



The history and homology of the os paradoxum or dumb-bell-shaped bone of the platypus *Ornithorhynchus anatinus* (Mammalia, Monotremata)

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Abstract

The os paradoxum or dumb-bell-shaped bone is a paired bone occurring in the middle of the specialized bill of the platypus *Ornithorhynchus anatinus*. It has been variously considered as a neomorph of the platypus, as the homologue of the paired vomer of sauropsids, or as a part of the paired premaxillae. A review of the near 200-year history of this element strongly supports the os paradoxum as a remnant of the medial palatine processes of the premaxillae given its ontogenetic continuity with the premaxillae and association with the vomeronasal organ and cartilage, incisive foramen, and cartilaginous nasal septum. In conjunction with this hypothesis, homologies of the unpaired vomer of extant mammals and the paired vomer of extant sauropsids are also supported. These views are reinforced with observations from CT scans of *O. anatinus*, the Miocene ornithorhynchid *Obdurodon dicksoni*, and the extant didelphid marsupial *Didelphis marsupialis*. At the choanae, *Obdurodon* has what appears to be a separate parasphenoid bone unknown in extant monotremes.

Key Words

Didelphis marsupialis, *Obdurodon dicksoni*, parasphenoid, premaxilla, vomer, vomeronasal organ

Introduction

First illustrated by Meckel (1826), the bill of the platypus, *Ornithorhynchus anatinus*, contains an unusual median bone anterior to the maxillae. As summarized by van Bemmelen (1901), as many as ten names were applied to this element, with most authors settling on either the os paradoxum (Albrecht 1883, cited in van Bemmelen 1901) or dumb-bell or dumb-bell-shaped bone (Turner

1884). The homologies of the os paradoxum have been the subject of long-term debate by some of the leading embryologists, comparative anatomists, and paleontologists of the times. Three principal views regarding it were expressed: (1) it is part of the premaxilla (e.g., Meckel 1826; Presley and Steel 1978); (2) it is a neomorph (e.g., Owen 1866; Flower 1876); and (3) it is the homologue of

the vomer occurring in extant lizards (e.g., Broom 1895; De Beer 1937). Relevant to this debate are the homologies of the mammalian vomer, a midline bone, which is equated with two different bones in sauropsids, either with the paired vomer (e.g., Gaupp 1906; Starck 1967) or the midline parasphenoid (e.g., Broom 1902; De Beer 1937). Although some may argue, including this author, that these matters were convincingly laid to rest by Parrington and Westoll (1940), doubts about the homology of the os paradoxum continue to occur in the recent literature (e.g., Musser and Archer 1998; Sidor 2001; Musser 2013; Cheng et al. 2019). It is my goal here to present the history of study of the os paradoxum and evaluate its homologies, hopefully quelling continued debate. Included are relevant original observations on CT scans of *Ornithorhynchus anatinus*, the Miocene platypus *Obdurodon dicksoni*, and the didelphid marsupial *Didelphis marsupialis*.

Anatomical Background

To aid the reader in following the history of study regarding the os paradoxum, an overview of the anatomical domain in a placental and a lizard is presented.

Figure 1 shows fetal and young crania of a placental, the Philippine colugo, *Cynocephalus volans*, taken from Parker (1885b). The bony anterior palate is formed by the paired premaxilla (= intermaxilla of Meckel 1826; os incisivum of NAV 2017) lodging the incisors and the paired maxilla lodging the canines and postcanine dentition. The bodies of the premaxillae meet on the midline and each sends a narrow medial palatine process posteriorly (usually referred to as the palatine process in the older literature). Each medial palatine process abuts the paraseptal (Jacobson's, vomeronasal) cartilage, which in turn shelters the vomeronasal (Jacobson's) organ (Fig.

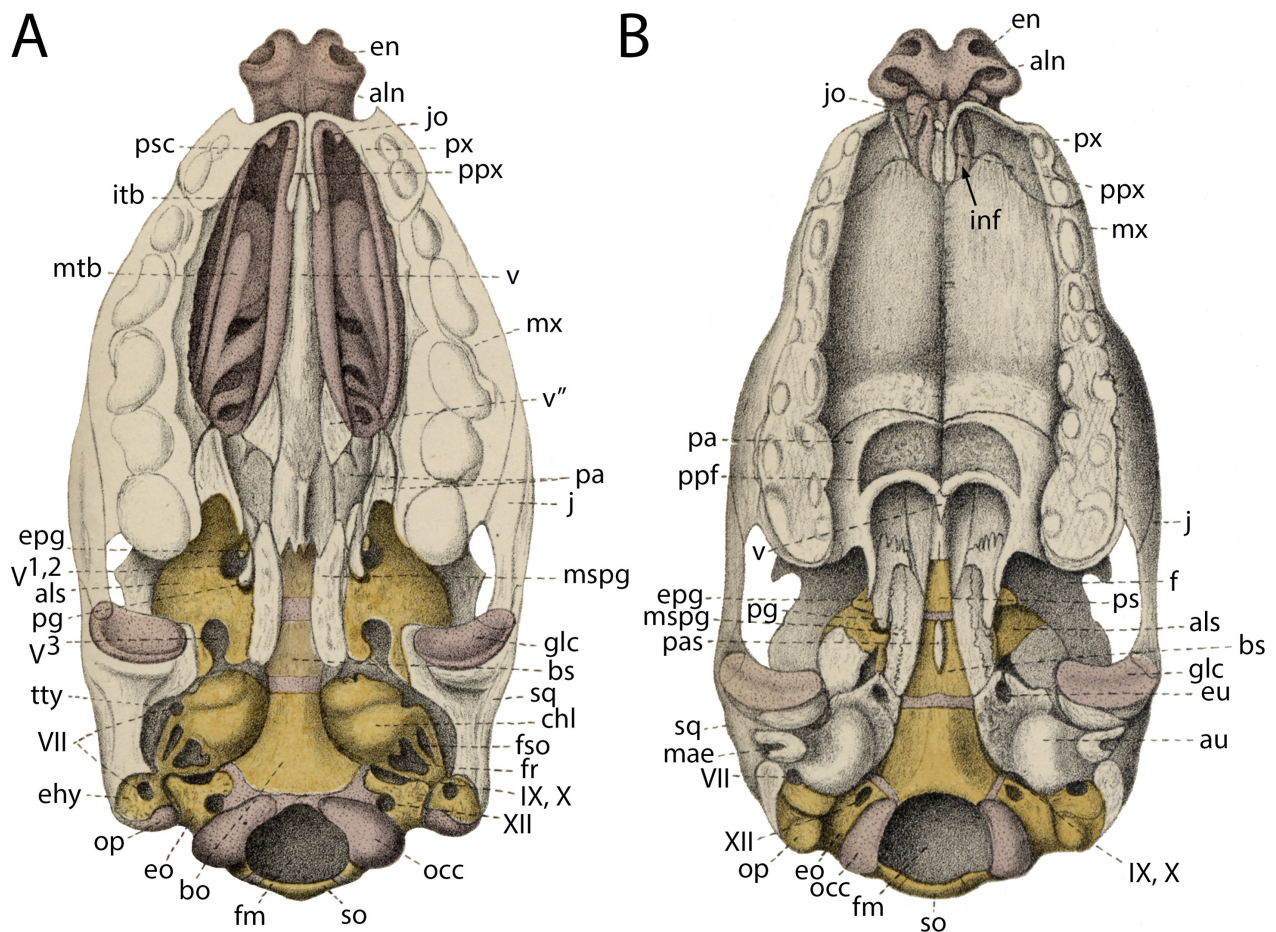


Figure 1. *Cynocephalus volans* (= *Galeopithecus philippinensis*, *G. volans*), cranium in ventral view. **A**, fetus, 14 cm from snout to root of tail, with palatal parts of maxillae and palatines removed to expose the nasal cartilages; modified from Parker (1885b: plate 39, fig. 1); **B**, young, 20 cm from snout to root of tail, with anteriormost part of right premaxilla removed; modified from Parker (1885b: plate 37, fig. 6). Cartilage (puce); ossifying chondrocranium (orange); bone (beige). Parker's original abbreviations: aln, alin-nasal; als, alisphenoid; au, auditory capsule; bo, basioccipital; bs, basisphenoid; chl, cochlea; ehy, epihyal; en, external nostrils; eo, exoccipital; epg, external pterygoid; eu, eustachian tube; f, frontal; fm, foramen magnum; fr, fenestra rotunda; fso, fenestra ovalis; glc, glenoid cavity; inf, incisive foramen [added by author]; itb, inferior turbinal; IX, X, glossopharyngeal and vagus nerves; j, jugal; jo, Jacobson's organ; mspg, mesopterygoid; mtb, middle turbinal; mx, maxilla; occ, occipital condyle; op, opisthotic; pa, palatine; pg, pterygoid; ppf, posterior palatine foramen ppx, [medial] palatine process of premaxillary; ps, presphenoid; psc, paraseptal cartilage (recurrent cartilage); px, premaxillary; so, supraoccipital; sq, squamosal; tty, tegmen tympani; v, v'', vomer; V^{1,2}, ophthalmic and maxillary nerves; V³, mandibular nerve; VII, facial nerve; XII, hypoglossal nerve.

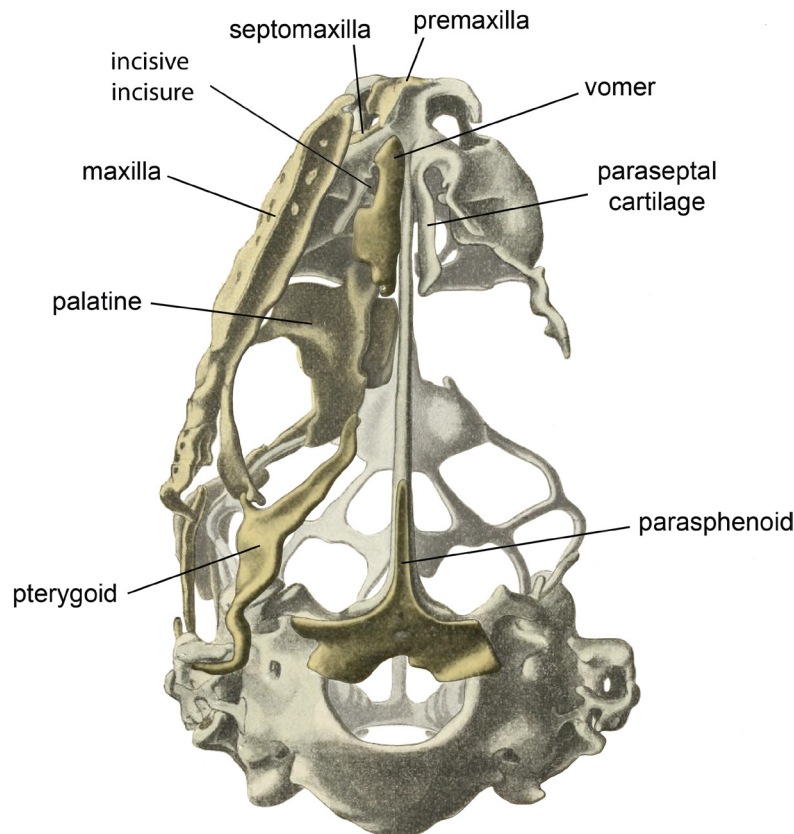


Figure 2. *Lacerta agilis*, cranium of a 47 mm long embryo in ventral view, modified from Gaupp (1906: fig. 383). Dermal bones have been removed from the specimen's left side to show the chondrocranium (gray).

1A). The medial palatine process forms the medial border of the incisive foramen (Fig. 1B), which transmits the nasopalatine duct from the vomeronasal organ. At their posterior terminus (Fig. 1A), the medial palatine processes diverge from each other, lie dorsal to the maxillae, and contact a long midline bone, the vomer, which on its dorsal aspect lodges the nasal septum. A final bone of interest here found in the young colugo (Fig. 1B) is the submarine-shaped parasphenoid, a small midline bone positioned ventral to the basisphenoid.

Each of the elements named above exhibits considerable diversity across mammals. Regarding the adult premaxilla, Chiroptera, for example, shows a broad range of morphologies (Giannini and Simmons 2007): the medial palatine processes may be wholly absent, the left and right bodies may be separated by a midline gap, and the body may be separated from the premaxillary body, the medial palatine process is reported to ossify from a separate center in, for example, the armadillo, *Dasypus novemcinctus* (= *Tatusia novemcincta*; Parker 1885a; Fawcett 1921). The paraseptal cartilage is generally much shorter than in the colugo (Fig. 1A), which has a remarkably long vomeronasal organ (Bhatnagar and Wible 1994). The paraseptal cartilage shows a variety of shapes in cross section and is reduced or absent in taxa lacking the vomeronasal organ (Wible and Bhatnagar 1996). The vomer generally arises from a single ossification, but paired centers are described in some taxa (De Beer 1837). The reports, for example, in *Homo sapiens* (Fawcett 1911; O'Rahilly and Gardner 1972) are supported by study of numerous onto-

genetic stages. On the other hand, Gaupp (1908) observed what he interpreted as paired centers in one stage of the echidna *Tachyglossus aculeatus* (= *Echidna aculeata*) even though there was a weak median connector that he interpreted as a later addition; Kuhn (1971) cautioned that dual centers though likely in the echidna are not proven by this single stage. Among extant mammals, the parasphenoid is absent in monotremes (Kuhn 1971; Zeller 1989), has a spotty distribution in placentals but recently has been shown to be widely distributed in didelphid marsupials (Wible et al. 2018).

Figure 2 shows the cranium of an embryo sand lizard, *Lacerta agilis*, taken from Gaupp (1906). A general correspondence regarding the elements highlighted above exists between the lizard and colugo, although there are differences. The sand lizard premaxilla, for example, has a prenasal (ascending) process that supports the egg-tooth and lacks a medial palatine process; the more substantial parasphenoid has large posterolateral wings covering much of the basicranium. The vomer is a paired element in the sand lizard in contrast to the single ossification in the colugo and most extant mammals. Each vomer generally forms from a single ossification in sauropsids (De Beer 1937), but there is variability. A recent study of the snake *Natrix natrix* (Sheverdyukova 2019) reported three ossification centers for each vomer. Turtles have an unpaired vomer in the adult (Gaffney 1979), but at least in some this condition results from fusion of paired ossifications during ontogeny (e.g., Kunkel 1912; Tokita et al. 2021). Lastly, the vomer in the sand lizard has an incisive incisure on its lateral margin marking the exit of the nasopalatine duct (Fig. 2).

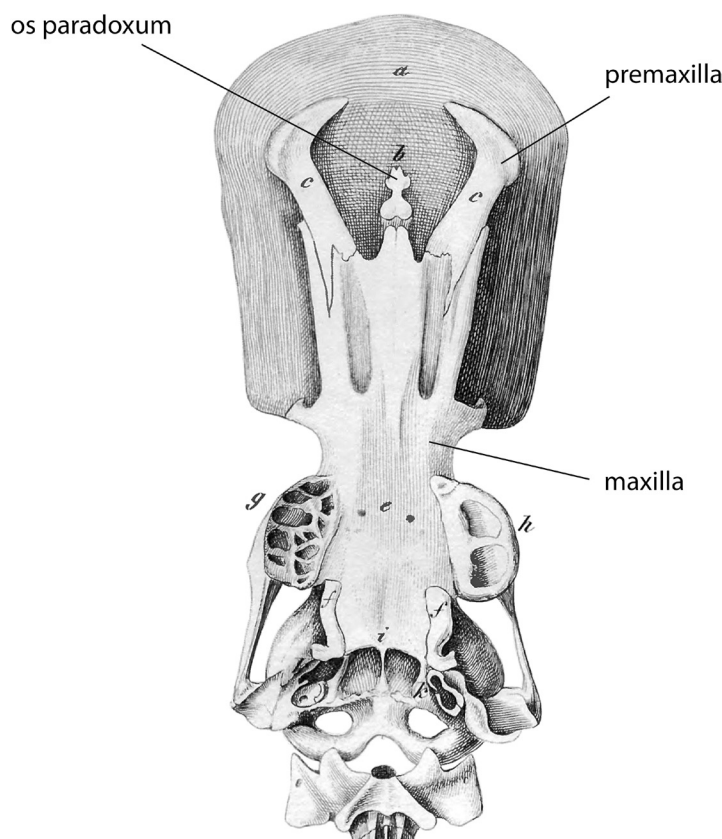


Figure 3. *Ornithorhynchus anatinus*, cranium, atlas, and partial axis in ventral view, modified from Meckel (1826: table IV, fig. I). Meckel's original abbreviations: a, cartilago naso-labialis; b, os intermaxillare internum; c, os intermaxillare externum; e, os maxillare superius et palatinum; f, apophyses pterygoideae, mobiles; g, alveolus dexter; h, dens molaris sinister; i, choana; k, porus acusticus, in sinistro latere adstant annulus et os posticum, aut stylum aut malleum referens.

Historical Background

Van Bemmelen (1901) provided a detailed literature review of the os paradoxum (his praevomer) to which the reader is referred. Here, I focus on the highlights prior to and after 1901 as they pertain to the three major views on the homologies of this bone.

Nearly 200 years ago, Johann Friedrich Meckel (1826) published his monographic descriptions of the platypus. His table IV has the earliest illustrations of the skeleton, with his figure I showing a ventral view of the cranium (Fig. 3). Within the bill, Meckel labeled two disjunct parts of the paired os intermaxillare, his internum and externum, which in current terminology are the medial palatine process and body of the paired premaxillae, respectively. Meckel recognized that although the os paradoxum was a midline element, it was a paired bone. As noted above, the premaxillae exhibit considerable diversity among extant mammals, but to my knowledge this separation between the bodies and palatine processes is unique to the platypus.

The first alternative view on the homologies of the os paradoxum came from Owen (1866) and Flower (1876) who equated it with the neomorphic prenasal bone of the pig (os rostrale of NAV 2017). However, the persuasive paper by Turner (1884) presenting details of the adult

anatomy of both elements left little doubt that the two were not homologues. The os paradoxum is in the palate, bound to the premaxilla and maxilla by membrane, supports the nasal septum and the vomeronasal organ and cartilage, and forms the medial border of the incisive foramina; the unique prenasal bone of the pig lies anterior to the palate and in a plane dorsal to it. Flower (1885) abandoned his prior view, citing Turner (1884), and replaced it with Meckel's identification of the bone as part of the premaxilla. A neomorphic origin for the os paradoxum has not been given serious consideration since Turner (1884), although it was recently posed by Sidor (2001) without additional justification.

After Turner (1884) came an interchange of papers documenting the anatomy of the anterior nasal cavity of adult *Ornithorhynchus* based on serial sections. The main controversy was whether or not posterior spurs on the os paradoxum were in the plane of the vomer. Wilson (1894) claimed the spurs were in the plane of the vomer, making the os paradoxum a vomerine element, which he called the anterior vomers. In contrast, Symington (1891, 1896) claimed they were not in the plane of the vomer and continued to support the os paradoxum as the medial palatine processes of the premaxillae.

Broom (1895) agreed with Wilson (1894) that the os paradoxum was a vomerine element, replacing the term anterior vomer with a new term, prevomer, which he also

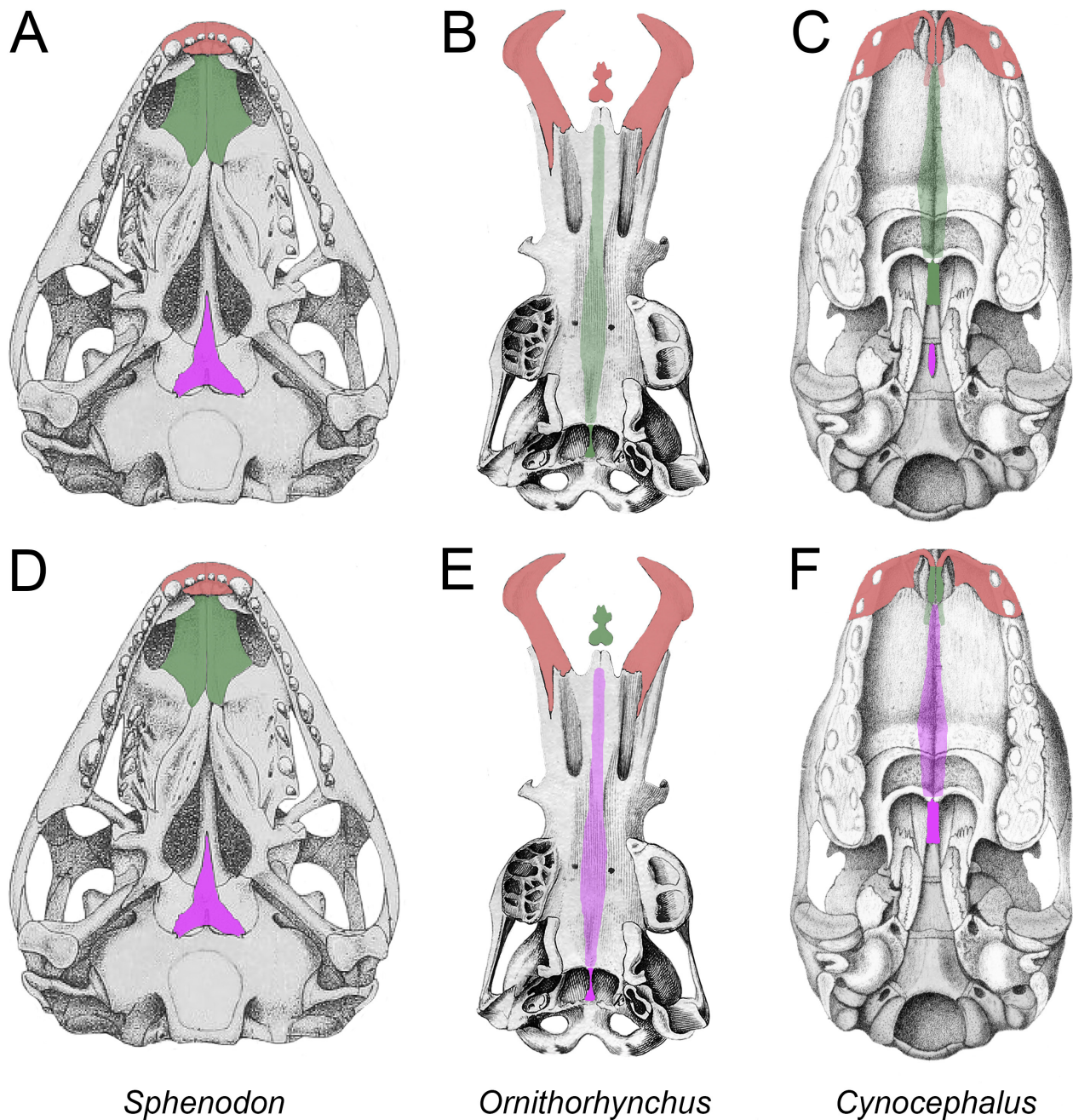


Figure 4. Crania in ventral view. **A, D**, *Sphenodon punctatus* (modified from Howes and Swinnerton 1901: plate IV, fig. 6); **B, E**, *Ornithorhynchus anatinus* (modified from Meckel 1826: table IV, fig. 1); **C, F**, *Cynocephalus volans* (modified from Parker 1885b: plate 37, fig. 6). In A–C, bones are color coded following the hypothesis that the saurosid vomer (prevomer of Broom 1895) = the mammalian vomer [green], the platypus os paradoxum = the therian medial palatine process of the premaxilla [red], and the saurosid parasphenoid = the therian parasphenoid [purple]. In D–F, the bones are color coded following the hypothesis that the saurosid vomer = the platypus os paradoxum = the therian medial palatine process of the premaxilla [green] and the saurosid parasphenoid = the mammalian vomer [purple]. Parasphenoid [purple in C] is removed in F to make the morphology congruent with the hypothesis. The parts of bones hidden by the palate in B, C, E, and F are indicated by semi-transparency.

applied to the paired vomer in lizards (Fig. 2). Broom did not just equate the os paradoxum with the lizard prevomer but also with the medial palatine process of the premaxilla of marsupials and placentals; that is, Broom considered the medial palatine process of the premaxilla as a composite structure formed by fusion with the prevomer (Fig. 4F). He supported this with prior observations by Parker (1885a, 1885b) and others that the medial palatine process in some placentals (e.g., *Dasypus*, *Erinaceus*)

forms from an ossification (Parker's anterior vomer) separate from the rest of the premaxilla. Reinforcing this was Wilson's (1901) observation of two 'mammary foetuses' of *Ornithorhynchus*. In the earlier stage (Fig. 5A), the bodies of the premaxillae are fused on the midline to support the egg-tooth (os carunculae) and there are short medial palatine processes. In the later stage (Fig. 5B), a pair of ossifications appear posterior to and separated by a broad gap from the stubbles of the medial palatine pro-

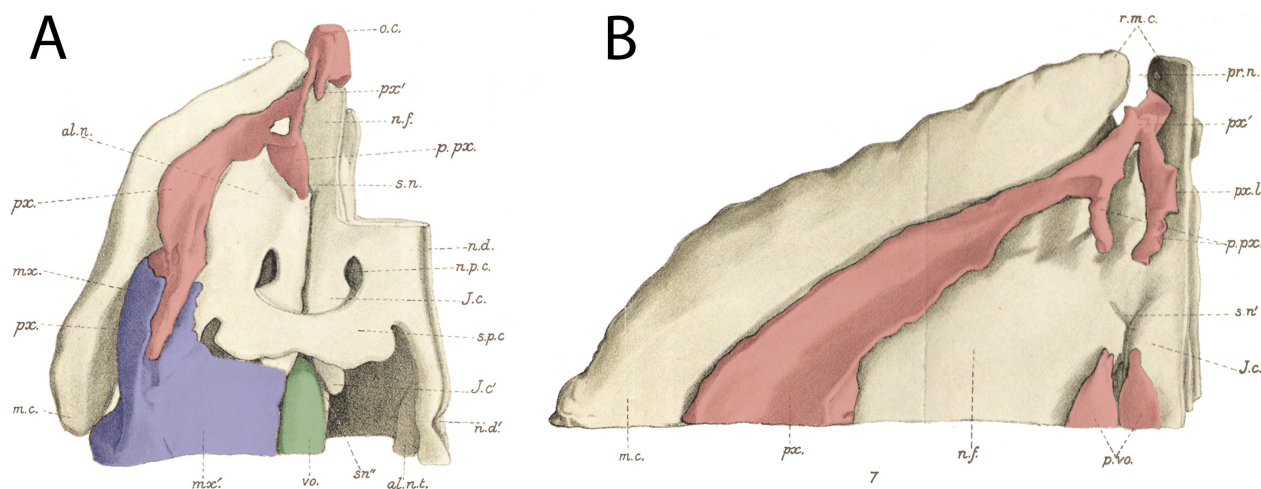


Figure 5. *Ornithorhynchus anatinus*, anterior rostrum of 'mammary foetuses' in ventral view, modified from Wilson (1901). **A**, model i (Wilson 1901: plate xxxvii, fig. 3); **B**, model ii (Wilson 1901: plate xxxviii, fig. 7). For broader anatomical context, see Figure 6. Wilson's original abbreviations: al.n., alinasal cartilage; al.n.t., alinasal turbinal ridge; J.c., Jacobson's (vomeronasal) cartilage; J.c', posterior extremity of Jacobson's cartilage; J.o., Jacobson's (vomeronasal) organ; m.c., marginal cartilage; mx., maxilla; mx', palatine plate of maxilla; n.d., nasal duct proceeding along outer surface of alinasal wall; n.d', nasal duct passing inward and piercing alinasal near its ventral border; n.f., nasal floor cartilage; n.p.c., naso-palatine foramen (= incisive foramen); o.c., os carunculae; p.px., [medial] palatine process of premaxilla; pr.n., pre-rostral notch in marginal cartilage; p.vo., prevomer; px., body of premaxilla; px', cut left premaxilla; px.l, cut left premaxilla; r.m.c., rostral marginal cartilage; s.n., septum nasi; s.n', septum nasi where it descends and is intercalated into and continuous with nasal floor cartilage; sn'', edge of ventral border of septum nasi which is largely hidden by vomer; s.p.c., transverse cartilaginous lamina; vo., vomer.

cesses, suggesting origins distinct from the premaxillae. Following Broom (1895), Wilson (1901) identified these separate ossifications as prevomers. Broom (1897) added evidence from the fossil record, reporting the apparent incidence of separate prevomers in a non-mammalian cynodont, the tritylodontid *Gomphognathus*.

Five years later, Broom (1902) added another twist to the debate, repeating a homological issue raised previously by Sutton (1884). Broom accepted the prevailing view that the mammalian vomer, the median bone lodging the nasal septum in the nasal cavity (Fig. 1A), is homologous in monotremes, marsupials, and placentals. Yet, if the platypus os paradoxum is the homologue of the paired bone associated with the vomeronasal organ immediately behind the premaxilla in lizards (the prevomer of Broom 1895), then to what median bone in the lizard is the platypus and, therefore, the mammalian vomer homologous? According to Sutton (1884) and Broom (1902), the appropriate bone to equate the mammalian vomer with is the sauropsid parasphenoid (Fig. 4D–F). Although citing Parker (1885a, 1885b) in his paper, Broom (1902) did not mention Parker's (1885b; Fig. 1B) description of a small parasphenoid in the Philippine colugo (Figs 1B, 4C), which if true would negate the proposed homology between the sauropsid parasphenoid and mammalian vomer. Not everyone was convinced by Broom regarding the homologies of the platypus os paradoxum and the mammalian vomer: notable among the skeptics was Gaupp (1905, 1906), considered to be the most learned student of the skull of the day.

In 1929, De Beer, a proponent of Wilson's and Broom's view on the os paradoxum, proposed the following three stages in the evolution of the prevomer and premaxilla:

(1) forming from separate ossifications, as in sauropsids (Fig. 4D); (2) forming from separate ossifications but the premaxilla secondarily developing a medial palatine process to buttress the vomeronasal organ that may secondarily fuse with the prevomer (as in some placentals; Fig. 4F) or not (as in *Ornithorhynchus*; Fig. 4E); and (3) forming from a single ossification (as in most placentals). Green (1930) reported on an ontogenetic stage of *Ornithorhynchus* that was not entirely congruent with De Beer's scenario. In Green's specimen, which was younger than that with a separate os paradoxum observed by Wilson (1901; Fig. 5B), there was a continuous "thread of ossification" connecting the os paradoxum and the stubble of the medial palatine process of the premaxilla. Green interpreted this thread as the product of resorption from an earlier stage where the os paradoxum was merely the posterior end of the medial palatine process of the premaxilla. He concluded that the existence of a separate prevomer in *Ornithorhynchus* was yet to be proven.

The ontogeny of the platypus skull was notably documented by Watson (1916), but based on a series of only two specimens. To fill in the gaps, De Beer and Fell (1936) reported on an ontogenetic series of five *Ornithorhynchus*, with the largest specimen the one previously described by Green (1930). Contra Green's observation of this specimen, De Beer and Fell observed no thread of ossification connecting the premaxilla and os paradoxum (Fig. 6B), although they admitted this was not entirely clear in the available transverse sections. However, they stated (p. 20) even if Green was correct that the os paradoxum was secondarily separated from the premaxilla during ontogeny, that was not opposed to a prevomer origin for the os paradoxum, "since it might be supposed

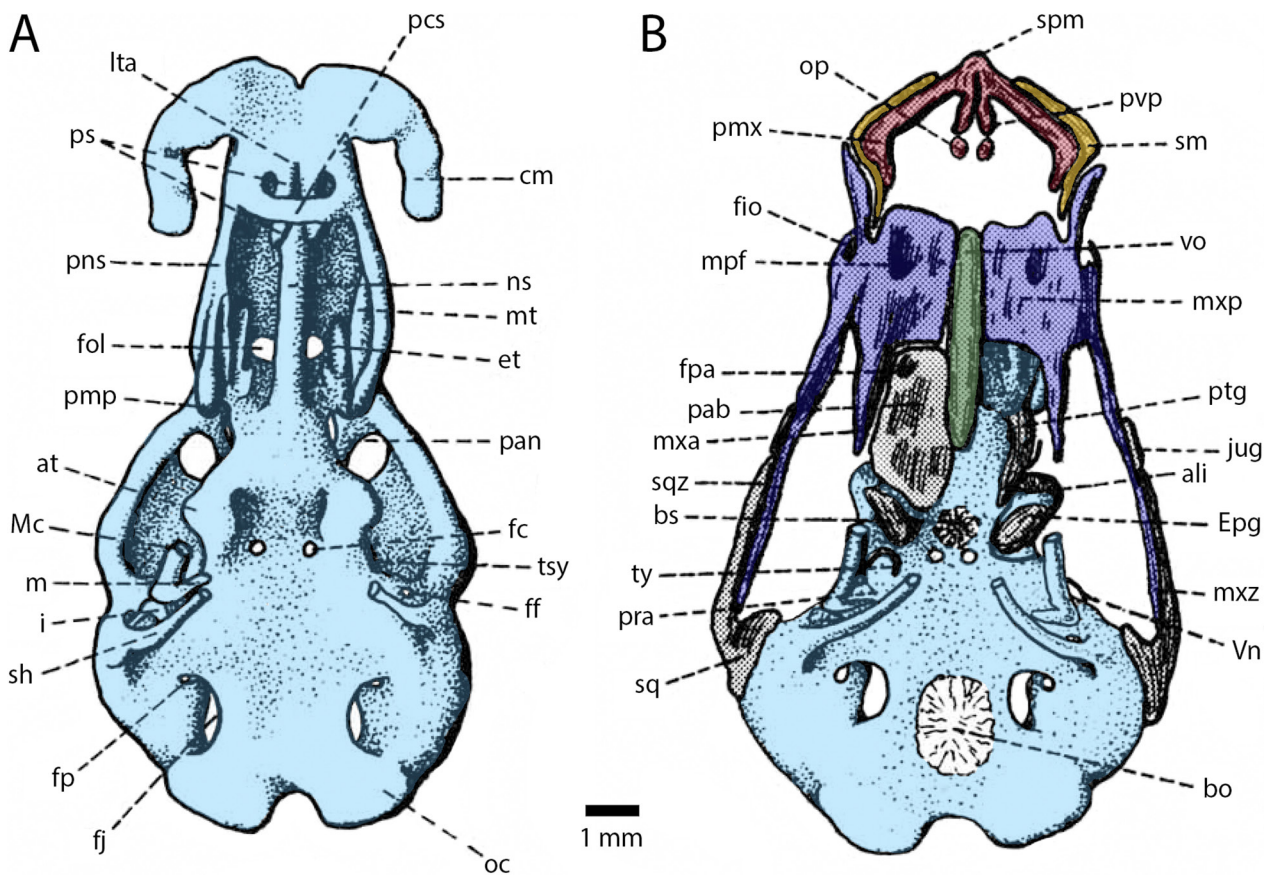


Figure 6. *Ornithorhynchus anatinus*, 122 snout-tail length posthatchling, modified from De Beer and Fell (1936: table VI, figs. 22, 24). **A**, chondrocranium and **B**, posterior two-thirds of chondrocranium with bones in situ in ventral view (palatine removed from left side). De Beer and Fell's original abbreviations: ali, Alisphenoid bone; at, Ala temporalis; bo, Basioccipital bone; bs, Basisphenoid bone; cm, Marginal cartilage of snout (crista marginalis); Epg, "Echidna-pterygoid"; et, Ethmoturbinal; fc, Carotid foramen; ff, Foramen for facial nerve; fio, Infraorbital foramen; fj, Foramen jugulare; fol, Foramen olfactorium advehens; fp, Foramen perilymphaticum; fpa, Palatine foramen; i, Incus; jug, Jugal bone; Ita, Lamina transversalis anterior; m, Malleus; Mc, Meckel's cartilage; mpf, Maxillopalatine foramen; mt, Maxilloturbinal; mxa, Alveolar process of maxilla; mxp, Palatine process of maxilla; mxz, Zygomatic process of maxilla; ns, Nasal septum; oc, Occipital condyle; pab, Palatine bone; pan, Pila antotica; pcs, Palatine commissure (of ectochoanal cartilage); pmp, Processus maxillaris posterior; pmx, Premaxillary bone; pns, Paries nasi; pra, Prearticular bone; ps, Paraseptal cartilage; ptg, Pterygoid ("mammalian") bone; pv, Prevomer bone; pvp, Prevomerine process of premaxilla; sh, Stylohyal cartilage; sm, septomaxilla; spm, Egg-tooth fused to symphysis of premaxillae; sq, Squamosal bone; sqz, Zygomatic process of squamosal; tsy, Tectum synoticum; ty, Tympanic bone; Vn, Vidian nerve (palatine); vo, Vomer bone.

that the centres of ossification of the prevomers had previously become fused with those of the premaxillae, and subsequently separated, perhaps in consequence of the changes which are associated with the precocious development of the premaxillae, their fusion in the mid-line, and the carrying of the egg-tooth." The views of De Beer and Fell (1936) were endorsed in De Beer's (1937) highly influential book "The Development of the Vertebrate Skull," as were the views of Sutton (1884) and Broom (1902) regarding the homology of the mammalian vomer and sauropsid parasphenoid.

In 1940, two paleontologists, Parrington and Westoll, revisited the evidence from embryology and the fossil record. Their synthesis convincingly debunked the homological hypotheses that the prevomer of lizards = the os paradoxum of the platypus = the medial palatine process of the premaxilla of therians (Broom 1895, 1935) and that the parasphenoid of lizards = the vomer of mammals (Sutton 1884; Broom 1902, 1935) (Fig. 4D–F). Par-

rington and Westoll (1940) noted recent discoveries in the fossil record of the parasphenoid in synapsids, including non-mammalian cynodonts that also have a vomer resembling that in mammals. With both the parasphenoid and vomer present in these fossils, the mammalian vomer is not homologous with the sauropsid parasphenoid. As additional support, they also noted the discovery of a parasphenoid in the extant placental *Cynocephalus* by Parker (1885b; Figs 1B, 4C) and the extant marsupial *Didelphis* by Fuchs (1910). Parrington and Westoll (1940) also showed the prevomers are paired in basal synapsids, such as *Dimetrodon*, and in the same position as the paired element in lizards. In the theriodont clade (p. 322), "The prevomers fuse, and come to support the secondary palate in a manner indistinguishable from that of the mammalian vomer; the palatine processes of the premaxillae become more important, and attain mammal-like proportions." In other words, the paired prevomer of lizards equals the vomer of mammals, and the os paradoxum of

Ornithorhynchus is the detached rear of the medial palatine processes of the premaxillae (Fig. 4A–C). The years after 1940 saw little appetite for the proposals of Broom (1895, 1902, 1935). For example, Gregory (1947) identified the platypus os paradoxum as part of the premaxilla, even though according to Broom (1935), Gregory was an early advocate of the alternate hypotheses.

In his monograph on the development of the skull of the echidna *Tachyglossus aculeatus*, Kuhn (1971) found a stage with a short, thin medial palatine process of the premaxilla in continuity with the body, which was not present in the stages studied by Gaupp (1908). This process must disappear in later stages as it is wholly absent in the adult echidna (van Bemmelen 1901). Kuhn (1971) strongly supported the homologies of the vomer in mammals and reptiles as well as the os paradoxum as part of the premaxilla.

In 1978, Presley and Steel reported on an ontogenetic series of ten stages of *Ornithorhynchus*, including some specimens studied previously by Green (1930) and De Beer and Fell (1936). In specimens with snout-tail lengths of 80, 122 (contra the observations of De Beer and Fell on this specimen; Fig. 6B), 170, and 200 mm, the os paradoxum was continuous anteriorly with the premaxilla, while in specimens of 140, 225, and 240 mm, the attenuated connection breaks down. From this, Presley and Steel (1978) concluded that the os paradoxum is a detached portion of the premaxilla (see also Green and Presley 1978). Additionally, they reiterated that the mammalian vomer is equivalent to the paired vomer (Broom's prevomer) in sauropsids.

In his 1981 book "The Mammalian Skull," Moore included a synopsis of the arguments for and against the hypotheses of Wilson and Broom, and he clearly settled on the 'against' side. He questioned the value of ossification centers as a guide to a bone's phylogenetic history, and the case of the two centers in the human vomer I noted above is one of many appropriate examples of this issue. He noted that the embryological evidence used by Wilson and Broom and supported by De Beer and Fell (1936) that the os paradoxum develops independent of the premaxilla is flawed, citing Green and Presley (1978) and Presley and Steel (1978). Lastly, he observed the overwhelming paleontological evidence raised first by Parrington and Westoll (1940) against the homologies of the mammalian vomer and sauropsid parasphenoid.

Zeller (1989) published a monograph on the development of the skull in *Ornithorhynchus*, which because of its synthetic treatment and comprehensive index became widely used by researchers studying early mammal phylogeny. For example, Musser and Archer (1998) extensively cited Zeller (1989) in their descriptions of the cranium of the Miocene platypus, *Obdurodon dicksoni*. Regarding the os paradoxum, Musser and Archer (1998: p. 1066) concluded that its origins were unknown and wrote that Zeller "could not positively identify this bone as either a prevomer or as part of the premaxillae." This was an unfortunate comment because Zeller (1989: p. 72) could not have been clearer about his view on this bone: "Morphologisch ist das Os paradoxum ein Teil des Praemaxillare."

The three most recent views on the os paradoxum that I have found in the literature cover the possible hypotheses about this bone except for the one settled on by most researchers in the wake of Parrington and Westoll (1940). Sidor (2001) described it as a possible neomorph; Musser (2013) equated it with the prevomer; and Cheng et al. (2019) called it "mysterious." The last moniker suggests to me that the authors consider the os paradoxum of unknown origin. Rather than a neomorph, a prevomer, or mysterious, a review of the history of the os paradoxum clearly identifies it as part of the premaxillae.

Materials and Methods

CT scans of the following specimens were studied, with structures of interest segmented in Avizo 2020.3 (© FEI SAS a part of Thermo Fisher Scientific).

1) The head, neck, and thorax of male *Ornithorhynchus anatinus*, MVZ MAMM 32885 [<http://arctos.database.museum/guid/MVZ:Mamm:32885>]. Museum of Vertebrate Zoology, University of California, Berkeley provided access to these data, the collection of which was funded by oVert TCN, NSF DBI-1702442, and NSF DBI-1701714. The files were downloaded from www.MorphoSource.org, Duke University. The CT image series included 1,878 tiff images [<https://www.morphosource.org/concern/media/000059596?locale=en;ark:/87602/m4/M59596>]. X, Y, and Z spacing is 0.0768222 mm.

2) The cranium of the Miocene ornithorhynchid *Obdurodon dicksoni*, QM F20568. This specimen from the Riversleigh Formation, the only known cranium of a fossil ornithorhynchid, was scanned by Dr. Richard Ketcham at the University of Texas High resolution X-ray Computed Tomography Facility on 12–13 November 1998 along the coronal axis for a total of 612 512×512 pixel slices with each slice 0.26 mm thick, with an interslice spacing of 0.22 mm. For more information, visit http://www.digimorph.org/specimens/Obdurodon_dicksoni. For permission to access the scans, I acknowledge Dr. Michael Archer, University of New South Wales, and Dr. Ted Macrini, St. Mary's University. The cranium of this specimen is described in Archer et al. (1992, 1993) and Musser and Archer (1998) prior to the CT scans, and the endocast of this specimen is described in Macrini et al. (2006) based on the scans.

3) The cranium of *Didelphis marsupialis*, du baa 0164. Duke University provided access to these data, the collection of which was funded by NSF BCS 1552848 (to D.M. Boyer) and NSF DBI 1458192 (to G.F. Gunnell). The CT image series included 1,910 tiff images [doi:10.17602/M2/M58076]. X, Y, and Z spacing is 0.0690778 mm.

As with any anatomical contribution, it is important to acknowledge the source of terminology. The substance

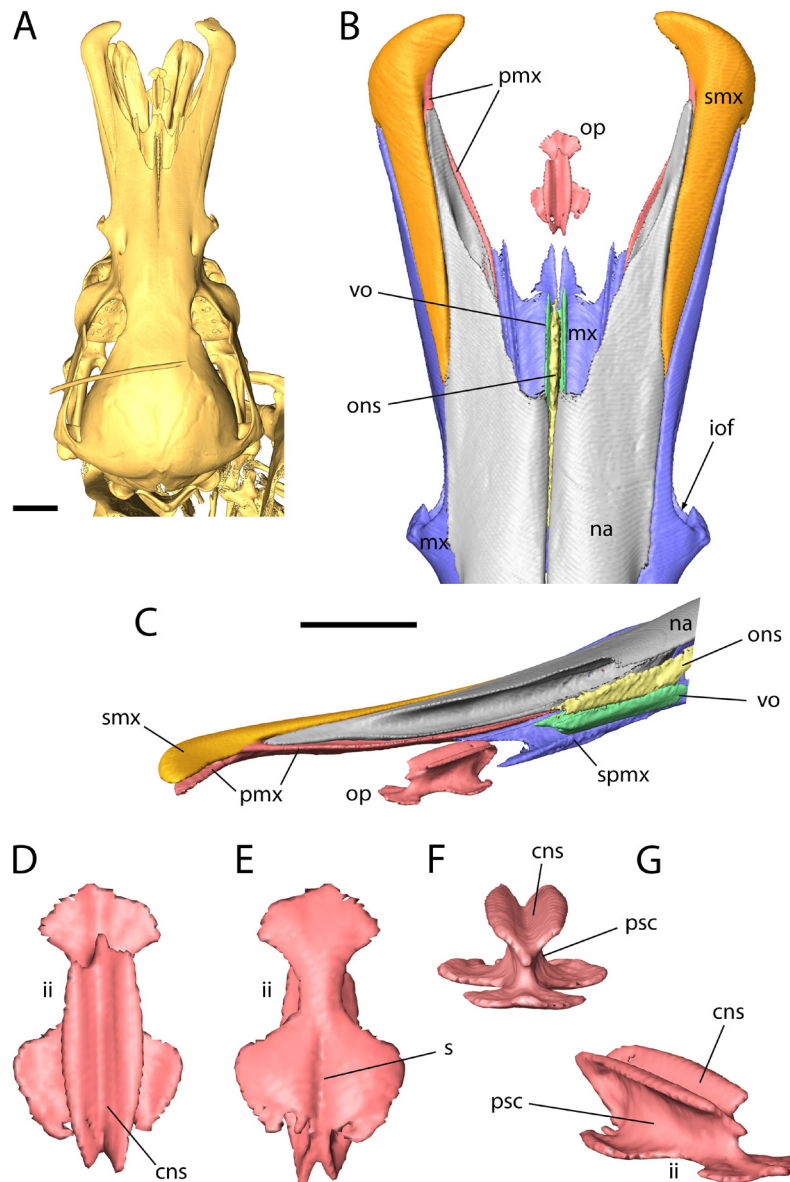


Figure 7. *Ornithorhynchus anatinus*, MVZ MAMM 32885, bone isosurfaces derived from CT scans. **A**, skull in dorsal view; **B**, rostrum in dorsal view; **C**, right rostrum in oblique medial view; **D–G**, os paradoxum in **D**, dorsal, **E**, ventral, **F**, anterior, and **G**, oblique anteromedial views. Scale for **A** = 10 mm; scale for **B–C** = 10 mm; scale for **D–G** = 5 mm. Septomaxilla and premaxilla are fused but colored separately based on their inferred relationships. Abbreviations: *cns*, surface for cartilaginous nasal septum; *ii*, incisive incisure; *iof*, infraorbital foramen; *mx*, maxilla; *na*, nasal; *ons*, ossified nasal septum; *pmx*, premaxilla; *psc*, surface for paraseptal cartilage; *s*, sulcus; *smx*, septomaxilla; *spmx*, septal process of maxilla; *vo*, vomer.

of this paper concerns a near 200-year debate concerning the homologies of bony elements of the mammalian rostrum. The terminology employed is wholly dependent on the side of the debate taken. Here, I follow the terms used by the main proponents of the debate. I usually try to conform to the *Nomina Anatomica Veterinaria* (NAV 2017), using anglicized versions of the Latin terms. However, NAV (2017) has a limited number of terms for the anterior rostrum.

Institutional Abbreviations: du baa, Duke University, Biological Anthropology and Anatomy, Durham, North Carolina, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; QM, Queensland Museum, Brisbane, Australia.

Results

Os Paradoxum in *Ornithorhynchus anatinus*, MVZ MAMM 32885

This male platypus specimen (Fig. 7) preserved in ethanol is considered here as not fully adult, with open epiphyses on the proximal humerus and distal ulna and radius, although its greatest skull length of 103 mm is at the high end of the 32 measured by Asahara et al. (2016). Study of the CT scans reveals there are few open sutures on the cranium, all of them on the rostrum with the exception of that delimiting the ectopterygoid. The premaxilla

and septomaxilla are fused, as generally occurs in extant monotremes such that some early workers did not differentiate a separate septomaxilla (e.g., van Bemmelen 1901; Kesteven and Furst 1929). Despite the fusion, the two bones are colored separately here (Fig. 7B, C) based on their inferred positions. Anteriorly, the two bones are separated by a deep sulcus (Fig. 7C) marking the location of the marginal cartilage of the chondrocranium supporting the bill (Figs 5, 6A), which is interposed between the two bones in early ontogenetic stages (Watson 1916; De Beer and Fell 1936; Zeller 1989).

The os paradoxum, here accepted as the fused medial palatine processes of the premaxillae, lies anterior to the palatal processes of the maxillae, separated from them by a narrow gap (Fig. 7B). In general, the os paradoxum has rough margins, unlike the smooth margins encountered with other cranial bones (Fig. 7D–G). It has a dumb-bell-shaped ventral base, with the posterior part of the dumb-bell larger than the anterior. The constriction between the anterior and posterior dumb-bells represents the incisive incisure (Fig. 7D–E, G), that is, the location of the left and right incisive foramina (Turner 1884), which are not closed by bone laterally. A midline sulcus on the ventral surface of the posterior half reflects the bone's paired origin (Fig. 7E); the ventral surfaces on either side of this sulcus are gently convex. The posterior two-thirds of the ventral base supports a Y-shaped vertical process that represents the fused septal processes of the premaxillae. While the base lies in the same plane as the palatal processes of the maxillae, the top of the Y is in the same plane as the vomer posterior to it (Fig. 7C). The slightly convex medial aspects of the arms of the Y accommodate the cartilaginous nasal septum (Fig. 7D, F–G), and the concave lateral aspects of the arms and base of the Y abut the paired paraseptal cartilage (Fig. 7F–G), which in turn supports the vomeronasal organ (Symington 1891, 1896; Wilson and Martin 1891).

The vomer is recessed posteriorly from the anterior margin of the palatal processes of the maxillae and sits on short septal processes of the maxillae (Fig. 7C). The vomer is U-shaped in cross section with the U accommodating the base of the nasal septum. The nasal septum dorsal to the vomer has an osseous base (preserved in the CT scans) and a presumed cartilaginous cap. The contribution of the ossified portion increases in height posteriorly.

Premaxillae in *Didelphis marsupialis*, du baa 0164

For comparison between the os paradoxum and the corresponding bones in therians, Figure 8 shows the premaxillae of the extant common opossum, *Didelphis marsupialis*, a didelphid marsupial. The premaxilla has a body housing the roots of the five upper incisors, an alveolar process for the alveoli of the incisor alveoli, a facial process (processus nasalis of NAV 2017), and an elongate medial palatine process (processus palatinus of NAV 2017). The body includes a pronounced paracanine fossa accommodating the lower canine. This specimen

shows considerable asymmetry between the two sides, in particular in the length of the facial and medial palatine processes. The incisive incisure lies between the medial and lateral palatine processes, which in the intact cranium is closed by the maxilla posteriorly to form the incisive foramen (fissure palatina of NAV 2017), transmitting the nasopalatine duct from the vomeronasal organ (Sánchez-Villagra 2001).

For descriptive purposes, the medial palatine process can be divided into anterior and posterior parts, which are roughly subequal in length on the right premaxilla. In the anterior part, the left and right medial palatine processes contact on the midline and their convex ventral surfaces are exposed on the palate (Fig. 8E). In contrast, in the posterior part a midline gap separates the two sides and they lie entirely within the nasal cavity, dorsal to the maxillae, with a facet for that bone on their ventral surface (Fig. 8E). Except at its anteriormost end, the anterior part is J-shaped in cross section, with the stem of the J, the septal process, on the midline. The tops of the stems on the right and left sides diverge laterally from each other, creating a V-shaped space between them that holds the cartilaginous nasal septum. The concavity of the J, the paraseptal shelf of Rowe et al. (2005), accommodates the paraseptal cartilage, which in turn supports the vomeronasal organ (Sánchez-Villagra 2001). The posterior part of the medial palatine process in cross section has a U-shape medially and a horizontal ledge laterally except at its posteriormost end where it is horizontal. The medial arm of the U contacts the vomer (Fig. 8F) with the concavity of the U and the horizontal ledge representing the posterior continuation of the paraseptal shelf. Likely, part of the U accommodates the vomeronasal organ. In the didelphid *Monodelphis domestica*, the vomeronasal organ is at the level between the ultimate incisor and the canine (Poran 1998); if the vomeronasal organ is of similar dimensions in *D. marsupialis*, then it would extend onto the posterior part of the medial palatine process. It is unknown if the paraseptal cartilage extends as far posteriorly. In the pouch young *D. marsupialis* studied by Toeplitz (1920), the paraseptal cartilage does not extend posterior to the anterior limit of the vomer.

Parasphenoid in *Obdurodon dicksoni*, QM F20568

Musser and Archer (1998) described the external surfaces of the cranium of the Miocene ornithorhynchid *Obdurodon dicksoni* QM F20568. An os paradoxum is not preserved, but was reconstructed (Musser and Archer 1998: fig. 1a, b) based on the remarkable similarity of the bony bill of *Obdurodon* with that of *Ornithorhynchus*. The basisphenoid was reported to have a thick midline crest, slightly bulbous at its posterior end, extending well posterior to the choanae; Musser and Archer (1998) contrasted this prominent crest with the similarly situated thin one in *Ornithorhynchus* (Fig. 4B). Wible et al. (2018) suggested that this so-called basisphenoid crest in *Obdurodon* is formed by a separate parasphenoid based on the sagittal

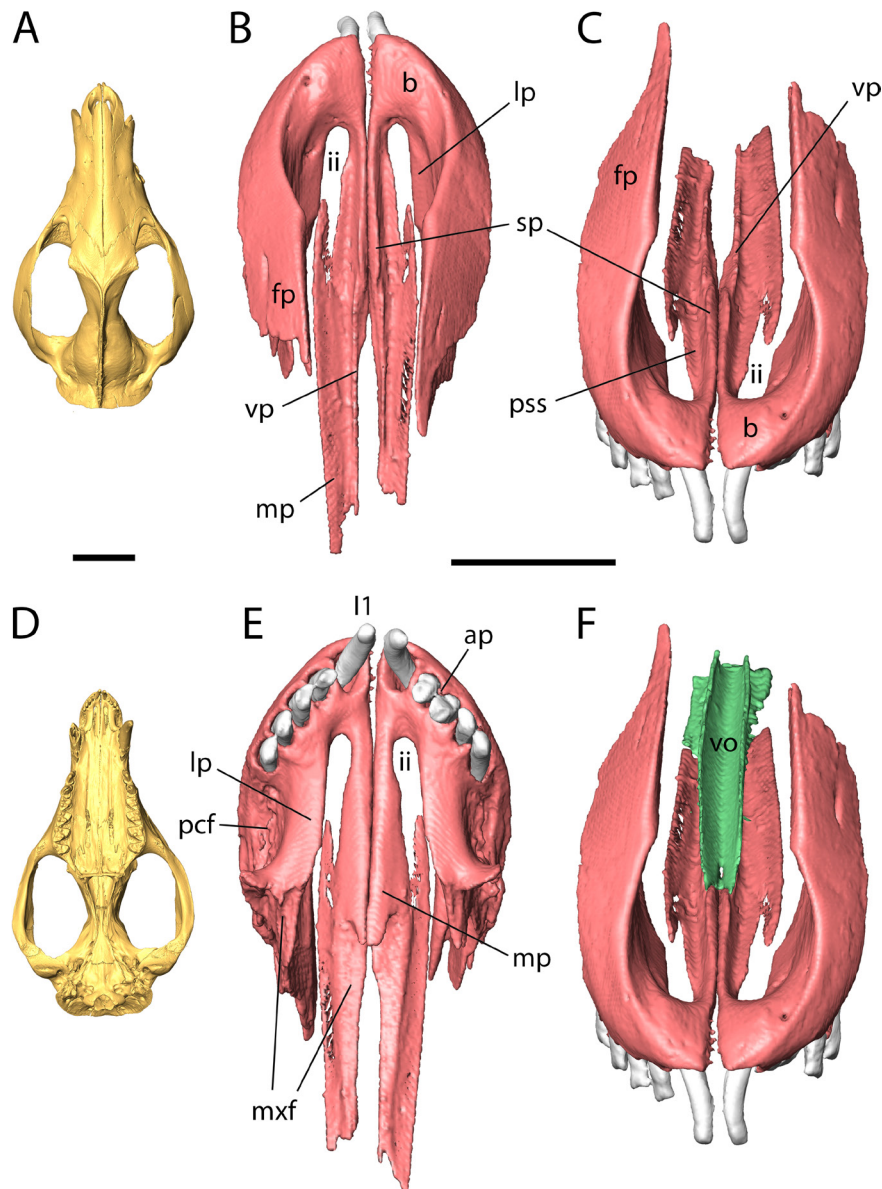


Figure 8. *Didelphis marsupialis*, du baa 0164, bone isosurfaces derived from CT scans. Cranium in **A**, dorsal and **D**, ventral views. Premaxillae in **B**, dorsal, **C**, anterior, and **E**, ventral views. **F**, premaxillae and vomer (anterior part) in anterior view. Scale for **A** and **D** is 25 mm; scale for **B–C** and **E–F** is 10 mm. Abbreviations: ap, alveolar process; b, body, fp, facial process; I1, upper first incisor; ii, incisive incisure; lp, lateral palatine process; mp, medial palatine process; mx, facet for maxilla; pcf, paracanine fossa; pss, paraseptal shelf; sp, septal process; vo, vomer; vp, vomeric process; vs, vomer shelf.

slice movie of the CT scans of QM F20568 on the DigiMorph website (http://www.digimorph.org/specimens/Obdurodon_dicksoni). Thanks to Drs. Mike Archer and Ted Macrini, I have studied the CT scans of this specimen and report what appears to be a separate bone on the midline dividing the nasopharyngeal passage posterior to the choanae (Fig. 9). As noted by Wible et al. (2018), in its position and size it is reminiscent of the parasphenoid reconstructed in the Miocene meridiolestidan *Necrolestes* by Wible and Rougier (2017). The CT scans show that the midline bone in *Obdurodon* is not only posterior to the choanae but extends anteriorly dorsal to the palatine bones (Fig. 9B), separating the left and right nasopharyngeal meatuses. A near vertical crack in the fossil separates the parts of the midline bone anterior and posterior to the choanae (Fig. 9D). The posterior part is roughly rectan-

gular in lateral view (Fig. 9C, D), underlies the basisphenoid, and has a point contact with the basioccipital; the anterior part in lateral view tapers to a point rostrally and is wedged between the palatines and presphenoid (Fig. 9D). Sutures delimiting this bone are most evident along the midline sagittal plane; the lack of clear sutures laterally suggests some fusion with neighboring bones has occurred.

To date, a parasphenoid has not been reported for extant monotremes, despite the number of ontogenetic stages that have been studied (e.g., Gaupp 1908; Watson 1916; De Beer and Fell 1936; Kuhn 1971; Presley and Steel 1978; Zeller 1989). Given the absence of this bone in extant *Ornithorhynchus* and *Tachyglossus*, its presence in *Obdurodon* is not expected. As in *Obdurodon*, *Ornithorhynchus* has a midline crest dividing the naso-

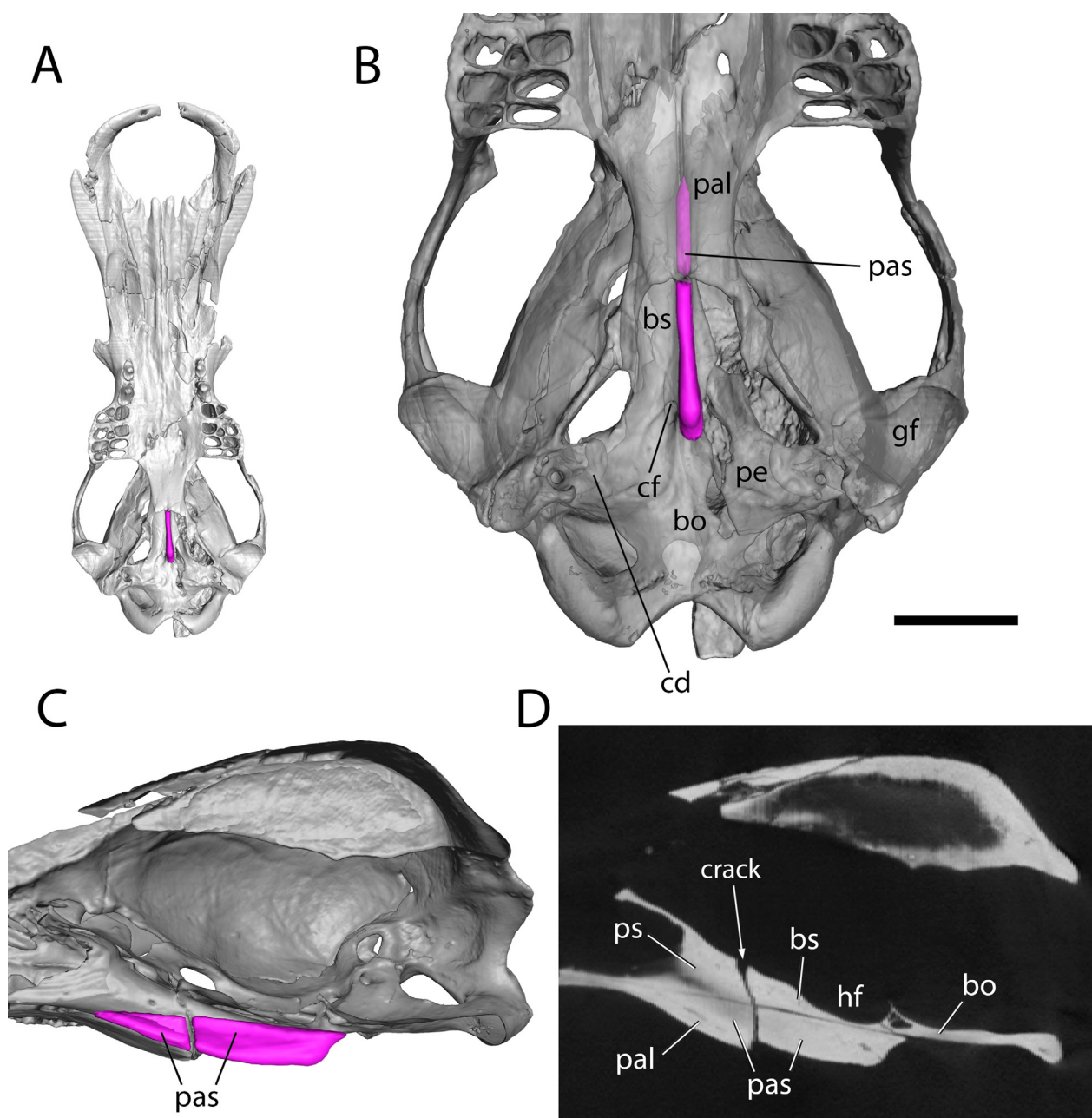


Figure 9. *Obdurodon dicksoni*, QM F20568, cranium. **A–C**, bone isosurfaces derived from CT scans. **A**, cranium in ventral view; **B**, semi-transparent posterior cranium in ventral view showing extension of parasphenoid dorsal to palatine bones; and **C**, right “half” of posterior cranium in medial view, sectioned to the left of the midline. **D**, CT slice in parasagittal plane corresponding to C. Scale bar for B–D is 10 mm. Pre- and basisphenoid are fused but identified based on their positions. Abbreviations: bo, basioccipital; bs, basisphenoid; cd, cochlear duct; cf, carotid foramen; gf, glenoid fossa; hf, hypophyseal fossa; pal, palatine; pas, parasphenoid; pe, petrosal; ps, presphenoid.

pharyngeal meatuses and extending posterior to the choanae, but it is formed by the posteriorly elongate vomer (van Bemmelen 1901; Kesteven and Furst 1929; Zeller 1989; Fig. 4B). In the CT scans of *Obdurodon*, the vomer is readily separable from other bones in the anterior nasal cavity, but posteriorly it appears fused to the ossified nasal septum and presphenoid. Nevertheless, this fused structure appears separable from the midline bone identified in Fig. 9. With the caveat that as a fossil the *Obdurodon* cranium is imperfectly preserved, I consider the presence of a separate parasphenoid as the appropriate explanation for this midline bone. Short of finding more

fossils, a higher resolution scan of QM F20568 might help in differentiating structures in the rear of the nasal cavity.

Discussion

The mammalian skull has ossifications widely considered as evolutionary novelties. Well-known examples include entotympanics, independent elements in the auditory bul-

la (e.g., MacPhee 1979, 2014; Maier 2013) and the rostral or prenasal bone of the pig (e.g., Herring 1972; Hou et al. 2014; NAV 2017). More obscure examples include the os proboscidis of *Solenodon paradoxus* (Wible 2008) and the internasal bone of the two-toed sloth *Choloepus* (Gaudin et al. 2021). The origin of another bone in the anterior rostrum remains controversial, the xenarthran os nariale, considered a neomorph by some (e.g., Wible et al. 1990; Wible and Gaudin 2004) and a transformed septomaxilla by others (e.g., Zeller et al. 1993). Recently, a hypothesis that the therian premaxilla results from fusion with the septomaxilla, traceable back to Gaupp (1905, 1906), has received support from comparative embryological studies distinguishing the therian premaxilla from that in monotremes and other tetrapods (Higashiyama et al. 2021). If true, this hypothesis supports the element in xenarthrans as a novelty and may also explain why the neomorph examples above, with the exception of the entotympanics, are from the tip of the snout, an anatomical domain transformed in therians (Higashiyama et al. 2021).

Although the mammalian skull includes neomorphic structures, the usual first course of action for neontologists and paleontologists is to identify and name structures in the context of elements already known in other taxa, with the implicit assumption that creating novelties is less parsimonious. The platypus os paradoxum is an instructive example in that early invocations of novelty by Owen (1866) and Flower (1876) were abandoned when detailed anatomy (e.g., Turner 1884; Wilson 1901) supported linkage to pre-existing bones in related forms. The controversy was that two camps promoted different bony origins using the same ontogenetic database. The Wilson-Broom-De Beer camp (Fig. 4D–F) determined the os paradoxum to be a separate paired ossification, which was used to support its homologies with the paired sauropsid vomer (Broom's prevomer), with the corollary that the unpaired mammalian vomer was the equivalent of the unpaired sauropsid parasphenoid. This camp held sway for the first forty years of the nineteenth century, although acceptance was not universal (e.g., Gaupp 1905, 1906). The second camp (Fig. 4A–C), traceable back to Meckel (1826) and Turner (1884), determined the os paradoxum to be part of the premaxillae ontogenetically through the studies of Green (1930), Green and Presley (1978), and Presley and Steel (1978). Moreover, this camp incorporated new discoveries in the fossil record that the parasphenoid is present in non-mammalian synapsids and that the paired vomer in early synapsids gave way in later taxa to an unpaired vomer resembling that in extant mammals (Parrington and Westoll 1940). Wible et al. (2018) further strengthened this view with new observations of the parasphenoid in extant marsupials and the suggestion, bolstered here, of a parasphenoid in the Miocene platypus *Obdurodon* (Fig. 9). The presence of a parasphenoid in the mammalian lineage complicates the Wilson-Broom-De Beer camp by debunking the hypothesis that the mammalian vomer is homologous with

the sauropsid parasphenoid (see also Atkins and Franz-Odenaal 2016). With the mammalian vomer the homologue of the sauropsid vomer (Broom's prevomer), the os paradoxum cannot be the prevomer.

Ontogeny has identified the os paradoxum as forming as part of the medial palatine processes of the premaxillae. Anatomical comparison of the elements in adult *Ornithorhynchus* (Fig. 7) and *Didelphis* (Fig. 8) reinforces the correspondence in structure, with concavities for the paraseptal cartilages (and vomeronasal organs) and V-shaped septal processes supporting the cartilaginous nasal septum. Recent fossil discoveries reveal that this arrangement predates the origin of Mammalia. For most non-mammalian eutheriodonts, the location of the vomeronasal organ is interpreted to be in concavities on the vomer (e.g., Maier et al. 1996; Hillenius 2000; Crompton et al. 2017; Pusch et al. 2019). However, Ruf et al. (2014) showed that the Late Triassic advanced non-mammalian cynodont *Brasilitherium*, widely considered to be the sister group to Mammaliaformes (e.g., Soares et al. 2014; Martinelli et al. 2017), had medial palatine processes resembling those in *Didelphis* with concavities for the vomeronasal organs and septal processes. Not surprisingly, the absence of medial palatine processes in adult *Tachyglossus* and the isolation of the os paradoxum from the rest of the premaxillae in adult *Ornithorhynchus* are derived conditions likely related to their specialized lifestyles. It is not known if *Obdurodon* had an os paradoxum; Musser and Archer (1998) reconstructed one, noting the remarkable similarities to the bony rostrum of *Ornithorhynchus*. One clear point is that the premaxillae in *Obdurodon* are not as reduced as in *Ornithorhynchus* because its right and left premaxillary bodies approximated each other on the midline (Fig. 9A). It is my conclusion that the os paradoxum of *Ornithorhynchus* should not be labeled as mysterious, a novelty, or the prevomers but as a retained portion of the premaxillae that were undergoing reduction in the monotreme lineage.

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