiary boundary or postdating the Cretaceous (Flannery *et al.* 1995). Accepting this, Ornithorhynchidae in the sense of Archer *et al.* (1985) would be paraphyletic. Reference of *S. galmani* to a distinct family of its own resolved the problem (Flannery *et al.* 1995).

That monotremes were once far more diverse and that the line is capable of extreme specialization is demonstrated by *Kollikodon ritchiei* (Flannery *et al.* 1995). The highly specialized echidnas have either lost or are in the process of losing features considered platypus-like, in particular teeth and the marginal cartilage that might have supported a wider, more platypus-like bill.

(a) *Relationships within Ornithorhynchidae*

Archer *et al.* (1993) suggest that the middle Miocene *Ob. dicksoni* might be ancestral to species of *Ornithorhynchus*. Many features of the Miocene taxon may be plesiomorphic (e.g. the structure of the bill and development of the dentary). In development of the angular and coronoid processes of the dentary, *Ob. dicksoni* may even be more plesiomorphic than the late Oligocene *Ob. insignis*, whose small dentary with its apparently reduced angular process suggests a trend towards reduction in this lineage.

Other features of *Ob. dicksoni* are not clearly plesiomorphic. Although the basic bill structure (with rostral crura meeting at the midline) may be plesiomorphic in *Ob. dicksoni*, it is possible that the extreme development (hypertrophy) of the bill represents an autapomorphic specialization in the Riversleigh animal. The flat skull and low angle of the dentary in *Ob. dicksoni* may also be an autapomorphic condition because the dentary of *Ob. insignis* appears to have been relatively 'normal' (i.e. with an upwardly angled ascending ramus). Specialization in the bill and skull of *Ob. dicksoni* may therefore preclude it from being ancestral to species of *Ornithorhynchus*. *Ob. insignis*, with its smaller bill and less flattened skull, may have been closer to the ancestral form for species of *Ornithorhynchus*. Both the Palaeocene *Monotrematum sudamericanum* and the Miocene *Ob. dicksoni* appear to have been large and robust animals. All of the *Ob. insignis* material suggests a more gracile animal which, in this regard, more closely resembles *Or. anatinus*.

The nature of the sediments in the central Australian and Riversleigh fossil deposits supports this interpretation. The Etadunna and Namba Formations (containing *Ob. insignis*) consist primarily of claystones and mudstones and some fine-grained sandy lenses, evidence that the palaeoenvironments were dominated by fluvio-lacustrine conditions (Woodburne *et al.* 1993), probably surrounded by cool, scrubby wet forest (Archer *et al.* 1995). The benthic substrate in these waters would probably have been silty, bordered by banks of semiconsolidated clay and mud. In this regard, these central Australian environments would have been closer to those that today support *Or. anatinus*. At Riversleigh, although much of the area was lacustrine, the lime-rich waters would have produced limey muds rather than clays or gravels and possibly carbonate-cemented banks (Archer *et al.* 1994, 1995).

ADDENDUM

After the present paper was sent for review a new Early Cretaceous mammal from southeastern Australia was reported, *Ausktribosphenos nyktos*, described by Rich *et al.* (1997) as an early placental mammal. Rich *et al.* (1997) cite similarities in molar count, tooth and mandibular morphology between *A. nyktos* and early placentals such as *Prokennalestes* in making their case for inclusion of *A. nyktos* within the infraclass Placentalia. However, one of us (M.A.) has seen the specimen and is convinced that this small jaw is not that of a placental mammal but instead may share a relationship with peramurids or possibly with monotremes.

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