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The development of the external features of the platypus (*Ornithorhynchus anatinus*)

Paul R. Manger[1], **Leslie S. Hall**[2] **and John D. Pettigrew**[1*]

[1]*Vision, Touch and Hearing Research Centre, Department of Physiology and Pharmacology, and*
[2]*Department of Anatomical Sciences, University of Queensland, Brisbane, Queensland 4072, Australia*

The present study describes the post-hatching development of the external features of the platypus. Specimens range in age from the day of hatching through to 6 months old, and provide the first comprehensive view of the developmental sequence of these features. Various features, those specific to the platypus, those specific to monotremes and those shared with marsupials and eutherians, are described. Features specific to the platypus, including the bill and webbing of the forefeet, are seen to develop precociously. Many features show similarities to marsupials, although marsupials show differential development both in timing and in morphology. The developmental progression is related to the age, in days, although the exact age of the specimens is unclear, and relies on ages given to the specimens at the time of collection, sometimes as long as 70 years ago. Despite this, the progression of development of these features suggests that the ageing given is relatively accurate.

Keywords: Monotremata; development; platypus; anatomy

1. INTRODUCTION

The post-hatching development of monotremes, the nestling stages, has been a subject of sporadic study over the past century. This is mainly due to the problem of obtaining an accurately dated set of specimens of monotremes through this period of development. Much of the information on post-hatching development is based upon isolated observations on one or a few specimens (Wilson 1901; Hill & De Beer 1949; Griffiths *et al.* 1969; Green 1930; Hughes 1993). Most of these studies have detailed the development of the chondrocranium and the ossification of this into the skull, with the major emphasis being placed upon the phylogenetic classification of the monotremes from these features (e.g. Wilson 1906; De Beer & Fell 1936; Kuhn 1971; for a review, see Griffiths (1978)). The appearance and development of the external features of developing monotremes has been largely ignored, with only a few notes regarding these features appearing throughout these studies. It is therefore very difficult to age a developing monotreme from the external appearance of the live young. Second, all the information regarding platypus development relies mainly on specimens caught from the wild, during the late 1800s and early 1900s, and much of this material is unaged, or unreliably aged. However, accurate growth curves of the echidna have been published, with notes on how size of the pouch young echidna is related to the size of the mother (Green *et al.* 1985)

The study of the development of monotremes before hatching has received far more attention. The pre-hatching development of monotremes has been reviewed by Griffiths (1978), Hughes (1993) and Hughes & Hall (this issue). Monotremes lay cleidoic eggs that show a meroblastic cleavage, similar in manner to that of the sauropsid vertebrates. During the intrauterine stages of development, supposed to be about 28 days in length, a degree of organogenetic complexity that parallels the development of kangaroo-like marsupials is seen. The timing of the appearance of the primitive streak in monotremes is unknown, but presumed to be approximately three days before the laying of the egg. At term, the definitive embryo of the monotremes is constituted of around 19 somites, with the primitive streak at the caudal end of the embryo being vastly shrunken. During this intrauterine development, Hughes (1993) noted that the development of the trigeminal ganglionic primordia was expressed early, a feature shared with marsupial species. At full term, the trigeminal ganglionic primordia are seen as two large, semicircular plates, which constitute the major feature of the head plate.

The period of incubation of the laid egg in monotremes is uncertain; however, most observations give a range of 9–11 days (Griffiths 1978). Hughes (1993) has separated the incubation period into three stages, early, middle and terminal, each with their own marked features. The newly laid embryo has no functional organs, and the extra-embryonic yolk sac undertakes the role of respiration for the embryo. At this early incubation period, the embryo is seen to have forelimb buds, and a degree of cephalic differentiation where the head fold is seen to invest the underlying yolk sac, with approximately 25 somites present. This early stage is presumed to occupy the first third of the incubation period. At the middle stage of incubation the brachial arches have smoothed over, the manus plate shows five digit rays, and a simple pes plate has formed. At the terminal stage of incubation the embryo is seen to have formed an oscaruncle, and egg tooth,

*Author for correspondence (jpettigrew@vthrc.uq.edu.au).

presumably to aid in rupture of the shell during hatching. The developing eyes and external auditory meatus are not yet covered by an epitrichial shield of periderm. The digits of the manus plate are separated and clawed, and believed to be capable of digitopalmar prehension (Hughes 1993). The pes plate shows five digit rays, and the whole embryo has reached a length of *ca.* 9 mm. It is at this stage of development that the embryo ruptures the egg, and where the description of the development of the external features presented in this study commences.

Monotremes have many external features that differ greatly from those of other mammals. These features show very little individual difference and so make for reliable markers upon which to base a description of the external development of the monotremes. This particular study deals with the external development of the platypus, and thus the features described herein relate to the external anatomy of the adult platypus. In particular, the development of the bill, webbing of the forefoot, functional orientation of the hindlimb and paws and their differentiation into separate digits, the tail, and external auditory meatus are invaluable markers of the progress of the development of the platypus, especially in relation to development of the echidna. The development of other external features, including the timing of the opening of the eye, the onset of the growth of fur and the growth of the nails of fore and hind paws, provide us with developmental markers with which we can compare monotreme development with other mammals, and possibly also reptiles.

The first specimens of adult platypus to be described by western science were met with incredulity (Home 1802). The appearance of a duck's bill attached to the body of a water rat, with a tail like a beaver, made many scientists of the time suspicious of the existence of such an unusual creature. The head of the platypus, with its 'duck's bill', is the most distinctive feature. The bill consists of a large upper bill, which gains its form and size from the extension of the maxillary and premaxillary bones by a cartilaginous plate. Effectively, the upper bill is spade-like in shape. In addition, at the posterior portion of the upper bill is an extended flap of similarly glabrous skin that extends over the face and finishes just anterior to the eyes and is called the upper shield. The skin of the bill is soft and pliable, although it is also very thick and strong. The lower bill is slightly smaller than the upper bill, but is contrived in a similar manner by cartilaginous extensions from the mandible. The lower bill closes loosely into the upper bill. At the posterior end of the lower bill is a similar extension of glabrous skin, which folds posteriorly over the neck. This flap is referred to as the lower shield. Two features of the bill are distinctive: first, the anteriorly placed nostrils on the cutaneous surface of the upper bill, and second, the mediolateral grooves found along the lateral aspect of the lingual surface of the lower bill.

The external opening of the eyes and ears of the platypus is unique. The eyes are placed anteriorly and dorsally on the head, presumably in a position to scan the sky and river banks when the platypus is floating at the surface of the water. The unusual feature of the eyes and ears is that they both open into the one groove, anterior and dorsal on the head. The external auditory meatus in the skull of the platypus is found in the normal mammalian position. A cartilaginous tube extends anteriorly and dorsally from this meatus, to pierce the skin at a position immediately posterior to the eye. Both eye and ear can be closed by the action of the same sphincter muscle upon diving. This conjunction of eye and ear openings does not occur in the echidna, or in any other mammal, and so can be presumed to be a specialization of the platypus for diving. The head of the platypus is flattened in its form, a result, presumably, of the expansive development of the bill and the need for streamlining in an aquatic environment.

The forelimbs of the platypus are sprawled either side of the trunk in a fashion similar to that seen in reptiles. This is a consequence of the retention of the interclavicle bone in the pectoral girdle. The forefeet, facing anteriorly, have five digits all with long sturdy nails. The forefeet are specialized for swimming, and beneath the digits is an expansion of skin that forms a large webbing used for underwater propulsion. When walking on land, the webbing is tucked in under the palm, and the platypus walks on its knuckles. The hindlimbs of the adult platypus are unusual in their position. The hindfeet are seen to form an axis that is orthogonal to the spine. The position of the acetabulum is lateralized in the pelvic girdle, which allows the platypus to direct the axis of the femur orthogonal to the spine, but in the same plane, and so developing the sprawling stance. The tibia and fibula are orthogonal to the femur, and the metacarpal and phalangeal bones of the hindfoot are orthogonal to the tibia and fibula. A small amount of webbing is found between the five digits, all of which have nails similar to that of the digits on the forefeet. During swimming the hindfeet act as rudders and brakes and are not used for propulsion. The hindlimb is also not used extensively when walking on land.

The trunk of the platypus is elongated and flattened, usually described as streamlined. There are no particularly distinguishing features on the trunk except for the dense fur. The fur of the platypus is so dense that a part cannot be made. The tail of the platypus completes the streamlined composition of the body. It is flattened and rounded posteriorly, and serves as a place where the platypus can store excess fat. Indices of the thickness of the tail of the platypus have been used to determine the health of individual animals. There is only sparse fur on the ventral aspect of the tail.

This brief description of the embryology and external anatomy of the platypus provides the necessary background to the present description of the development of the external characteristics of the platypus. The present description was determined from a range of specimens aged from the day of hatching until 6 months of age. No other description of this kind is currently available.

2. MATERIALS AND METHODS

In this study, the examination of 33 nestling platypus was undertaken, which represents the largest collection of nestling platypus examined in any single study. The ages of these platypus ranged from the day of hatching through to approximately 6 months of age. The specimens used in this study were obtained from four museums throughout Australia: the Museum of Victoria (Melbourne), the

Table 1. *Details of the specimens used in the present study, including various measurements of body parts, the museum where the specimen is located and specimen collection reference number, and age as given by Burrell (1927)*

(N.M. of A., National Museum of Australia, Canberra; M. of Vic., Museum of Victoria, Melbourne; Aust. Mus., Australian Museum, Sydney; Qld Mus., Queensland Museum, Brisbane.)

museum	specimen number	age (days, weeks or months)	crown–rump length (mm)	tail length (mm)	head length (mm)	bill length (mm)	bill width (mm)	inter-ocular width (mm)	inter-aural width (mm)
N.M. of A.	684	0 d	13.5	1.7	—	—	—	—	—
N.M. of A.	685	2 d	16.2	2.0	—	—	—	—	—
N.M. of A.	686	4 d	21.1	4.2	—	—	—	—	—
N.M. of A.	687	5 d	26.1	6.1	—	—	—	—	—
N.M. of A.	688	5 d	—	—	—	—	—	—	—
N.M. of A.	689	6 d	31.6	5.6	—	—	—	—	—
N.M. of A.	690	7 d	37.6	16.1	14.3	4.5	6.8	6.9	—
N.M. of A.	691	10 d	43.2	15.3	17.3	5.2	7.1	8.3	—
N.M. of A.	692	12 d	56.6	18.6	23.3	8.6	11.0	11.4	—
N.M. of A.	693	14 d	—	—	—	—	—	—	—
N.M. of A.	694	24 d	68.0	24.8	22.6	8.4	13.6	13.0	—
N.M. of A.	695	28 d	68.3	26.6	29.1	10.0	14.5	13.6	19.1
N.M. of A.	696	6 w	70.9	29.1	30.5	11.7	14.7	14.0	18.6
N.M. of A.	697	7 w	92.2	34.4	33.1	12.7	16.4	16.2	21.5
N.M. of A.	698	14 w	150.0	62.0	47.1	17.6	20.8	18.4	25.9
M. of Vic.	C922	28 d	—	—	34.5	10.6	14.4	13.5	17.7
M. of Vic.	C25037	5 w	—	—	37.9	12.8	15.0	14.6	19.1
M. of Vic.	C5715	7.5 w	—	—	43.5	13.2	14.6	16.6	21.0
M. of Vic.	C27576	11 w	101.3	45.0	48.8	17.1	19.2	18.4	23.2
Aust. Mus.	M5017	15 d	—	—	18.9	7.2	7.8	7.6	—
Aust. Mus.	M2783	7 w	—	—	36.0	13.1	17.0	16.5	—
Aust. Mus.	M2780	11 w	—	—	47.0	15.0	20.0	18.6	—
Qld Mus.	J6098	6+ m	—	—	75.0	30.0	24.5	23.7	—
—	—	adult	—	—	—	56.3	47.5	—	—

Queensland Museum (Brisbane), the Australian Museum (Sydney) and the National Museum of Australia (Canberra). The specimens obtained from the National Museum of Australia had been fixed in 10% formalin, and mounted for display before the 1930s. Despite this prolonged fixation, the external features of the specimens were in ideal condition for the procedures required for this study. These 26 specimens, and one of the specimens obtained from the Australian Museum, were collected by Burrell (1927), during his many years of observation of the platypus both in the wild and in captivity. The remaining specimens obtained from the Australian Museum (two specimens), and the specimens obtained from the Museum of Victoria (four specimens), were fixed in alcohol, all having been in alcohol for a period of more than 40 years. These specimens were obtained from the general public and donated to the museums at sporadic intervals. The specimen obtained from the Queensland Museum had been fixed in 10% formalin for an indeterminate period. However, as with all the specimens obtained, the condition of the external anatomy served the present purposes. A summary of the protocols of the specimens is given in table 1.

Throughout this paper the ages of the nestling platypuses are given. The derivation of these ages come from the 'Burrell' collection housed at the National Museum of Australia in Canberra. It is assumed that Burrell himself aged these animals, and although we cannot definitively state that the ages used here are correct, we consider that at the present time these ages, from Burrell's estimation, are most likely to be the best approximation available. Until breeding colonies of platypus are established, which seems unlikely given the present problems of actually keeping platypuses in captivity (Whittington 1991), and given the political aura surrounding the platypus, we will not be certain of the precision of Burrell's ageing. One problem associated with age determination is that similar-aged monotreme young appear to vary in size according to the size of the mother (Green *et al.* 1985). However, it is convenient to use the ages designated by Burrell, and hopefully, with added information from the occasional 'fortunate incident', the size and development of the platypus with the correct ages can be determined.

All of the specimens in this study were photographed and, from these, scale drawings of the external features were made. Drawings were used in preference to photographs, as often the specimens were fixed in unnatural postures, which we have artistically corrected. Further, many of the specimens had previously undergone some form of dissection, and all larger specimens have had their abdominal walls slit to allow for the infiltration of the fixative. The drawings also provide a much clearer view of important features such as the splitting of digits and webbing of the paws, and the opening of the various

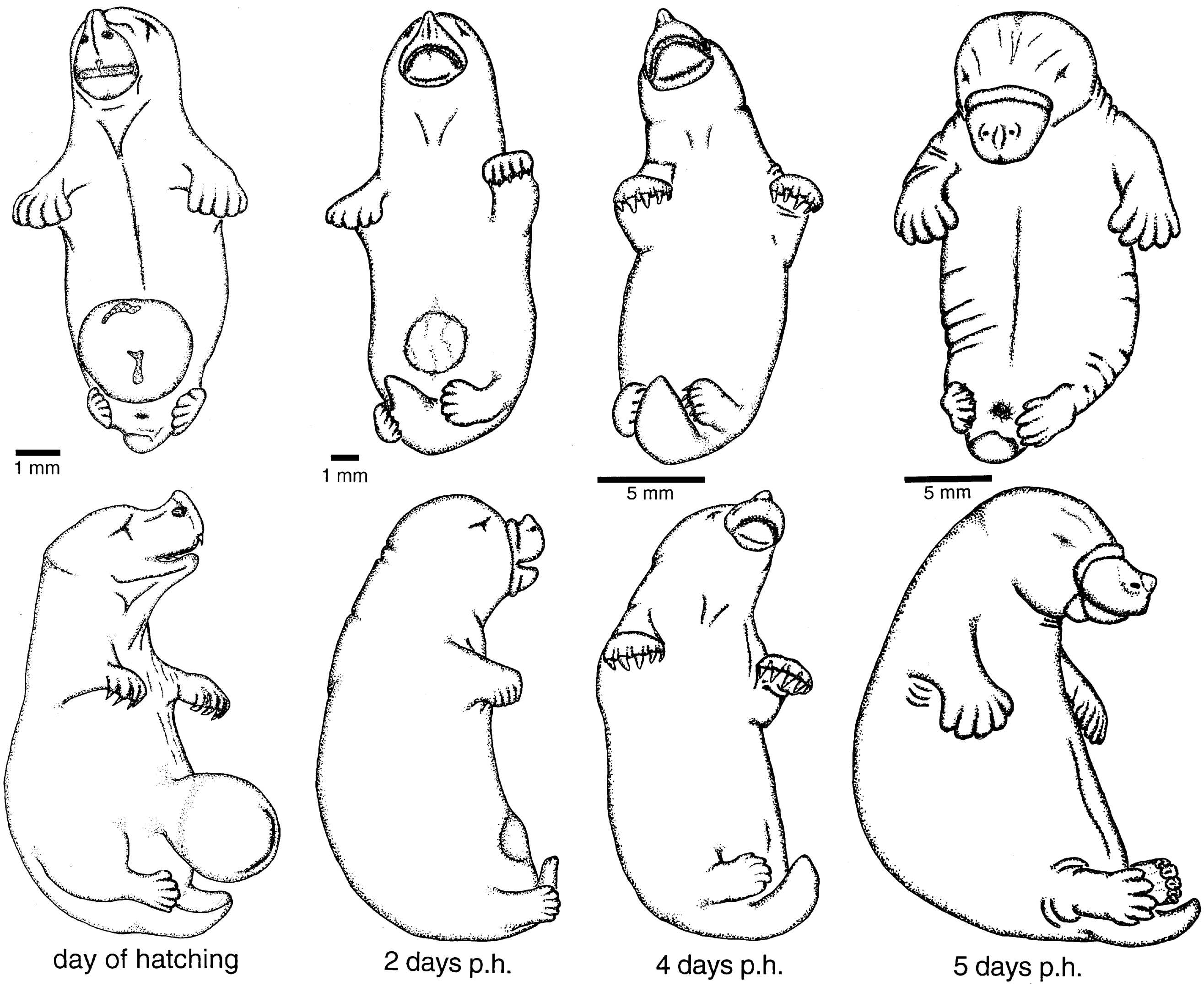

Figure 1. Line drawings of the external anatomy of the developing platypus from the day of hatching through to 5 days post-hatching (p.h.) Features of note include: day of hatching, egg tooth, large caruncle, unregressed yolk-sac, pronated forelimbs and epithrichial claws; 2 days p.h., upper and lower shields of bill apparent, egg tooth lost, regressed yolk-sac, true nails have replaced epitrichial claws, C-shape curvature to body beginning to develop; 4 days p.h., neck region apparent; 5 days p.h., upper and lower shields prominent, retinal pigment apparent.

orifii. Drawings of the ventral surface and the lateral surface are provided for each age examined in this study.

3. RESULTS

(a) *Development of the head and bill*

At hatching the head is relatively large in comparison to the rest of the body and there is no apparent region which could be described as a neck (figure 1). The future position of the eye and ear opening is marked by a branched groove positioned laterally and at the middle of the antero-posterior dimension of the head. The mouth is open, and appears as a slit in the coronal plane. The nostrils are prominent and are located anteroventrally either side of a large caruncle. The caruncle forms a large (0.5 mm) protuberance at the most rostral, dorsal portion of the head. Within the median rostral extremity of the upper portion of the oral cavity, is a sharp keratinous spine, the egg tooth (Green 1930). The egg tooth is curved inwards, towards the mouth, and is 0.3 mm long. At hatching the future area of the bill cannot be distinguished from the rest of the head area. The general shape of the head is not flattened in a dorsoventral plane as is found in the adult. The whole area of the nose, mouth and jaws resembles an early stage typical of early mammalian development.

By 2 days post-hatching (p.h.), the area of the future bill becomes distinguishable, and the regions that will form the upper and lower shields are discernible (figure 1). The egg tooth has been shed, but the caruncle still forms a prominent protuberance at the anterior dorsal portion of the future bill. The nostrils remain located relatively close together either side at the base of the caruncle, although they are proportionately smaller than those seen at the day of hatching. The eye and ear groove is still branched, and the overall shape of the head has become more rounded. By 4 days p.h., the bill primordium has commenced to elongate, and a discernible neck region is seen (figure 1). The upper and lower shields are prominent by 5 days p.h., although they have not separated from the skin surface to form flaps (figure 1). At this stage the

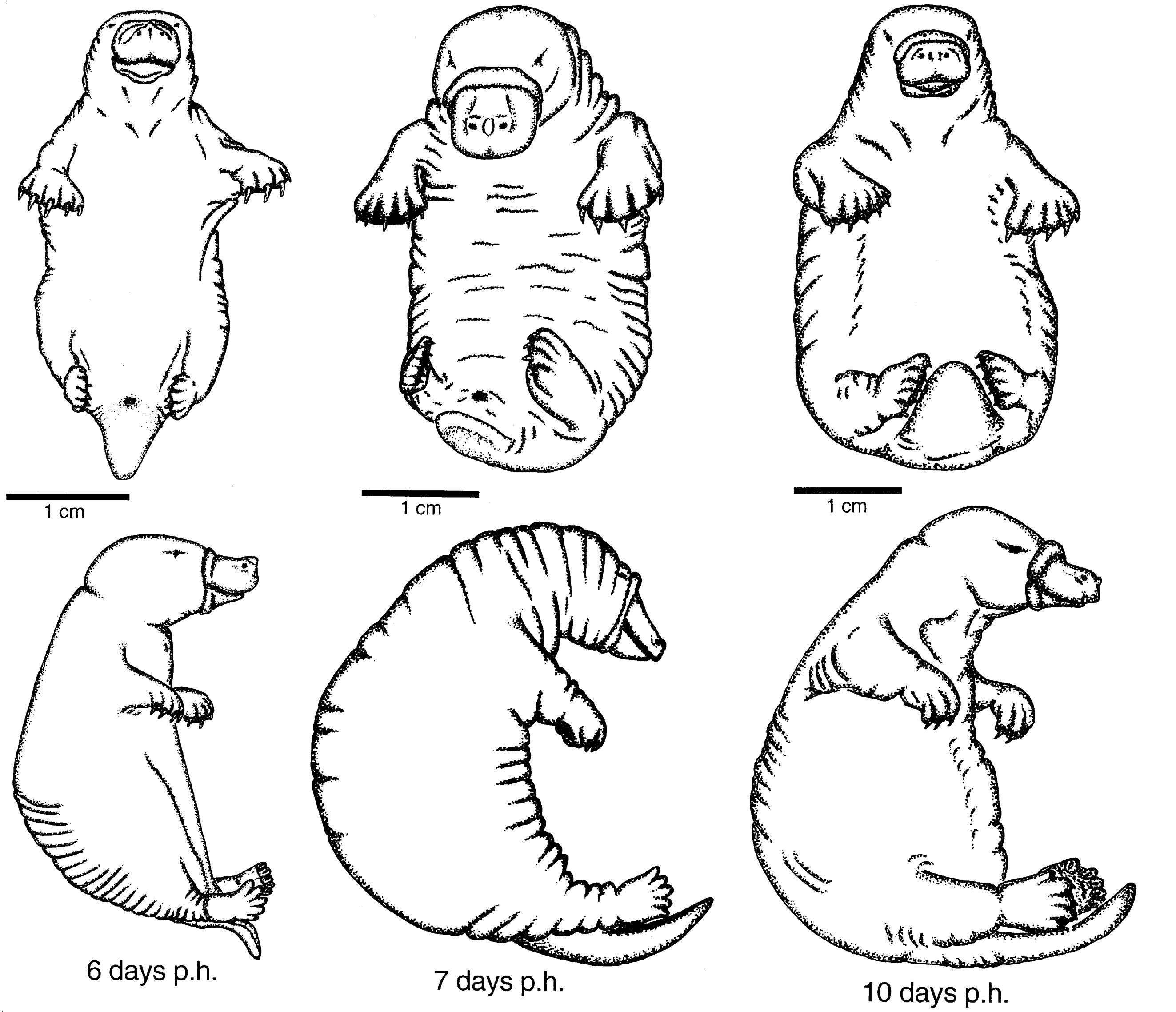

Figure 2. Line drawings of the external anatomy of the developing platypus from 6 days p.h. to 10 days p.h. Features of note include: 6 days p.h., upper and lower shields begin to form their own flap of skin; 7 days p.h., caruncle less prominent, webbing below digits on forefoot begins to form; 10 days p.h., retinal pigment prominent, lower jaw outline defines head and neck, webbing begins to develop between digits on hindfoot.

pigment of the retina is visible in the eye and ear groove, which is now shallow and unbranched. At 6 days p.h., the bill is seen to be roughly circular in cross section. However, the shape of the entire head is beginning to form a flattened appearance (figure 2). The eye groove is quite shallow and the neck region is obvious. Both the upper and lower shields have begun to detach from the skin of the face.

The eye groove deepens at 7 days p.h. and the bill and the head continue to flatten (figure 2). The rostrally located caruncle is now far less prominent, and is just a small, elevated knob located between the nostrils. By 10 days p.h., the retinal pigmentation is prominent in the eye and ear groove, the posterior portion of which has begun to extend and deepen (figure 2). The outline of the lower jaw can be seen posterior to the lower bill, which clearly defines the head from the neck. The head and bill shape continues to flatten. The caruncle rudiment is still apparent, and the upper and lower shields have formed visible flaps of skin. At 12 days p.h., the cornea of the eye is visible in the anterior portion of the eye and ear groove (figure 3). At this stage the width of the bill has increased to 11 mm.

There is little change in the gross surface morphology of the head until 28 days p.h., when the external auditory tube becomes visible in the posterior region of the eye and ear groove (figure 3). At this stage, the bill has increased in width to 15 mm, and is semicircular in outline. The remnant of the caruncle continues to be found positioned slightly anteriorly to the nostrils. The eye and ear groove is much more pronounced, and deeper posteriorly, at 7 weeks p.h. (figure 4). Interestingly, the remnant of the caruncle at this stage is located posterior to the nostrils, although at 6 weeks p.h. the caruncle is still anterior to the nostrils. The caruncle maintains this location until sometime between 11 and 14 weeks after hatching, when it is lost (figure 5). After 7 weeks the profile of the head is quite flat, and closely resembles the profile of the adult head. The bill becomes more elongated during the period between 7 and 14 weeks after

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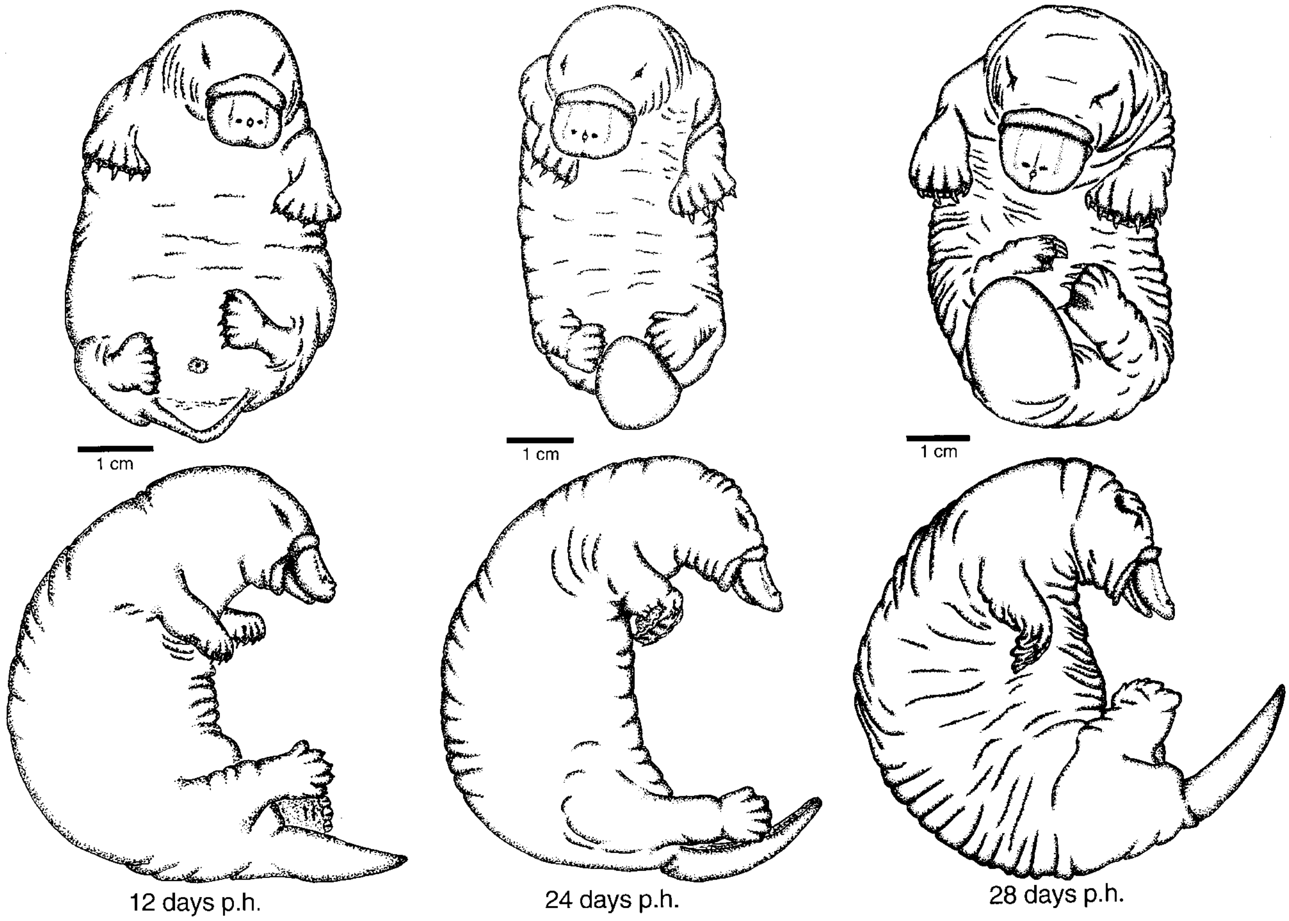

Figure 3. Line drawings of the external anatomy of the developing platypus from 12 days p.h. to 28 days p.h. Features of note include: 12 days p.h., cornea of eye visible; 24 days p.h., position of forelimb begins to alter with palm facing lateral to body axis; 28 days p.h., external auditory tube seen in posterior portion of eye/ear groove, bill increases in width, webbing on forefoot extends beyond digits.

hatching and begins to more closely approximate the proportions of the adult bill.

During the course of development, the bill undergoes unexpected changes in shape. If the width of the bill is divided by the length of the bill, and expressed as a percentage, and if this is plotted against age, it can be shown that over certain periods of development, the width of the bill is greater than the length (figure 6). During the first 24 days of growth, the width of the platypus bill is significantly greater than the length. Between 10 and 24 days p.h., the length begins to approach the same size as the width. However, between 24 and 28 days p.h., concurrent with other changes in structures in the bill (see Manger, Collins & Pettigrew, this issue), there is a relative growth spurt in the width of the bill. After this short growth spurt, the length of the bill slowly achieves the same size as the width, and before the platypus emerges from the nest, at around 6 months, the length of the bill is greater than that of the width and closely resembles, in proportion, the same ratio as that found in the adult.

(b) *Development of the forelimb and hindlimb*

At hatching the forelimbs have distinct and clawed digits (figure 1). These recurved claws appear to be composed of epitrichium, and finish in a sharp point. The forearms are pronated, whereas the hindlimbs have their plantar surfaces closely opposed in the sagittal plane. The hindlimb has distinct digits, but at hatching do not display any claws. The forelimb is composed of the digits, wrist and only a small amount of forearm that extends from the body wall. The hindlimb has digits, an ankle and a lower leg that protrudes from the abdominal wall. At this stage the hindlimb is slightly longer than the forelimb.

By 2 days p.h., the sharp, recurved, epitrichial claws on the forelimb digits have been replaced by shorter, true nails on all digits (figure 1). There are small nails appearing on the hindlimb digits. Digitopalmar prehension of the forelimb is apparent by the position of the digits and limb. The plantar surfaces of the hindlimbs are pressed against, and almost enclose, the tail.

There is an elongation of the digital claws by 4 days p.h., the forelimb claws being far larger than those found on the digits of the hindlimb (figure 1). The hindlimbs now lie beside the tail, no longer appearing to clasp it. The forelimbs protrude to the level of the elbow, and the hindlimbs to the level of the ankle at 6 days p.h. (figure 2). At 7 days p.h., webbing appears below the digits of the forelimb on the palmar surface (figure 2). Webbing appears between the digits of the hindlimb at 10 days p.h. (figure

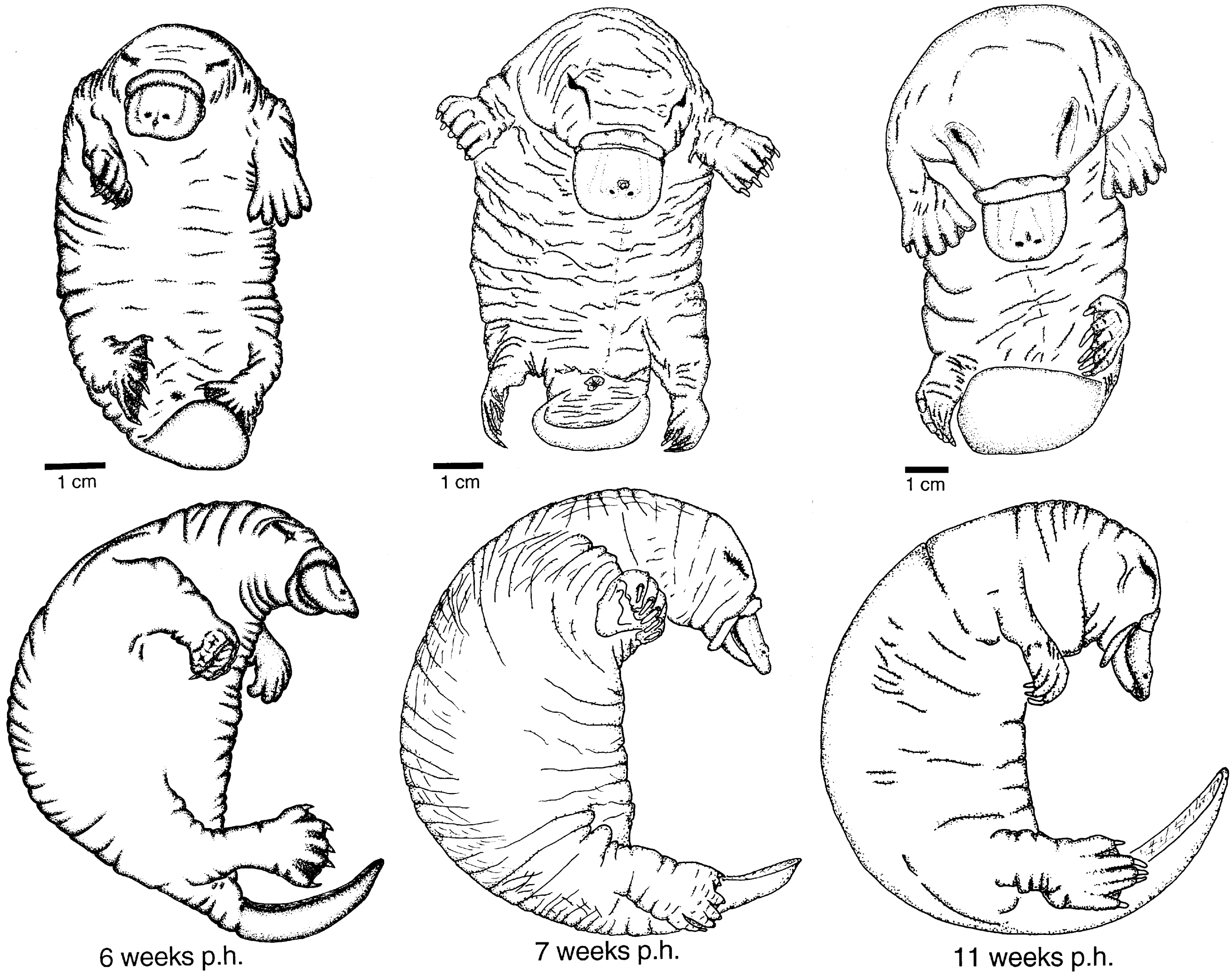

Figure 4. Line drawings of the external anatomy of the developing platypus from 6 weeks p.h. to 11 weeks p.h. Features of note include: 6 weeks p.h., webbing on forefoot at adult proportions; 7 weeks p.h., head profile flattened as in adult; 11 weeks p.h., caruncle vestigial, very short fur on body.

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2). The webbing of the digits of the forelimb is much longer at 28 days p.h., and is seen to extend beyond the digits at this stage (figure 3). This webbing progressively increases in size until it has reached the proportions seen in the adult, which occurs at 6 weeks p.h. (figure 4). The webbing of the hindlimb digits remains between the digits, not extending beyond as for the forelimb. The hindlimb digit webbing elongates as the digits grow in size, but is restricted to the regions between the digits.

Throughout development the position of the limbs alters, possibly reflecting some changes in the functional ability of the limbs. From hatching until 12 days, the forelimb is in a pronated position, allowing digitopalmar prehension (figures 1–3). During this time the forelimb presumably allows the nestling to cling to and climb over the mother's body. The position of the forelimb is altered progressively until 11 weeks p.h. The first signs of altered positioning arise at 24 days p.h., when the lower arm is seen to be capable of rotation to a position to allow the palm of the forefoot to face away from the body wall (figure 3). Following this, the elbow begins to extend from the body wall and along with this the shoulder region begins to become more distinct. This occurs from 28 days until 11 weeks p.h. (figures 3 and 4). At 14 weeks p.h., the forearm is positioned below the body, in a position similar to that seen in the adult, and is now presumably in a position to allow movement of the forelimb for 'knuckle' walking and swimming (figure 5).

The hindlimb of the adult platypus, as mentioned earlier, is unusual in its positioning, with a lateralized acetabulum and lack of rotation during development, leading to feet that have an axis orthogonal to the body. During the first 14 weeks of development the hindlimb of the platypus maintains the same position in a sagittal plane (figures 1–4). It is not until the animal is at least 6 months old that the adult position is attained (figure 5). Another unusual feature of the hindlimb development is that, during the period from 7 days to 6 weeks after hatching, the hindlimb is disproportionately long compared with the forelimb.

(c) *Development of the body and tail*

At hatching the crown–rump length is 15 mm (figures 1 and 6). The head is disproportionately large in comparison

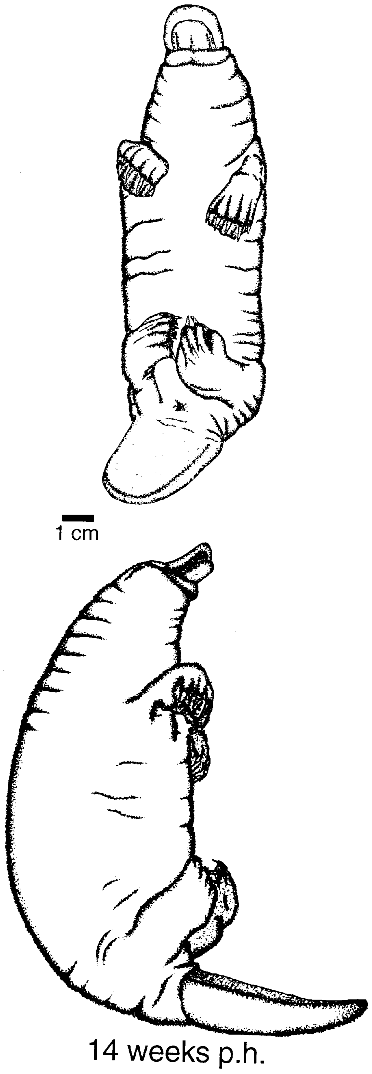

Figure 5. Line drawings of the external anatomy of the developing platypus at 14 weeks p.h. Features of note include: caruncle resorbed, forelimbs in adult position, hindlimbs still in sagittal plane, body loses C-shape curvature, longer fur on body. At 6 months p.h., the hindlimb has altered to be in the same positon as the adult, the fur has become far more dense and all features are almost identical to the adult.

with the body. There is no obvious neck and the body tapers towards the tail. The tail is short, and the ventral surface is flat. The cloaca is visible between the base of the tail, as is the unregressed yolk-sac, which protrudes from the ventral midgut area. The yolk-sac remnant is spherical with a 3 mm diameter. The surface of the vestigial yolk-sac is smooth and numerous blood vitelline vessels can be seen. The lumbar region shows a marked lordosis, although this flexion is not seen in the thoracic region. The tail is similarly curved, and is located posterior to the hindlimbs.

The yolk-sac has regressed by 2 days p.h., leaving an area of marked tissue, 3 mm in diameter, in the lower mid-ventral region (figure 1). The trunk is longer, and the head not so disproportionate. The taper towards the tail is not as marked, and the tail has grown and curved to cover the cloaca. The thoracic region at this stage has begun to show the lordosis seen in the lumbar region at the day of hatching.

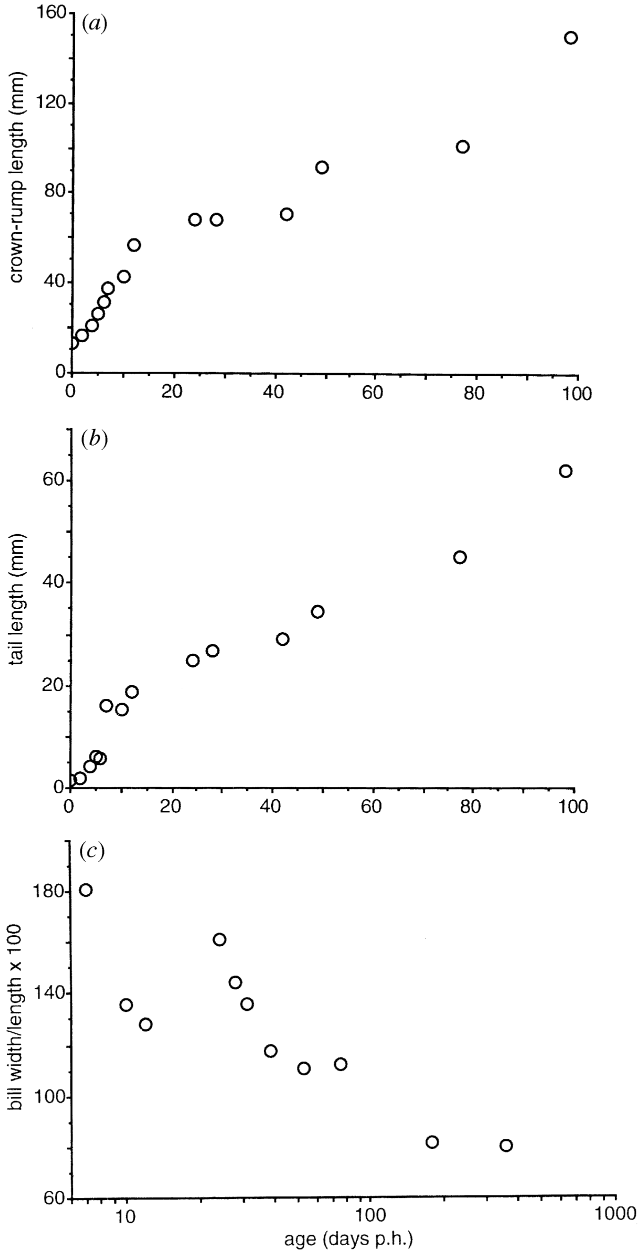

Figure 6. Plots of the growth of different features of the developing platypus against age in days post-hatching (p.h.). (*a*) Changes in the crown–rump length of the developing platypus plotted against age. The crown–rump length can be seen to increase rapidly in the first 12 days p.h., following which the rate of growth shows a steady increase over the rest of the sampled period. (*b*) The growth rate of the length of the tail, measured from the cloacal aperture to the tip of the tail. As with the crown–rump length, the first 12 days p.h. show rapid growth, followed by a steady increase in length over the period sampled. The consistency of these two plots, as well as the growth pattern of other features of the developing platypus, provide evidence supporting the ageing of the specimens by Burrell (1927). (*c*) The ratio of the bill width:bill length expressed as a percentage plotted against age (see table 1 for measurements). Over the first 24 days p.h., the bill shows increases in the length, although the width of the bill is still greater than that of the adult. Between 24 and 28 days p.h., a marked increase in the width of the bill relative to its length is seen. Over time, the length of the bill increases proportionally, until the adult ratio is reached, where the width of the bill is seen to be significantly less than the length. Despite the change of ratio between 24 and 28 days p.h., the rest of the plot is very consistent, and provides further evidence for accurate ageing of the developing platypus by Burrell.

Table 2. *List of the significant changes of the external anatomy throughout development of the platypus*

age (post-hatching)	features apparent or altered
0 (day of hatching)	egg tooth, large caruncle, ear and eye groove apparent, epitrichial claws on forelimb digits, forearms pronated, digit rays apparent on hindfoot, hindfoot in sagittal position, allantois unregressed, cloaca visible
2 days	egg tooth lost, upper and lower shields apparent, true nails replace epitrichial claws on forefoot, true nails apparent on hindfoot, allantois regressed, C-shape of body curvature apparent
4 days	neck region apparent
5 days	upper and lower shields prominent, retinal pigment apparent
6 days	upper and lower shields begin to form own flap of skin
7 days	caruncle less prominent, webbing appears below digits on forefoot
10 days	retinal pigment prominent, lower jaw outline separates head and neck, webbing appears between digits on hindfoot
12 days	cornea of eye visible
24 days	position of forelimbs begins to alter
28 days	external auditory opening in posterior portion of eye and ear groove, bill increases markedly in width, webbing on forefoot extends beyond digits
6 weeks	webbing on forefoot at adult proportions
7 weeks	head profile flat as in adult
11 weeks	vestige of caruncle, very short fur appears
14 weeks	caruncle gone, forelimbs in adult position, hindlimbs still in sagittal position, body loses C-shape curvature, fur longer
6 months	hindlimbs in adult position, dense fur, closely resembles adult in all features

This gives the whole body a shallow C-shaped curvature. At this stage the tail is located between the hindlimbs.

There is no evidence of the regressed yolk-sac at 4 days p.h. (figure 1). The body has increased in size, and the tail has increased in length and is again located posterior to the hindlimbs. By 5 days p.h., the developing nestling has attained a distinct C-shaped curvature to the body, this shape being exaggerated by the positioning of the head and the similar curvature of the tail (figure 1). The tail is now free of the hindlimbs, and no longer covers the cloaca, which is quite distinct on the lower ventral surface of the body. The body is now no longer tapered towards the tail, and has increased in width relative to length.

A pronounced C-shaped curvature of the body persists until sometime between 11 and 14 weeks after hatching (figures 4 and 5). At 14 weeks the body has straightened out. Very short fur first appears at 11 weeks after hatching, and is considerably longer at 14 weeks, where it covers the entire body surface except for the bill, ventral surfaces of the forefoot and hindfoot, the webbing of both paws and the flattened, ventral surface of the tail. No vibrissae hairs were observed at any stage.

4. DISCUSSION

This paper presents, to our knowledge for the first time, a description of the sequential development of the external anatomy of a monotreme. The age range of the specimens was from the day of hatching until 6 months. The specimens used in this study were collected and aged by Burrell (1927), the first naturalist to comprehensively study the platypus. However, doubt as to the accuracy of the ageing of the specimens has been cast by Grant (1989), owing to the fact that the specimens were collected over a wide area from different platypus populations, and because of the variability of the platypus breeding season. However, as it is unlikely that an accurate series of specimens will be produced in the near future (Hughes 1993), the present collection, with the assigned ages, is the best available. Apart from some radical changes in the morphology of the growing platypus (figure 6), there appears to be a reasonable degree of consistency to the ageing of the specimens by Burrell. Whether some of the ages were educated guesses, or whether Burrell had a system for ageing, is also unknown.

There have been various descriptions of the external appearance of monotremes at the moment of hatching (Griffiths *et al.* 1969; Hughes 1993). The specimen used in the present study correlates both in appearance and in size with these other descriptions. The presence of the yolk-sac rudiment and the egg tooth in the present description indicates that this specimen is actually from the day of hatching. Hughes (1984, 1993) and Hughes & Hall (this issue) have described, and reviewed, the embryology of the monotremes up until the day of hatching. Hughes (1993) describes the external anatomy of a specimen of platypus aged 2 or 3 days prior to birth. Several features of this specimen are of particular interest when compared with the day-of-hatching specimen described in the present study. First, the specimen of Hughes has a large vascular yolk-sac (10 mm × 6.5 mm), the specimen being only 9 mm in length. The specimen described in the present study is larger, being 15 mm in length, and has only a small (3 mm) avascular yolk-sac remnant.

Second, the eye of the specimen described by Hughes (1993) is uncovered, as is the external auditory canal. The hatchling platypus in the present study had both the eye and external auditory canal covered by a sheath of epitrichium. The most interesting point regarding the uncovered eyes and ear canals is the position on the head of these two openings. The eye of the 9 mm specimen is placed laterally on the head, whereas the eye in the adult platypus is situated dorsolaterally on the head. The external auditory canal of this 9 mm specimen is located laterally and posteriorly on the head, in a position somewhat similar to that seen for the adult echidna, and for other mammals (Hughes 1993). However, the external auditory canal in the adult platypus is located immediately posterior to the eye in a large groove around which a sphincter of muscle contracts to close of this groove when the platypus dives. In the adult platypus the external auditory meatus is connected to the external ear by a cartilaginous canal, which extends forwards. At hatching the external auditory opening described by Hughes (1993) is covered by epitrichium, leaving two options as to the fate of this opening. First, the cells forming the external auditory opening in the pre-hatching platypus migrate forwards to a position behind the eye. This, however, is unlikely. A more likely scenario is that the pre-hatching auditory opening is permanently plugged by the epitrichium, and as the cartilaginous tube develops it grows anteriorly, deep to the skin surface, and forms a secondary opening in the adult position, which from the observations of the present study occurs at around 28 days p.h.

The specimen described as day of hatching in the present study has a body length of 15 mm. This is very close to the dimensions given for hatchling platypus (16.5 mm (Green 1930) and 15.3 mm (Grant 1989)), and is also similar to the dimensions given for a newly hatched echidna by Griffiths *et al.* (1969). Flynn & Hill (1942, 1947) and Hughes (1993) both comment that there is a striking similarity in developmental morphogenesis between *Tachyglossus* and *Ornithorhynchus* with respect to microanatomy and histology at hatching. Griffiths *et al.* (1969) also consider that the newly hatched monotreme is similar in many respects to that of a newly born macropodid marsupial. Hughes (1993) agrees with this observation, but adds that the development of the monotreme at hatching is similar to that of a grade 3 marsupial (Hughes & Hall 1988).

Despite the similarities, several differences exist between a newborn macropod marsupial (Hughes *et al.* 1989) and a newly hatched monotreme. The most prominent difference is the large caruncle and egg tooth, which are presumed to aid the hatchling in rupturing the shell of the egg. Second, the eye of the platypus is located in a groove, which is characteristic of the platypus, and may be related to the fact that adult platypus have a cartilage ring around their eye (Griffiths 1978). There is no superficial indication of the ear at hatching. The mouth of the hatchling platypus forms a slit across the anterior portion of the head, and is not specialized for nipple attachment as is seen in marsupials (Hughes & Hall 1988). An extra abdominal yolk-sac remnant is present in the hatchling platypus, but not evident in the newborn marsupial. The hindfeet of the hatchling platypus, although not as advanced as the forefeet in development, appear to be only a day or so behind in development. This is unlike marsupial development, where the hindfeet lag significantly in development, and reflects more closely eutherian development, where the hindfeet develop only slightly slower than the forefeet (Moore 1988). At birth, dasyurid marsupials show a large swelling of tissue at the sternum (Hill & Osman Hill 1955; Hughes & Hall 1988). This swelling is seen neither in the hatchling platypus, nor in the embryonic eutherian. Finally, there were no signs whatsoever of specialized vibrissal hairs during development of the platypus. Hair was not seen on the developing platypus until at least 11 weeks after hatching.

Various features of note, which are specific to the platypus, were seen to develop at different times. The first species-specific feature to develop was the bill. The bill of the platypus is its major sensory organ, and occupies the majority of the brain and behaviour of the adult (Krubitzer *et al.* 1995; Manger & Pettigrew 1995). Two types of sensory receptors, electroreceptors and mechanoreceptors, are found in the bill skin (Manger *et al.* 1995; Manger & Pettigrew 1996). The development of these receptors is described in another study (Manger, Collins & Pettigrew, this issue). The development of the bill is precocious, and the major features of the bill are distinguished by 5 days p.h. Interestingly, the caruncle persists for many weeks after hatching. It has been suggested previously that the use of the caruncle is to stimulate secretion of milk by rubbing (Griffiths 1978), which may be causally linked to the extended retention of this feature.

The orientation of the forefeet of the platypus at hatching is similar to that of a marsupial. This orientation suggests that, similar to the marsupials, the platypus is capable of digitopalmar prehension. This reflex action would allow the hatchling platypus to climb to the mammary area on the ventral surface of the adult female platypuses, and would also allow the young platypuses to hang onto the fur of the adult. A locomotor generator and associated morphology similar to that described for marsupials (Hughes & Hall 1988; Hughes *et al.* 1989) is probably present in the monotremes. However, in marsupials, this locomotor generator is used solely to get the marsupial neonate to the nipple. The newly hatched monotreme does not attach to a nipple as the neonatal marsupial does, so it is possible that a more complex motor and sensory system is present in the newly hatched monotreme, and one that differs in some respects from marsupials.

A note of interest for the present study comes from Burrell's (1927) observation of young platypuses. During the collection of the specimens used in this study, Burrell noted that the young platypuses were very difficult to drown, this being his favoured method of killing them. Of particular interest is the fact that it took the youngest nestlings approximately 3 h to drown. An unresolved issue in platypus biology is how the female platypus spends her time during incubation and the weeks following hatching. The main reason for this curiosity is that a platypus will eat up to half its own weight in food every night. One explanation for this is that the female would live from fat stores in the tail. However, if the young platypuses were to climb into the fur of the female, which is quite dense and composed of two layers, and hang on tightly, the female may actually be able to leave the nest for short periods of time to eat.

As described earlier in this study, the position of the hindlimb of the platypus is unique, and is brought about by simple lateralization of the acetabulum in the pelvic girdle. It is not until 14 weeks after hatching that the hindfeet of the platypus begin to realign themselves from the sagittal plane into the position seen in the adult. The reason for this delayed repositioning is unclear, although it may be related to the low usage of the hindlimbs by the adult platypus. Underwater propulsion is taken on solely by the forelimb, the hindfeet being used mainly as rudders. During walking, the platypus almost drags the hindfeet, using the forelimb knuckle walking as its main propulsive force. Lack of development of hindlimbs is seen in many aquatic mammals, especially cetaceans and seals. It may be that the platypus is converging towards these animals, although the small amount of usage the platypus attains from the hindfeet may be sufficient to maintain them.

A feature unique to the platypus is the extensive webbing of the forefeet and slight webbing of the hindfeet. Normally, webbing is caused by the failure of cell death to mould the digits in eutherian mammals, e.g. syndactyly (Moore 1988). Cases where webbing persists naturally, such as in flippers or on waterfowl feet, is called zygodactyly. This appears to be the situation for the hindfeet of the platypus. However, the webbing on the forefeet is extensive. This webbing grows as a sheet of epithelium below the tips of the digits of the forelimb, from the palmar surface of the hand, and eventually forms a web independent of these digits. This extensive webbing is fully formed by 24 days p.h., and so is specialized in its development.

The present report details the development of the external anatomy of the platypus from the day of hatching until adulthood is reached. Several features of interest specific to the platypus were noted as being specialized in their development, the most prominent being the bill and the webbing of the forefeet. A dorsally placed caruncle persists as a rostral dorsal extremity of the upper jaw until 11 weeks after hatching, whereas the egg tooth is lost very rapidly after birth (within 48 h). Development of the forelimb suggests post-hatching digitopalmar prehension as in newborn marsupials. However, as the platypus does not attach to a nipple, and must repeatedly locate the mammary region, a more complex motor and sensory system than that found in the marsupials may be required and deserves special investigation. The development of the remainder of the external features show a mixture of developmental timing and morphological development that seems to overlap with marsupials and eutherians.

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