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The development of the electroreceptors of the platypus (*Ornithorhynchus anatinus*)

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A series of developmental stages of the platypus were examined to obtain an anatomical description of the development of the periphery of the electroreceptive system. Putative electroreceptors, composed of modified mucous glands, were observed to appear at 10 days post hatching (p.h.). The typical striped arrangement of peripheral electroreceptors in the platypus was seen at 12 days p.h. The arrangement of the stripes was modified during development with a range of additions and divisions of stripes occurring until the adult pattern is obtained, approximately 6 months p.h. After appearing at 10 days p.h., the number of electroreceptors increases rapidly until sometime between 24 and 28 days p.h. when there is massive death of electroreceptors, the number present at 28 days p.h. being 60% of the number present at 24 days p.h. This massive death of receptors is coincident with the appearance of other sensory structures in the epidermis of the bill skin, the push-rod mechanoreceptors and the sensory serous glands. Histological examination of a range of developmental stages demonstrated poorly differentiated innervation at 28 days p.h., which became differentiated and reached the adult configuration between 11 weeks p.h. and 6 months p.h., the time at which nestling platypuses leave the burrow. Lamination of the cells lining the duct of the electroreceptors showed a similar developmental profile. This study indicates that the electroreceptive system of the developing platypus is not functional, in a similar manner to the adult, until it is time for the platypus to leave the nesting burrow. However, the system may be functional in the developing platypus, and may be used speculatively in the location of the mammary region for suckling.

Keywords: electroreception; platypus; Monotremata; development; mechanoreception; anatomy

1. INTRODUCTION

The focus of the present study is the manner and manifestation of the development of the electroreceptors found in the skin of the bill of the platypus (Scheich *et al.* 1986). There are four structures found in the epidermis of the bill skin of the platypus, three of which are sensory (Andres & von During 1988; Manger *et al.* 1995; Manger & Pettigrew 1996). The three sensory structures are a mucous gland electroreceptor (Gregory *et al.* 1988), a sensory serous gland (putative electroreceptor) and a push-rod mechanoreceptor (Gregory *et al.* 1988). The fourth structure is a non-sensory mucous gland. The ultrastructural detail, distribution, number and innervation of all four of these structures has been reported previously (Andres & von During 1988; Manger & Pettigrew 1996), and so precludes the necessity for a detailed description of each to be included here. However, a brief overview of the structure, distribution and proposed function of the mucous gland electroreceptor aids in the understanding of the development of these receptors.

As is evident from it name, the mucous gland electroreceptor, is a mucous gland modified, and innervated, in such a manner as to receive weak electrical stimuli and initiate action potentials following stimulation. An intricate cuff of electrosensory nerve terminals is found around the epidermal papillary region of the duct of the mucous gland (Manger *et al.* 1995). These nerve terminals have four features of interest. A large bulbous portion of the terminal is located at the border of the epidermis and dermis, and is seen to lie on the epidermal side of the basal lamina. At the portion of the large bulb closest to the duct of the gland is a smaller bulbous portion, lying at the interface of two different layers of the epidermis, the germinative layer and the dense layer (Manger *et al.* 1995). From this small bulb, a terminal filament pierces the dense layer, and protrudes approximately 5 μm into the periluminal layers of the gland duct. Within the dense layer, small branches from the proximal portion of the terminal filament—circumferential arbors—are seen to branch orthogonally from the path of the terminal filament, and make putative connections with similar branches from adjacent terminal filaments, possibly forming a means of communication between adjacent electrosensory nerve terminals (Manger *et al.* 1995).

Andres & von During (1988) have shown that there is a great deal of elaboration of the keratinocytes surrounding the pore of the duct, forming a series of concentric rings around the pore for a diameter of *ca.* 100 μm. This makes these structures very easy to identify under low magnification. There are *ca.* 40 000 of these mucous gland electroreceptors in the bill skin of the adult platypus

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(Manger & Pettigrew 1996), and these receptors have a highly specialized distribution. Across the upper and lower surfaces of the bill, these electroreceptors can be seen to form ten parallel, parasagittal stripes (Andres & von During 1988; Manger & Pettigrew 1996). It has been demonstrated behaviourally (Manger & Pettigrew 1995) that the platypus can respond in a directional manner to electrical stimuli, rapidly and accurately locating the origin of an electrical transient. This ability is attributed, in part, to the distribution of these electroreceptors, the cortical representation of the electroreceptive periphery (Krubitzer *et al.* 1995; Manger *et al.* 1996*a*) and to the manner in which these electroreceptors respond to stimulation (Gregory *et al.* 1988). The distribution, anatomy and functional properties of these receptors are extremely important to the adult platypus, as all these features are used to obtain food. It is of interest to examine these features during development, thus possibly affording insight into the complex functional nature of the adult platypus electroreceptive system.

Three features of the mucous gland electroreceptors are examined in this study. First, the histological features of the electroreceptors at different stages of development demonstrate the time at which these electroreceptors can be thought of as functional. Second, the numbers of electroreceptors at the various stages of development are given, providing us with a time-scale for the development of the electroreceptive system. Finally, the aggregation of these receptors into a series of stripes has been plotted, allowing us an insight into the development of the complexity of the adult electroreceptive system. The appearance of the mechanoreceptors and the sensory serous gland is also described, although details of the histology, distribution and number of these receptors are limited in the present study.

2. MATERIALS AND METHODS

In this study, the examination of 33 nestling platypuses was undertaken, these specimens being the same as those previously described (Manger, Hall & Pettigrew, this issue). The ages of these platypuses ranged from the day of hatching through to approximately 6 months of age. The details of the acquisition, fixation, location and handling of these specimens have also been described elsewhere (Manger, Hall & Pettigrew, this issue). Despite a prolonged fixation, the histological detail and external features of the specimens were in more than adequate condition for the procedures required for this study.

Throughout this paper, the ages of the nestling platypuses are given. As stated previously (Manger, Hall & Pettigrew, this issue), the ages given here cannot be confirmed, although these are the best possible approximations available at the present. Until successful and repeated captive breeding of the platypus occurs, it will not be known if these ages are correct, although the experience of Burrell (1927) as the collector, and the analysis of developmental rates described for these specimens (Manger, Hall & Pettigrew, this issue), allows a reasonable amount of confidence regarding the ageing of these specimens.

The upper cutaneous surface of the bill of each specimen was examined at high power under a dissecting microscope. This allowed us to determine if the pores of the mucous glands, which in the adult stage show a marked elaboration of the surrounding superficial keratinocytes (Andres & von During 1988), were present. These pores, as will be shown later, allowed us to determine whether there were putative electroreceptors present or absent at any particular developmental stage. Further, in the older specimens, this examination allowed us to determine whether either the serous sensory glands or the push-rod mechanoreceptors were also present, as both of these, although smaller in size than the pores of the electroreceptors, have a specific superficial keratinous elaboration, which distinguishes them from the other receptors (Manger & Pettigrew 1996). Specimens younger than 10 days showed no pores. However, all specimens judged by Burrell (1927) to be older than 10 days did show the pores. High-power photographs, using either a dissecting microscope or a macro lens for the larger specimens, were taken systematically across the upper cutaneous surface of the bill. Enlargements of the photographs were fashioned into a montage of the upper cutaneous surface of the bill. A clear acetate sheet was placed over the montage, and a dot marked on the sheet for every pore. This acetate sheet was then photographed and a smaller working copy of the mapped pores was made. Each montage allowed us to determine the distribution and number of the pores present on the upper cutaneous surface of the bill. These working copies were then scanned into a computer and a grey-scale bitmap Canvas file was created. The scan was of sufficient resolution (800 d.p.i.) to allow all the previously hand-marked dots to be clearly visible. A computer-generated dot was pasted over each of the previously hand-marked dots, although in a separate drawing layer. The outline of the specimen was also assigned a separate layer and traced into the file. This gave a neat, accurate portrayal of the distribution and number of the pores on the upper cutaneous surface of the bill. This process was carried out for 15 specimens that were aged at older than 10 days.

From the specimens obtained from the Queensland Museum, the Museum of Victoria and the Australian Museum (for details, see Manger, Hall & Pettigrew, this issue), the skin from the lower cutaneous surface of the bill was dissected from the specimen and used for histological examination. The specimens housed at the National Museum of Australia were not available for dissection; rather, they were preserved in their undissected state for historical reasons. Seven developmental stages, ranging in age from 28 days to 6 months, were available for histological examination. This does not coincide with the appearance of the putative electroreceptors (at 10 days), although the limited number of specimens available for dissection precludes a full analysis of this kind. The skin specimens were sectioned in two planes, either tangentially to the skin surface, or orthogonally to the skin surface. This afforded us two views of the developing receptors, and also allowed examination of the innervation of the receptors in two planes.

Specimens of skin were processed for embedding in glycol methacrylate (Historesin, Jung). Sections (3 μm) were taken from these blocks and stained with 0.1% toluidine blue at room temperature for 5 min.

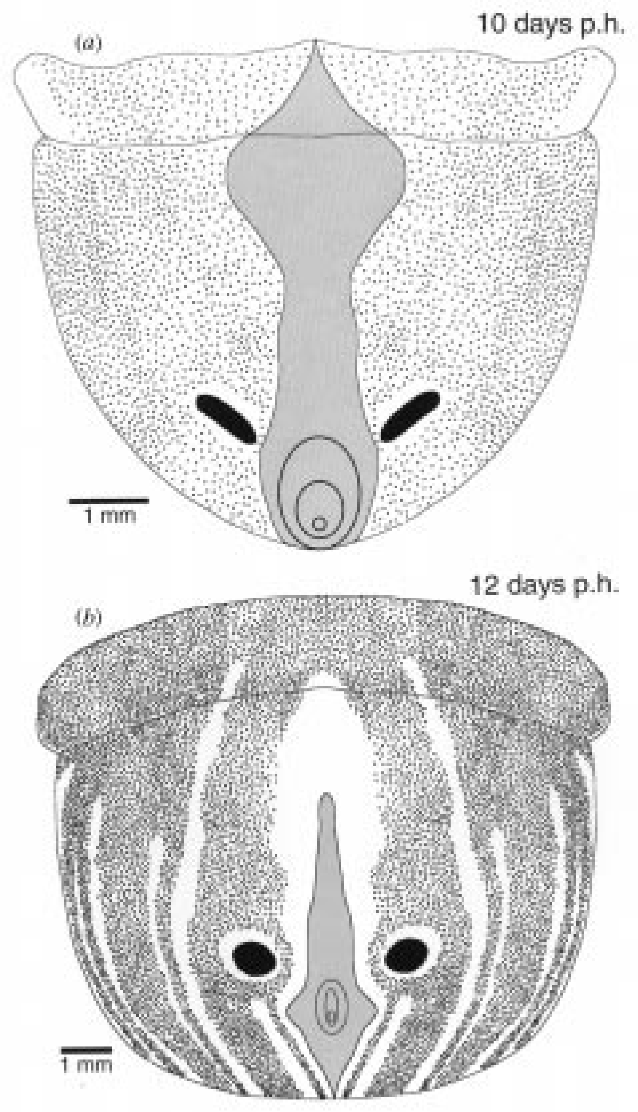

Figure 1. Two representations of the upper cutaneous surface of the bill of the developing platypus at (*a*) 10 days p.h. and (*b*) 12 days p.h. Each small black dot represents a putative mucous gland electroreceptor. The large black shapes represent the nostrils, and the shaded region is the portion of the upper cutaneous surface where no pores of any sort were found. The ectopic ovals in the shaded region represent the caruncle. Anterior is down, and the upper shield is demarcated at the posterior aspect of the bill skin. At 10 days p.h., the putative electroreceptors are distributed relatively evenly over the surface of the skin, apart from the region where no receptors were found. At 12 days p.h., the characteristic striped distribution of the putative electroreceptors can be seen. At this stage of development the medial group is composed of only two stripes, and the lateral group is composed of four stripes. The regions between the stripes contains pores that are associated with the non-sensory mucous glands. The region devoid of pores is relatively smaller, and the caruncle is located further posteriorly.

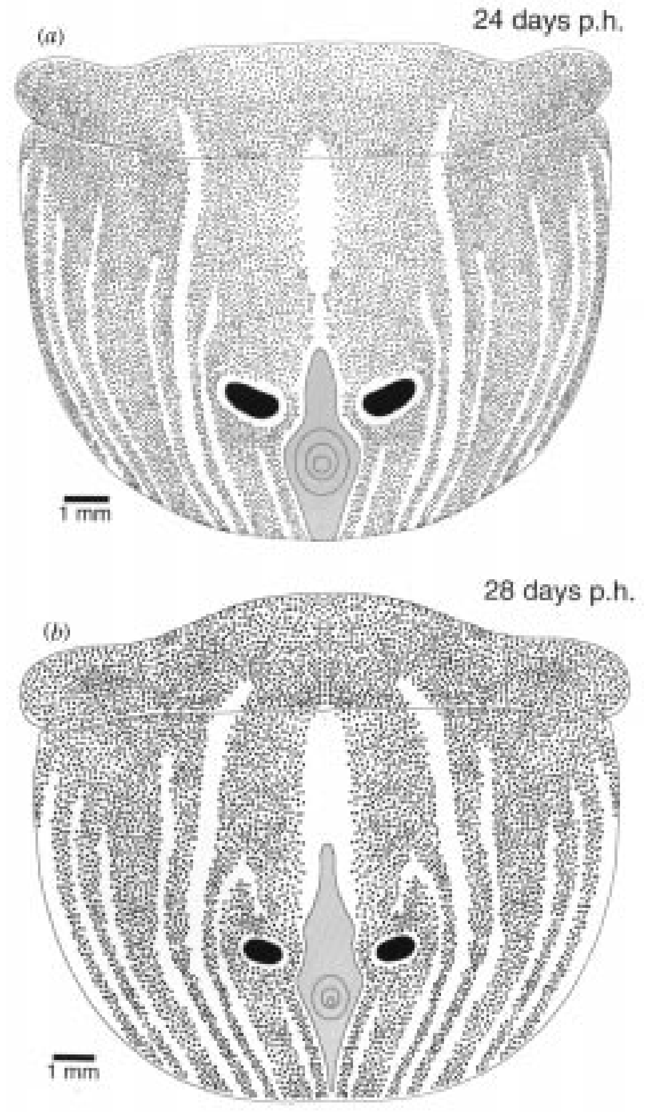

Figure 2. Diagrams of the upper cutaneous surface of the bill skin at (*a*) 24 days p.h. and (*b*) 28 days p.h. Conventions as in figure 1. At 24 days p.h., an additional stripe has been added to the lateral part of the lateral group of stripes, now totalling five. An extra stripe is also seen on the lateral portion of the medial group of stripes, bringing the total to three. At 28 days p.h., the newly added stripe of the lateral group is lost, and the newly added stripe of the medial group has a curved posterior aspect. The number of electroreceptors between these two stages in development is markedly different, with the earlier developmental stage having many more electroreceptors. It is between these stages of development that a large number of developing electroreceptors die, and this change of numbers is evident in the plots (for more details see figure 7).

3. RESULTS

Three points of major interest were found during the analysis of data for this study. First, the numbers of mucous gland electroreceptors, and their distinctive striped pattern, altered markedly through development. Second, although pores were located at the surface, and the mucous gland appeared fully formed, sensory innervation was not clearly evident until at least 6 weeks post-hatching (p.h.). However, a vague formation of cells resembling developing innervation were seen at 28 days p.h. Finally, the appearance of mucous gland electroreceptors occurred earlier in development than that of the push-rod mechanoreceptors and the sensory serous gland, which both appeared at 28 days p.h. This later appearance of the mechanoreceptors and the sensory serous glands was found to be concurrent with a massive reduction in the

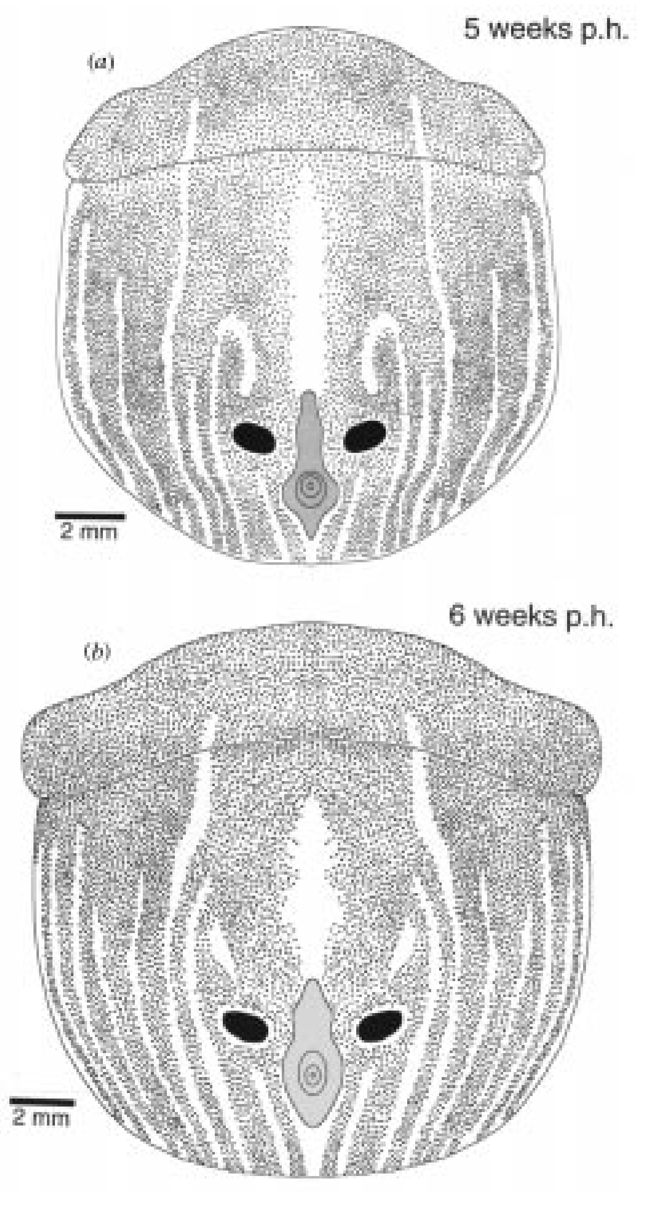

Figure 3. Plots of electroreceptors on the upper cutaneous surface of the bill of developing platypus at (*a*) 5 weeks p.h. and (*b*) 6 weeks p.h. Conventions as in figure 1. The lateral group of stripes in the 5 weeks p.h. specimen is unchanged, whereas an additional stripe has been added to the lateral portion of the medial group of stripes. At 6 weeks p.h., an additional stripe has been added to the lateral part of the lateral group of stripes and one stripe has been mostly lost from the lateral part of the medial group of stripes.

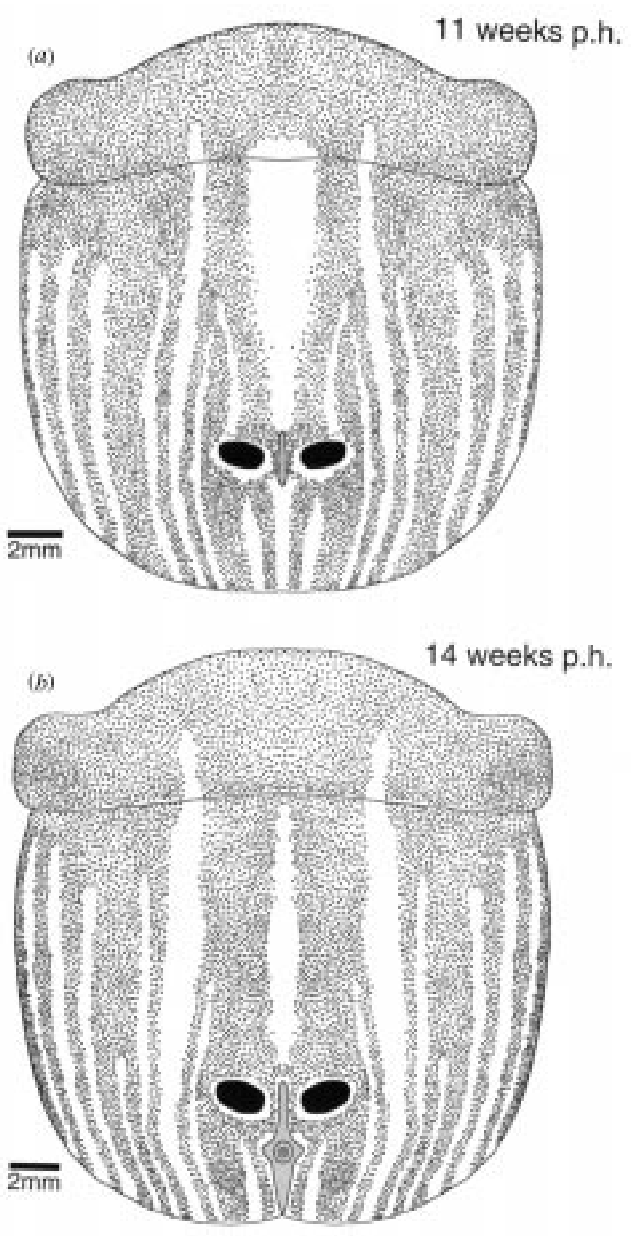

Figure 4. Plots of electroreceptors on the upper cutaneous surface of the bill of developing platypus at (*a*) 11 weeks p.h. and (*b*) 14 weeks p.h. Conventions as in figure 1. At 11 weeks p.h., the lateral group of stripes remains unchanged. The medial group of stripes is undergoing a change posterior to the nostril. At 14 weeks p.h., the thick stripe of the lateral group has bifurcated at its anterior one third. The changes occurring posterior to the nostril in the medial group of stripes appear to have ceased and the region that was undergoing change is now covered by electroreceptors.

number of mucous gland electroreceptors, and a change in the gross morphological development of the bill (Manger, Hall & Pettigrew, this issue).

(a) *Changes in number and the distribution of the stripes of electroreceptors during development*

The first sign of pores on the upper cutaneous surface of the bill of the nestling platypus occurs at 10 days p.h. These pores are not fully elaborated as the pores of the adult platypus and later nestling stages, although they were easy to discern under the dissecting microscope at a magnification of 40 times. There were 3040 of these pores located on the upper cutaneous surface (figures 1, 6 and 7), and a similar density of pores could be seen for the lower surface. The pores at this stage are not arranged in the striped pattern seen in adults; instead they are uniformly distributed over the surface of the bill. However, a stripe of skin approximately 2 mm wide, and located at the midline, was found to lack any of the pores. This stripe of skin contained the caruncle anteriorly, and extended posteriorly to include the midline portion of the upper shield.

At 12 days p.h., the striped pattern of distribution of the pores is apparent (figures 1 and 6). There are two types of pores discernible at this stage, one larger than the other. They are both arranged in a series of alternating parasagittal stripes. The largest pores, presumptive mucous gland electroreceptors, exhibit a series of six parasagittal stripes on each side of the bill, these being symmetrical. At the midline of the bill there is still a large area of skin that lacks pores, although the proportion of this is relatively less than the 10-day p.h. nestling. The most medial stripe of these pores is seen to extend anteriorly from the upper shield to the nostril, which it surrounds, and then as it progresses anterior from the nostril, this stripe bifurcates to form a thin medial stripe and a thicker lateral stripe. Lateral to these stripes is a set of four stripes that remain relatively unchanged throughout the development of the platypus. The most medial stripe of this series is thin, the adjacent stripe is thicker, and the remaining two stripes, on the lateral side of this group, are equal in width to that of the most medial stripe. These stripes are seen to extend from slightly anterior to the join of the upper shield and the upper cutaneous surface to the anterior lip of the bill. Except for a small stripe, the entire upper shield is covered by the larger pores. At all remaining areas of the upper cutaneous surface, except for the stripe at the midline, the smaller pores were seen. At this stage of development, the number of the larger pores has increased to 10 100, a marked rise in number compared with the 3000 of the nestling aged at only 2 days younger (figure 7). The remaining description of the changes in the stripes throughout development is based on this initial manifestation of the stripes. For ease of description, these stripes can be divided into two groups, the first, group 1, being the medial stripe and its two bifurcations, and the second, group 2, being the set of four stripes located laterally on the bill to group 1.

The next nestling examined was aged at 24 days p.h. At this stage, the number of presumptive mucous gland electroreceptors has again risen to 11 740 (figure 7). This rise is not as marked as that seen between the 10- and 12-day p.h. nestlings, and appears to indicate a lessening in the rate of addition of extra presumptive electroreceptors. At this stage, two changes have occurred in the manifestation of the striped distribution of the pores, showing a rise in the number of stripes across the bill from 12 stripes at 12 days p.h., up to 16 stripes at 24 days p.h. (figures 2 and 6). In group 1, the medial group of stripes, an additional stripe is seen. This is situated lateral to the two previously seen in the 12 days p.h. specimen. This additional stripe appears to originate slightly anterior to the junction of the upper shield and upper cutaneous surface, and proceeds anteriorly to the lip, describing a course parallel with the other two stripes of this group. Within group 2, the lateral group of stripes, an additional stripe is also seen. This has been added to the extreme lateral aspect of the group, and describes a course parallel with the other four stripes within this group. This stripe has a width approximately equal to the three thinner stripes in this group. Again, there is a portion of the upper cutaneous surface along the midline which lacks pores. This area has become proportionally smaller, and appears to be limited posteriorly at the level of the nostrils, and shows some expansion around the diminishing caruncle. The remainder of the upper cutaneous bill surface is covered with smaller pores, those of the non-sensory mucous glands.

A nestling platypus aged at 28 days p.h. was the next specimen to be examined. At this stage, one very important detail of the development of the electroreceptive system was noted. The number of presumptive electroreceptor pores was seen to decrease markedly, reduced to a total of 6914, approximately 60% of what was seen in a nestling only 4 days younger (figure 7). This stage is important as it defines the time at which the nestling platypus is undergoing the phase of cell death seen in many developing systems, and which was previously unknown for the monotremes. At this stage there appeared to be very little change in the manifestation of the stripes, although in both groups there is a change worth noting (figures 2 and 6). In group 1, the stripe of non-sensory mucous gland pores that delineated the additional stripe at the lateral aspect of this group is seen to extend at its posterior end, and curve in such a manner as to turn 180° and begin to describe a course towards the nostril. This extension invades the territory of the upper cutaneous surface of the bill previously occupied by the thicker medial stripe. Within group 2, the additional stripe observed in the 24-day p.h. specimen has been reduced, so that it is only evident at the most posterior aspect of the upper cutaneous surface. The portion of the surface barren of pores is still restricted to the midline, and is seen to extend from just posterior to the nostrils, around the caruncle, and tapers to a point at the anterior lip of the bill, thereby slightly changing its previous appearance. Proportionally however, this region appears to occupy the same extent as in the previous specimen.

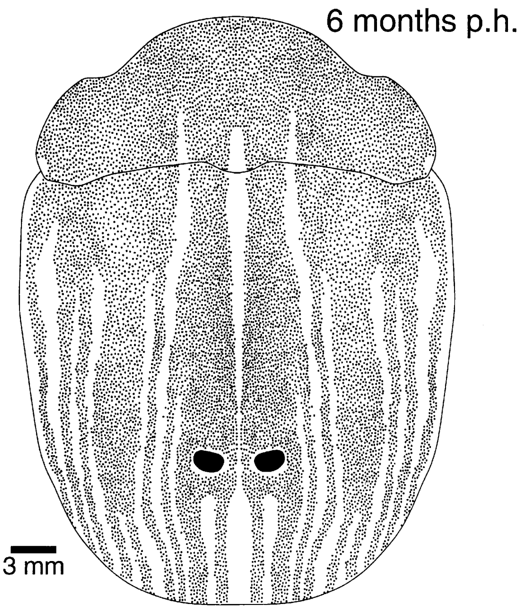

Figure 5. Plot of electroreceptors on the upper cutaneous surface of the bill of developing platypus at 6 months p.h. Conventions as in figure 1. The anterior bifurcation of the thick stripe in the medial group has lessened in length. The medial group of stripes remains unchanged. At this stage of development the entire upper cutaneous surface of the bill is covered with pores of either the mucous gland electroreceptors or the non-sensory mucous glands, and the last vestige of the caruncle has disappeared.

The next oldest specimen examined was aged at 5 weeks p.h. In this specimen the number of presumptive mucous gland

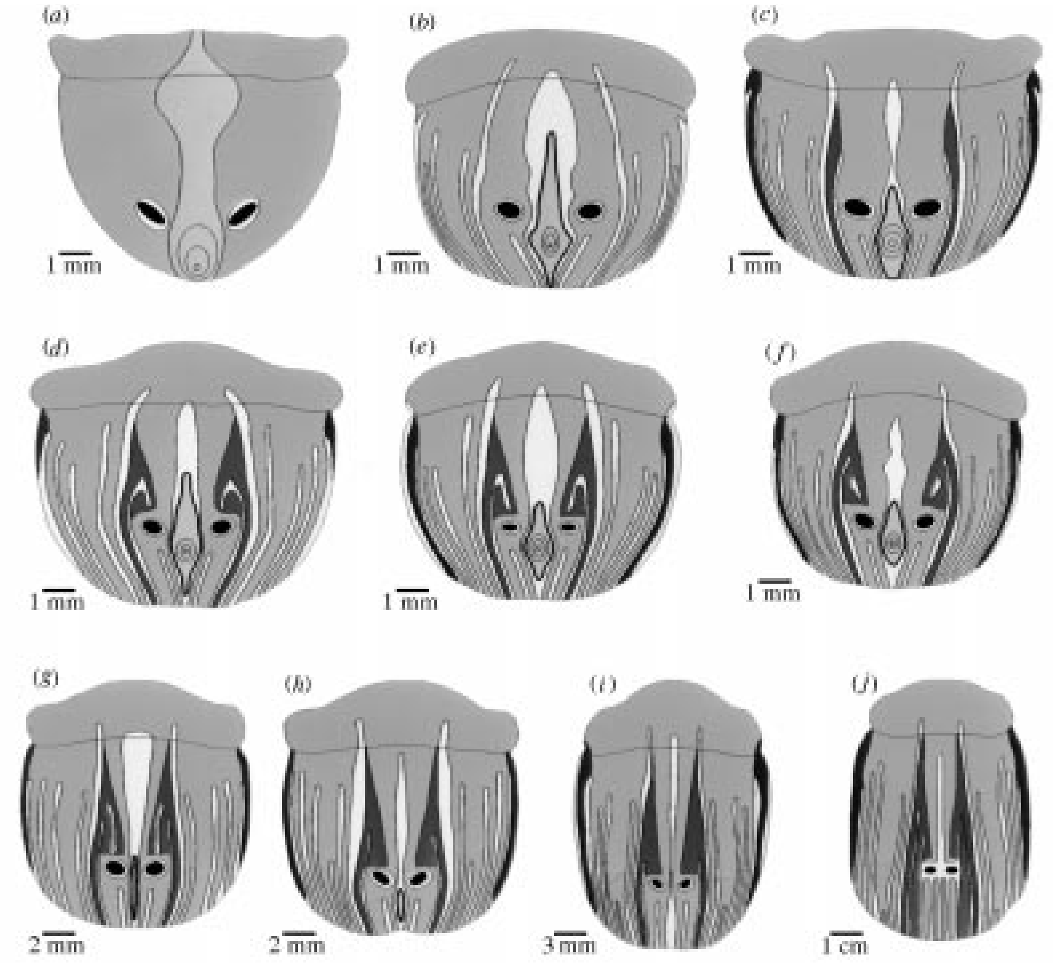

Figure 6. Summary of the changes in the array of stripes of electroreceptors during development. (*a*) 10 days p.h.; (*b*) 12 days p.h.; (*c*) 24 days p.h.; (*d*) 28 days p.h.; (*e*) 5 weeks p.h.; (*f*) 6 weeks p.h.; (*g*) 11 weeks p.h.; (*h*) 14 weeks p.h.; (*i*) 6 months p.h.; (*j*) adult. The blue colour represents the stripes that are found at 12 days p.h., and which persist throughout the development of the platypus. The different colours represent the stripes that have been added or altered during the course of development. First, this diagram clearly shows that most of the changes occur in the medial group of stripes. Second, it demonstrates that the changes continue until the platypus is an adult.

electroreceptor pores had risen to 9350, again a significant rise in the number of pores, although still markedly less than the number of pores present at 24 days p.h. (figure 7). Between 5 weeks and 28 days p.h., very little change has occurred to the pattern of distribution of the pores (figures 3 and 6). The stripes of pores within group 1 show virtually no change. Within group 2, the additional lateral stripe, the fifth of the group, which first appeared at 24 days p.h., and which was virtually absent at 28 days p.h., has reappeared; this change may be due to individual variation. The region devoid of pores at the anterior part of the midline has reduced in size and is restricted in its range around the caruncle, with only a very small portion of this region projecting posterior to the nostrils. The most significant change to this region is that the anterior portion no longer extends to the lip.

At 6 weeks p.h., the number of electroreceptors has not increased; in fact, probably owing to individual variation, the number is slightly less, at 9180 (figure 7). The stripes of electroreceptors posterior to the nostril in group 1 have slightly altered in appearance (figures 3 and 6). The curved appearance of the intermediate pores of the non-sensory mucous gland has been bisected by a small stripe of presumptive mucous gland electroreceptor pores, which leaves a small island of non-sensory mucous gland pores in the thick medial stripe, just posterior to the nostril. The stripes of group 2 have not altered in appearance. Again, the area containing no pores has slightly reduced in size, and retracted further from the anterior edge of the bill.

Five weeks later, at 11 weeks p.h., the number of presumptive electroreceptor pores has increased to 10 420, not a large increase in numbers (figure 7). Very little has happened to the striped pattern of pores (figures 4 and 6). In group 1, the island of non-sensory pores has elongated in a posterior direction, demarcating what can be identified as an additional stripe of electroreceptor pores, forming three parallel stripes within group 1 posterior to the nostril. This now matches the three stripes anterior to the nostrils in this group. The appearance of the stripes in group 2 has not altered. The region at the midline containing no pores has been greatly reduced in size, and is now seen as only a small strip approximately 0.5 mm in width. At this stage of development, as with the 24 day p.h. specimen, only 16 stripes of electroreceptors are seen, and

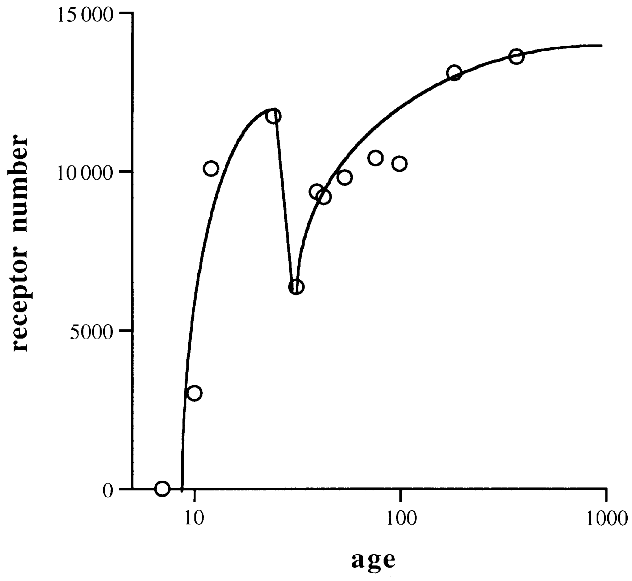

Figure 7. Graph of the numbers of electroreceptors found plotted against age in days p.h. (log scale). The numbers of electroreceptors rise rapidly between appearance at 10 days p.h. until 24 days p.h. Between 24 and 28 days p.h., there is a sharp decline in the number of electroreceptors. After this the numbers of receptors rise more slowly than in the first incident until the full complement of receptors found in the adult is reached.

this, apart from the 28 day p.h. specimen, has been consistent throughout this time period.

At 14 weeks p.h., the number of electroreceptor pores has remained stable, and, in the individual in this study, numbered 10 232 (figure 7). The striped pattern of these pores shows only two changes (figures 4 and 6). In group 1, the previously identified island of non-sensory mucous gland pores has disappeared, again fusing the electroreceptor pores into two stripes posterior to the nostrils. Within group 2, the anterior portion of the thickest stripe is seen to have divided into two stripes from the level of the nostrils. The patch of skin at the midline devoid of pores had reduced its anteroposterior extent, and now only occupies a small region surrounding the vestiges of the caruncle.

The next specimen to undergo examination was a young platypus, taken at large, presumably having recently emerged from the burrow, and so aged at approximately 6 months. The number of pores of electroreceptors has increased to 13 090, only a few hundred below the number of pores in the adult (figure 7). Within group 1, no significant change in the distribution of the pores is noticeable. Within group 2, the thickest stripe, which at 14 weeks p.h. had bifurcated at the level of the nostrils, is now seen to bifurcate at a position anterior to the nostrils. The region of bare skin is completely absent by this stage (figures 5 and 6).

Finally, in the adult platypus (Manger & Pettigrew 1996), a variety of changes can be seen when compared with the juvenile platypus. The number of pores has increased to 13 600 (figure 7). Within group 1, an additional stripe of electroreceptor pores can be seen. This stripe originates behind the nostril, in the region where many changes have occurred throughout development. This stripe projects forward, between the two medial stripes that were always present and the first stripe added to the lateral region of group 1, to the anterior edge of the upper lip. The final result in group 1 is three partial stripes posterior to the nostril, and four stripes anterior to the nostrils. In group 2, only one small change is seen, this being the reduction of the anteroposterior extent of the bifurcation of the thickest of the stripes in this group. Hence, in group 2 at the adult stage, five stripes, one with a small anterior bifurcation, are seen. Again, there is no region on the surface of the bill where pores, of some variety, cannot be found (figure 6).

In summary, two subsets of stripes appear at 12 days p.h. These subsets undergo a variety of changes over the course of development, and it is not until the adult stage is reached that these changes are completed (figure 6). The number of electroreceptors increase markedly between 12 and 24 days p.h., although many electroreceptors die off between 24 and 28 days p.h. The number of electroreceptors then slowly increases until the number found in the adult is reached (figure 7).

(b) *Histological observations on the development of the electroreceptors*

Five stages of the ontogeny of the bill skin and associated receptors were available for histological examination. These were at 28 days p.h., 6 weeks p.h, 7 weeks p.h., 11 weeks p.h. and 6 months p.h. Details of the histological appearance of the receptors in the bill skin of the adult platypus have been published previously (Andres & von During 1988; Manger *et al.* 1995; Manger & Pettigrew 1996).

At 28 days p.h., sensory mucous glands, non-sensory mucous glands, primordial mucous glands, primordial push-rod mechanoreceptors and primordial sensory serous glands were evident in the cutaneous surface of the skin of the lower bill (figures 8*a*,*c*, 10*d* and 11). The sensory mucous glands were the easiest and largest of the structures listed above to discern in the present preparations. They consisted of a large dermal gland, the duct of which traversed the epidermis, forming an elaboration that was particularly obvious below the level of the adjacent epidermal pegs. Approximately 100 µm below the surface of the adjacent epidermis, the duct of the mucous gland thickens greatly in diameter, up to 45 µm. In the adult platypus, it is around this papillary thickening that the electrosensory innervation occurs (Manger *et al.* 1995). At the basal epidermal portion of the mucous gland duct, a series of poorly defined, unmyelinated axons, in the position of the future nerve cuff, form a close association with the duct. This neural association resembles that seen for the mystacial vibrissae of *Macropus eugenii* at birth (Hughes & Hall 1988), although in the present preparation it is unclear whether nerve terminals have yet been formed. At this stage of development, the basal epidermal portion has six cells across its diameter. No evidence of the complicated layering of keratinocytes around the epidermal portion of the mucous gland duct, as that described for adults (Manger *et al.* 1995), is seen at this stage.

The density of these presumptively innervated mucous glands was seen to be *ca.* 160 mm^{-2} within the stripes,

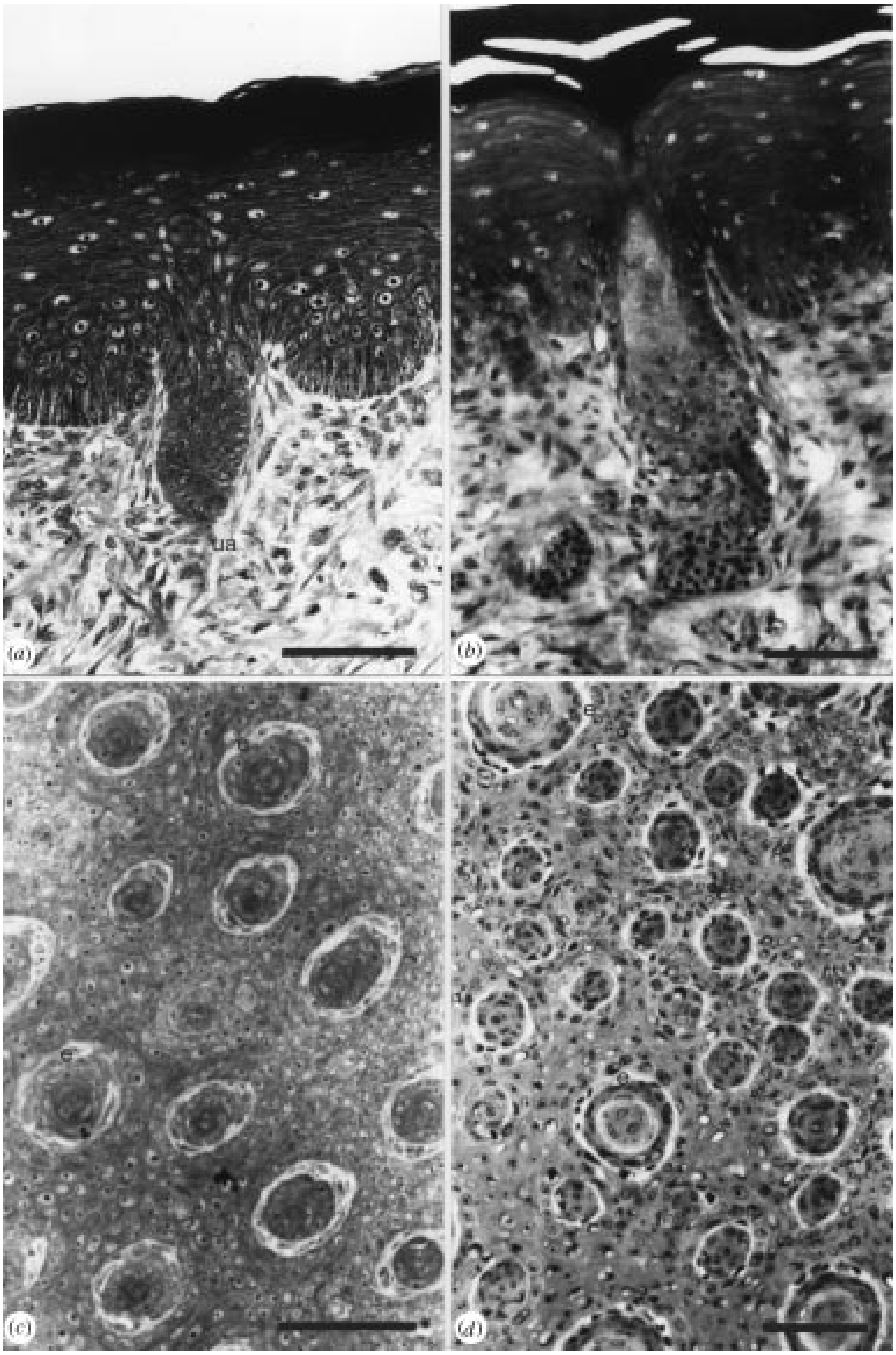

Figure 8. Histological sections of the developing electroreceptors taken orthogonal (*a*, *b*) and parallel to the skin surface (*c*, *d*). (*a*) Section through the epidermis and adjacent epidermal specialization of the duct of the developing electroreceptor at 28 days p.h. At this stage of development the epidermal portion of the duct is simple in its configuration and the nerve cuff, which surrounds the papillary portion of the duct, has not yet formed. A loosely formed series of developing unmyelinated axons (ua) is typically found in the region of the future nerve cuff at this stage. (*b*) Similar section to (*a*), but this section is taken from the skin of a 6 weeks p.h. platypus. The layering of the epidermal portion of the duct is distinct, and more cells with large nuclei, possibly Schwann cells, are located in the region of the future nerve cuff along with unmyelinated axons. (*c*) Section taken parallel to the bill skin surface from a 28-day p.h. platypus. The putative electroreceptors (e) are seen as the larger of the circular structures, with the developing glands, mechanoreceptors and serous glands being the smaller circular structures. (*d*) Similar section to (*c*), but taken from a 6-week p.h. platypus. The three layers that surround the electroreceptor duct (e) can be seen, and an occasional unmyelinated nerve terminal is seen. The density of the electroreceptors has dropped, although the density of other structures has increased. Scale bars, 50 µm.

whereas that of developing glands was slightly lower, being *ca*. 130 mm^{-2} over the entire bill. This density of receptors is far greater than that seen for the adult (Manger 1994). The epidermis of the bill skin was composed of four strata, as in the adult (Manger & Pettigrew 1996), which from deepest to most superficial were, the stratum germinativum (1 cell thick), stratum spinosum (4–5 cells thick), stratum granulosum (12–14 cells thick) and the stratum corneum (18–20 cells thick). The entire epidermis was 140 µm in thickness.

At 6 weeks p.h., the histological features of the presumptive electroreceptors described for 28 day p.h. specimen have changed considerably, and in many ways resemble the adult form (figure 8*b*,*d*). The most obvious change is the distinct lamination of the epidermal portion of the duct of the mucous gland. The basal epidermal portion of the duct, 100 µm below the level of the surrounding epidermis, shows the lamination most clearly. As in the adult platypus, three layers are seen. The outer most layer, the germanitive layer (Manger *et al.* 1995), consists of 1–2 cells, and closely resembles the stratum germinativum of normal epidermis. Luminal to the germinative layer is a layer of tightly packed, flattened keratinocytes, consisting of 3–4 cells, and termed the dense zone (Manger *et al.* 1995). Surrounding the lumen of the duct is the periluminal layer (Manger *et al.* 1995), which consists of 2–3 loosely packed keratinocytes. The cross-sectional width of the basal epidermal portion has increased to 60 µm. Once again, unmyelinated axons can be seen in the region of the future nerve cuff, and in some favourable sections taken parallel to the skin surface, occasional unmyelinated nerve terminals can be seen. Associated with the unmyelinated axons are a variety of cells, the most prominent of which have large nuclei, and probably represent the precursors of the Schwann cells. A similar pattern of unmyelinated axons associated with these precursor Schwann cells can be seen in the dermis, where, in cross-section, they show the typical appearance of axon bundles.

The density of these future electroreceptors has decreased markedly, despite the increase in number of these organs (figure 7), to *ca*. 125 mm^{-2}. Other structures in the bill skin, including developing mechanoreceptors, serous sensory glands and mucous glands, have increased in density, with up to 575 of these structures being found per square millimetre. The structure of the epidermis has not changed between the 28 days p.h. specimen and the 6 weeks p.h. specimen.

Between 6 weeks p.h. and 7 weeks p.h., very little in the structure of the electroreceptor changes; in particular, the numbers of cells in the laminations around the basal epidermal portion of the mucous gland duct remain unchanged. Similarly, the morphology of the epidermis remains unchanged. However, one major change of significance occurs, this being the existence of myelinated axons in the region of the nerve cuff, and bundles of myelinated axons in the dermis (figure 9*a*,*c*). The formation of the nerve cuff resembles that seen in the adult, although the nerve cuff still lacks much of the neural sheathing seen in the adult. Again, in favourable tangential sections occasional unmyelinated nerve terminals can be seen. The density of the electroreceptors has further diminished, down to 50 mm^{-2}. The remaining structures, including push-rod mechanoreceptors, sensory serous glands and non-sensory mucous glands, have become more defined in appearance and more closely resemble that seen in the adult. The density of these other structures has also dropped markedly, totalling at this stage only 110 mm^{-2}.

At 11 weeks p.h. there are two significant changes in the structure of the electroreceptor (figure 9*b*,*d*). The first of these is that extra layers of flattened keratinocytes have been added to the dense zone surrounding the duct. The number of cell layers in this zone has increased from 3–4 to 5–6. Second, the neural sheathing that surrounds the neural cuff is clearly defined. This neural sheathing is also more prominent surrounding the axon bundles found in the dermis. The electroreceptive nerve terminals are still unmyelinated. Within the rod of the push-rod mechanoreceptors, the peripheral and central vesicle chains can be seen, indicating that, at this stage of development, these receptor organs may be considered fully functional. The density of electroreceptors has dropped further to 40 mm^{-2}. The other epidermal structures show only a slightly higher density of 50 mm^{-2}.

At 11 weeks p.h., the epidermis has become slightly thicker, attaining a width of 160 µm, mainly due to thickening of the stratum corneum. At 6 months p.h., the epidermis has again increased slightly in width (170 µm). The density of the electroreceptors has dropped slightly to 35 mm^{-2}, this being only slightly more than the density of 30 mm^{-2} seen in the adult (Manger 1994). The remainder of the epidermal structures show a density of 45 mm^{-2}, again slightly less than that of the 11 weeks p.h. specimen, but slightly more than that seen in the adult. The change of most interest is the presence of myelinated electroreceptive nerve terminals in the germanitive layer of the basal epidermal portion of the mucous gland duct (figure 10*a*). The number of cells in the dense zone has increased and closely approximates the number seen in adults. The neural array of the mechanoreceptors is more clearly defined, as is the structure of the rod (figure 10*b*,*c*). Serous sensory glands are also innervated at this stage of development. The appearance of the receptors and the epidermis closely resembles that of the adult platypus at this stage.

4. DISCUSSION

The present description of the development of the electroreceptive system of the platypus has provided many points of major interest. These include: (i) the changing pattern of the stripes of electroreceptors during development; (ii) the apparent loss of many of the electroreceptors during ontogeny, and the coincidental appearance of other sensory receptors at the time when electroreceptors vacillate in number; (iii) the development of the general features of the electroreceptors, especially the layering of the epidermal portion of the mucous gland duct; (iv) the developmental timing and morphology of the innervation of the electroreceptors; and (v) the differential timing of development of the sensory receptors complexes in the bill skin.

(a) *Development of the striped pattern of electroreceptors*

As can be seen from the plots of the distributions of the electroreceptors during ontogeny, the pattern of striping

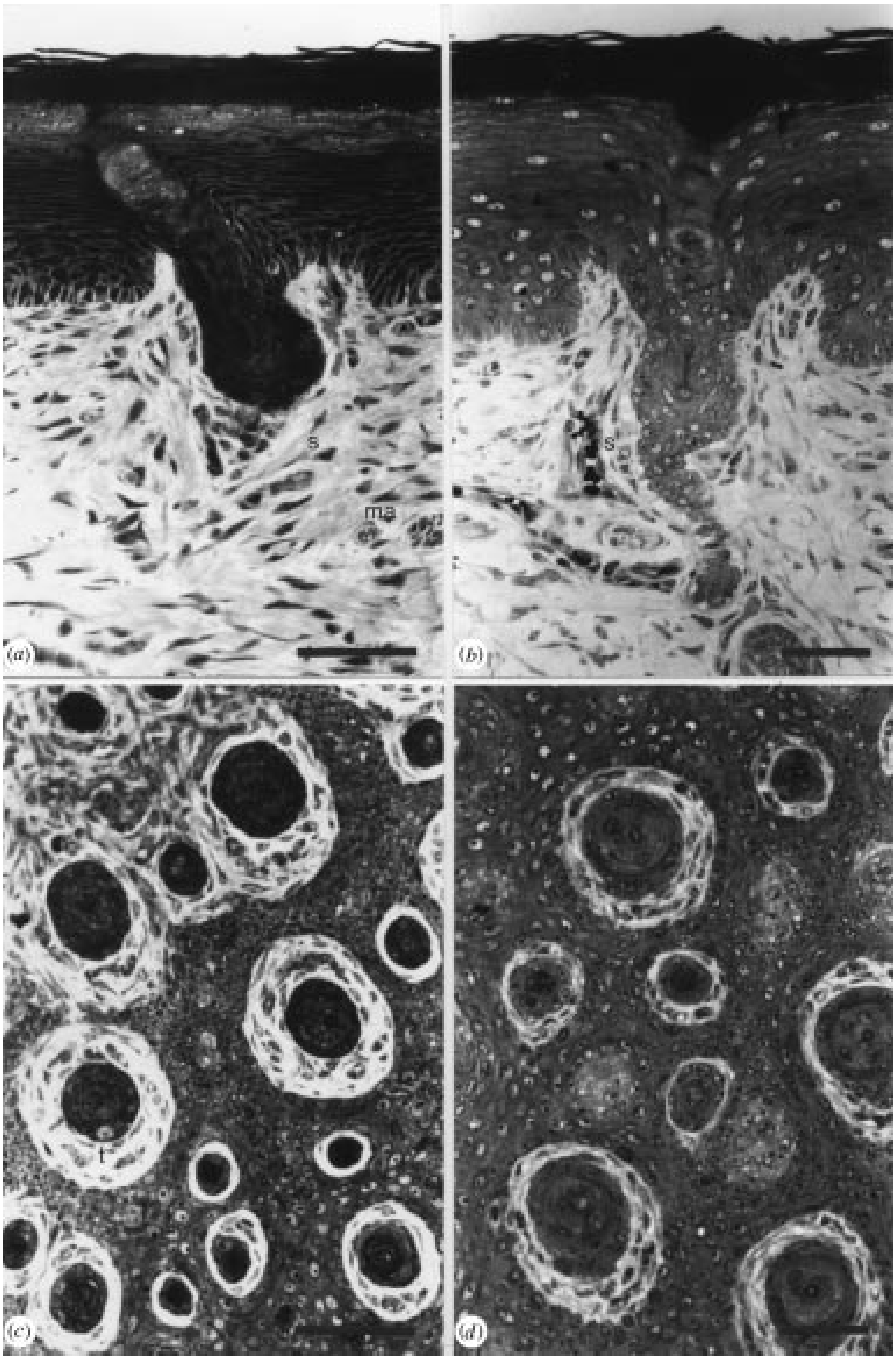

Figure 9. Histological sections of the developing electroreceptors taken orthogonal (*a*, *b*) and parallel to the skin surface (*c*, *d*). (*a*) Section through the epidermis and adjacent epidermal specialization of the duct of a developing electroreceptor at 7 weeks p.h. Two changes have occurred in the histological appearance of the developing electroreceptors and the surrounding dermis between this specimen and the 6-week p.h. specimen, these being the appearance of myelinated axons (ma) in the dermis close to the receptors and the appearance of some neural sheathing (s) around the region of the nerve cuff. (*b*) Section through the epidermis and adjacent epidermal specialization of the duct of a developing electroreceptor at 11 weeks p.h. At this stage of development the number of flattened keratinocytes in the dense zone have increased and the neural sheathing (s) surrounding the nerve cuff is more clearly defined. (*c*) Tangential section through the skin of the bill from the 7-week p.h. specimen. At this stage an occasional unmyelinated nerve terminals (t) in the developing electroreceptors can be seen. Mechanoreceptors and sensory serous glands are also evident in this view. The density of all structures is less at this stage of development. (*d*) Similar section to that shown in (*c*), but from an 11-week p.h. specimen. This view shows the differentiation of the dense zone in the electroreceptors clearly. This section is too superficial in the epidermis to demonstrate the nerve terminals at this stage of development (see text for description). Scale bars, 50 μm.

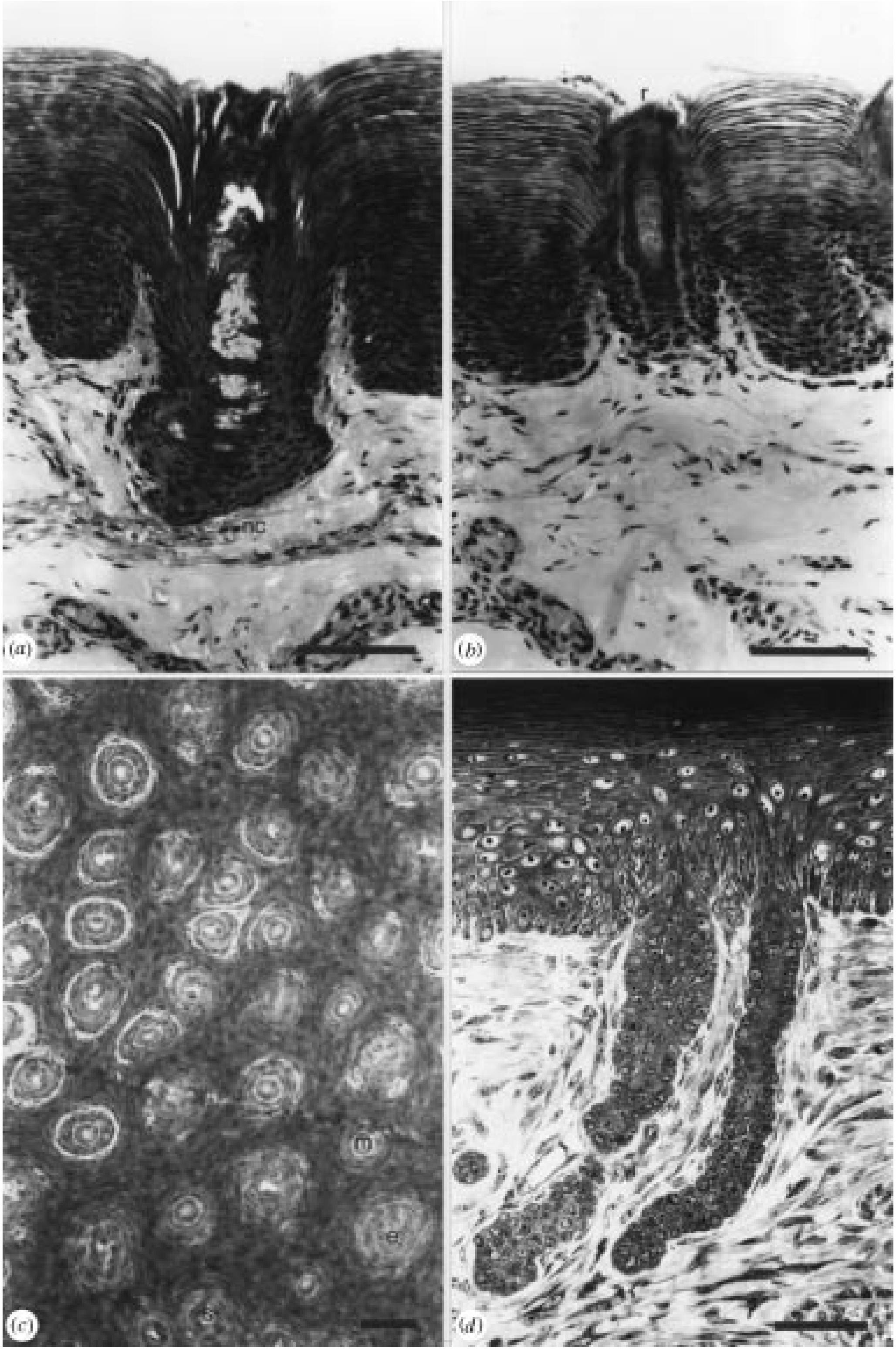

Figure 10. (*a–c*) Histological sections through platypus bill skin at 6 months p.h. (*a*) Section through an electroreceptor at 6 months p.h., showing all the features of the adult electroreceptor, including a complex nerve cuff (nc) and myelinated nerve terminals. (*b*) Sections through a fully developed push-rod mechanoreceptor at 6 months p.h., showing all the features described previously for the adult platypus, including central and peripheral vesicle chains through the core of the epidermal rod (r). (*c*) Section taken parallel to the surface of the epidermis from the 6 months p.h. specimen. All structures evident in the adult platypus were found in this specimen, including the electroreceptors (e), push-rod mechanoreceptors (m) and the sensory serous glands (s). (*d*) Section taken through the epidermis of the 6 week p.h. specimen showing the appearance of the developing mucous glands. These developing glands do not show the specialization of the epidermal portions of the duct, which are found in the future electroreceptors. It is these structures that form the electroreceptors. A simple columnar arrangement of cells is seen. No duct is yet present. Scale bars, 50 µm.

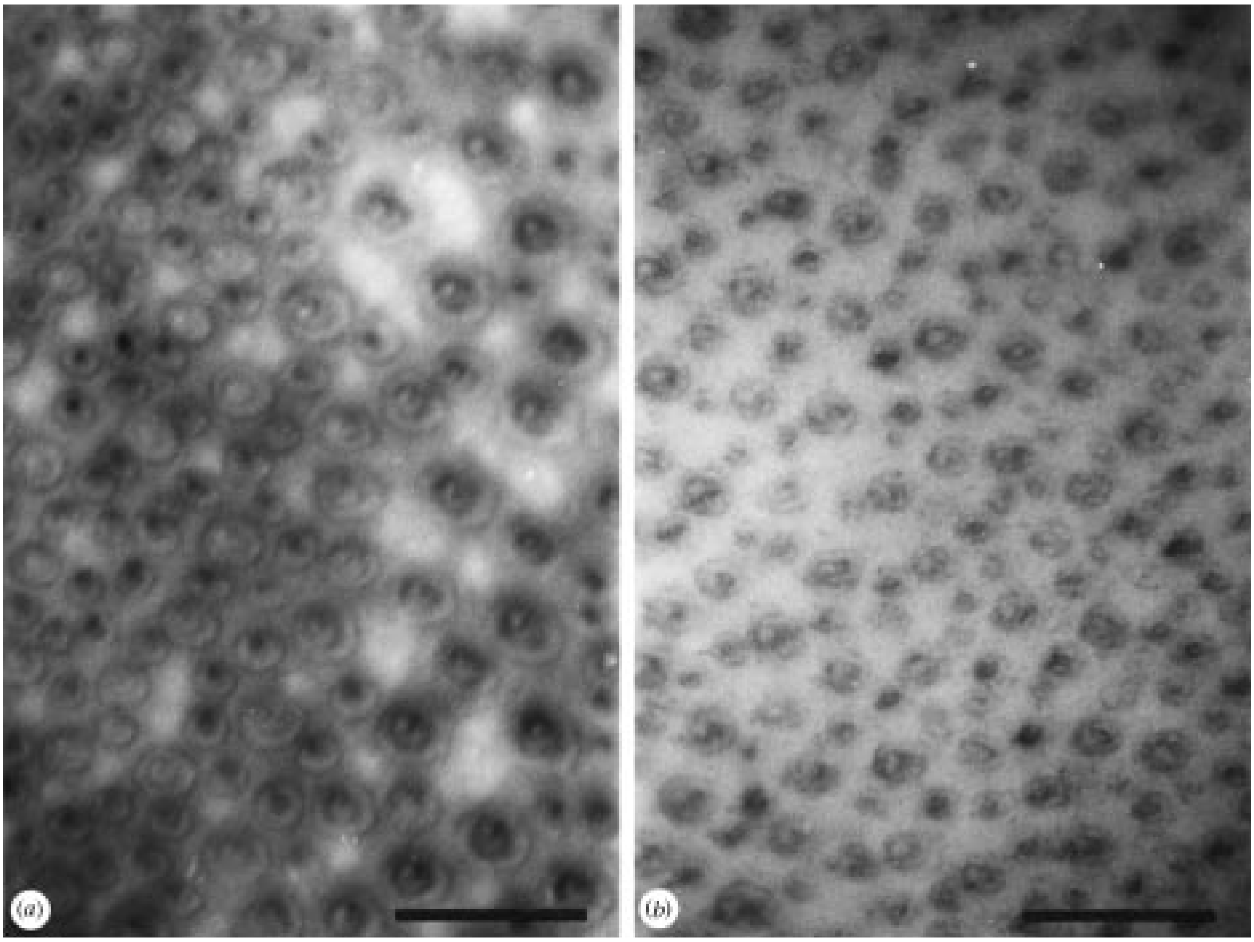

Figure 11. Microphotographs of the surface of the bill skin of the developing platypus at (*a*) 24 days p.h. and (*b*) 28 days p.h. At 24 days p.h., only future electroreceptors and developing mucous glands can be seen on the surface of the bill skin. At 28 days p.h., all sensory structures found in the adult platypus can be seen on the bill surface, these being the electroreceptors, the push-rod mechanoreceptors and the sensory serous glands. Scale bars, 250 µm.

seen in the adult platypus is achieved by the addition and alteration of stripes during development. Specifically, we have partitioned the stripes into a medial and a lateral group, which were evident at 12 days p.h., the first occurrence of the stripes. Preceding the development of stripes, at 10 days p.h., the presumptive electroreceptors were evenly distributed across the entire bill. After the development of stripes, the lateral group only undergoes one major change, the addition of an extra stripe to the lateral most part of this group. However, the medial group undergoes more changes, with many alterations, additions and subtractions of stripes from this group.

This variability of receptor distribution over development has correlates in other sensory systems. For example, in the development of lateral-line receptors in *Eigenmannia*, Vischer (1989*a*) has shown differential development of neuromasts between the head and the body, where cephalic development precedes the lateral-line development. This differential development has also been shown for the electroreceptive system of *Eigenmannia*, with a similar anteroposterior gradient of development (Vischer 1989*b*; Vischer *et al.* 1989). Gradients of change during development can also be seen in the retina of many mammals (Robinson 1991). For example, in the cat, there is a developmentally advanced region at the centre of the retina; however, over time, this developmentally advanced region becomes displaced temporally (Robinson 1987).

Despite these other examples of changes in distribution of peripheral receptors during development, neither is homologous or analogous to the case described in the present study for the platypus. As described earlier in this paper, the striped pattern of the electroreceptors in the bill skin form part of a complex processing system that allows the adult platypus to accurately and rapidly locate the origin of an electrical potential (Manger & Pettigrew 1995). One unanswered question that arises from this study is: why does the array of peripheral electroreceptors change during ontogeny?

The distribution of peripheral electroreceptors in the adult platypus surely reflects some evolutionary pressure to generate this pattern. This pressure could relate to two different possibilities: first, the type of electrical waveform, resulting from different prey items, which the platypus is detecting to find these prey items, and second, changes in the electrical parameters of the water, such as conductivity, could possibly produce conditions where a particular array of electroreceptors is more efficient at prey localization than other arrays. If this is the case, then the arrays of electroreceptor distribution seen during platypus ontogeny may reflect various arrays that at different times during the course of platypus evolution have been the most efficient at that time for the localization of prey items, the array being dependent on the electromyographic (EMG) activity of prey items and/or water conditions.

It is not unreasonable to assume that prey items of the platypus have changed over time (Archer *et al.* 1991), and with changes in morphology, or species, the 'signature' EMG waveform emitted during locomotion is likely to have changed (Taylor *et al.* 1992). In addition, during the evolutionary history of the platypus, there have been significant changes to the Australian climate. Most notable is the change from lush rainforests to a predominantly arid landscape (Archer *et al.* 1991), from which it is reasonable to conclude that changes in the physical parameters of the water associated with transmission of electrical transients have occurred. Biophysical modelling of the various arrays observed during the ontogeny of the platypus compared with those found in the adult, and how these arrays are related to the water conditions found in modern Australia, would provide useful data, not only for the modern platypus, but for understanding the variations in striping seen in the developing platypus. Further, this sort of study may help elucidate the physical properties of the water in prehistoric Australia. In addition, early platypuses may have had a less differentiated electroreceptive system, supplemented by vision. The stripes may represent a later development with extreme specialization of electroreception (stripes) and relative atrophy of vision (the Cretaceous–Tertiary boundary event may have eliminated 'platypuses' that depended too much on vision in the long dark period, and 'platypuses' with better electroreception may have been selected for).

(b) *Numbers of electroreceptors during development and the period of cell death*

The second major finding of importance is the observed changes in numbers of electroreceptors during development. Briefly, electroreceptors first appeared at 10 days p.h., and there is a marked rise in their number until sometime between 24 and 28 days p.h., when a sharp decline in numbers is seen. After this the numbers of electroreceptors rise until the full adult complement is reached.

The period of development between post-hatching days 24 and 28 is coincident with the death of large numbers of presumptive electroreceptors. Furthermore, this period of death is coincident with a change in the gross morphometric development of the bill (Manger, Hall & Pettigrew, this issue). Such large-scale cell death is seen in many vertebrate and invertebrate systems (Glücksmann 1951; Saunders 1966; Hurl 1988) and has been the focus of frequent study in the nervous system (Oppenheim 1991). A general hypothesis of large-scale cell death proposes that the function that it performs is that of an adaptive function during the development of an organism. Periods of death in the development of the electrosensory periphery of *Eigenmannia* have been reported (Vischer 1989*b*). Two different examples of death were noted for *Eigenmannia*. First, the sensory cells of the tuberous organs were seen to have a period where the average number of cells per organ decreased before again increasing in number to reach the adult complement. Second, during the first stage of cell proliferation, there was a significant decrease in the number of tuberous electroreceptors identified (Vischer 1989*b*). For *Eigenmannia*, the period of decreasing numbers of tuberous electroreceptors is coincident with the initial period of increasing numbers of sensory cells per organ. The second example of cell death in *Eigenmannia* is analogous to the cell death seen in the platypus, i.e. the loss of the entire receptor complex. As with the platypus, the loss of receptor complexes in *Eigenmannia* is extremely large. Cell death is also observed in the development of the retina (Young 1984; Robinson 1991), especially so in the ganglion cell layer, where approximately 10% of the cells located in this layer, in the mouse, are lost during development.

The rationale of cell death during development is still not understood, although some of the mechanisms behind this phenomenon are coming to light. Of most interest to the present study is the fact that cell death in the nervous system appears to be closely related to the maintenance of synapses (for reviews, see Oppenheim (1985, 1991)). This mechanism pertains to the observation that the death of electroreceptors is correlated to the appearance of other sensory receptor complexes during the development of the platypus. Before the appearance of other sensory structures the electroreceptors are the only sensory complexes found in the bill. Speculatively, they have the opportunity to control the targeting of the growing axons, by means that are presently unknown but probably involve trophic factors. After the appearance of other sensory complexes, the competition for the developing axons would increase, and so the developing axons would have more target choices. Many of the electroreceptors would then be lacking innervation and synapses, and may die.

The synapses referred to in the above speculation may be difficult to determine, as the platypus electroreceptor nerve terminals do not make synapses with a sensory cell, although putative connections form between these terminals (Manger *et al.* 1995). It may be these connections that are responsible for the maintenance of sensory innervation, and hence the electroreceptor complex, during development. A confounding factor in this hypothesis is the observation that the number of electroreceptors again rises after the period of death. Possibly a balance in the targeting of developing axons is achieved following an initial skew of innervation towards the newly appeared receptor complexes. Electron microscopic and immunohistological studies (e.g. Manger *et al.* 1995) of freshly acquired developing platypus tissue would help elucidate the factors causing the receptor complex death during platypus ontogeny. However, as there are no breeding colonies of platypuses, and are unlikely to be so in the future, we are limited to speculation on this issue.

(c) *Development of the lamination of the electroreceptor duct*

One of the crucial features of the peripheral electroreceptor complex in the adult platypus is the layering of the epidermal keratinocytes around the duct of the mucous gland. Within these layers, the dense zone appears to play an important part in the functioning of the adult electroreceptor (Manger *et al.* 1995). In the adult, a fine axonal projection from the electroreceptive nerve terminal pierces the dense zone, and neural communication between terminals is also carried out in the dense zone (Manger *et al.* 1995). The dense zone, owing to the integration of the peripheral electroreceptive neural circuitry, constitutes one of the most important aspects of the functioning electroreceptor. The lamination of the epidermal portion of the duct is not noticeable histologically until 6 weeks p.h., despite the presumptive electroreceptors being observed at much earlier times of development. Interestingly, this initial layering is not as complex as that found in the adult, and it is not until 11 weeks p.h. that the complexity of layering seen in the adult platypus is approximated by the developing young. It is therefore possible to assume that it is not until this time that the electroreceptors of the developing platypus have the possibility of functioning in a similar manner as the adult electroreceptors.

(d) *Development of the innervation of the electroreceptors*

The first developmental stage examined histologically in this study, 28 days p.h., demonstrated poorly defined, unmyelinated axons in the region of the future nerve cuff. However, it is unclear if nerve terminals have developed at this stage. At 6 weeks p.h., the unmyelinated axons can be more clearly seen, and occasional unmyelinated nerve terminals were evident. The nerve cuff becomes more distinct and demonstrates intricate neural sheathing by 11 weeks p.h. It was not until 6 months p.h. that any myelinated nerve terminals were found associated with the electroreceptor organ. Therefore, it is not until sometime between 11 weeks and 6 months p.h. that the anatomical array of the developing electroreceptors approximates closely enough that of the adult (see above discussion on lamination also) to be able to state that they are indeed functional in a similar manner to that of the adult platypus. This timing is also coincident with the striped array of electroreceptors forming a close approximation of that found in the adult.

Thus, it can be assumed, with some degree of confidence, that the electroreceptive system of the developing platypus is not functional, at least in the manner of the adult, until the platypus is at least 3–4 months of age. This age correlates to the time when the developing platypus is ready to leave the nesting burrow, which has been reported to occur sometime between 3 and 6 months after hatching (Griffiths 1978). This observation, that the electroreceptive system of the platypus is not functional, in the same manner as the adult, until the platypus is ready to leave the burrow, has correlates in other sensory systems. For example, the developing visual system of a range of mammals only becomes responsive to light at the time of eye opening (Dreher & Robinson 1988). This correlates to the present finding, where the electroreceptive system putatively becomes responsive to electrical stimuli, in the same manner as the adult, at the time the platypus leaves the burrow and enters the water for the first time. The complicated cytoarchitectural and physiological features of the bill representation in the adult platypus cortex (Krubitzer *et al.* 1995; Manger *et al.* 1996*a*) are probably refined following sensory experience.

We cannot dismiss the possibility that the developing electroreceptive system may provide some sensory function to the nestling young. This possibility is supported by some experimental evidence that a 20-day-old pouch young echidna will respond vigorously to electrical stimuli in the form of a coil placed around the end of the beak (P. R. Manger and R. L. Hughes, unpublished observation). Exactly what function the system may perform is unclear. Putative electroreceptors do not appear before the platypus is at least 10 days p.h. Burrell (1927, p. 184) states: 'The most remarkable and mysterious feature about the baby platypus is that it is not suckled at all by the mother for some days after hatching, for the very good reason that the maternal mammary glands are not yet actively functional. Investigations of this extraordinary phenomenon have advanced far enough to place the matter beyond doubt.' Burrell (1927, p. 185) furthers this by stating: 'An examination of a considerable series of mammary glands from nursing mothers which have been collected with their young has convinced me that during the first week, at least, after hatching there cannot be more than a very slight milk-secretion, if any at all, and I think this characteristic applies to the echidna also.' Griffiths (1978) strongly refutes Burrell's claim, and provides evidence that the echidna suckles shortly following hatching. We tend to agree with Griffiths' view, that it would be basically impossible for the newly hatched platypus to survive for a period of a week without suckling, although the observations of Burrell combined with the appearance of electroreceptors at sometime between 7 and 10 days p.h. is an interesting coincidence nonetheless.

This leads to the speculative function of the developing electroreceptive system. The adult platypus uses the electroreceptive system for locating food. It is not, therefore, a leap of faith to presume that if the electroreceptive system is functional in the developing platypus it is used in a similar manner. In this case the nestling platypus would use its electroreceptive system to locate the mammary region on the ventral surface of the nursing mother. For this to occur either the metabolic activity of the mammary gland must produce a large enough bioelectric potential to be detected by the young platypus, or the nursing mother may use a signal, such as contraction of fibres of the panniculus carnosus muscle over the mammary region to attract the young platypus. The second possibility is strengthened by the fact that the platypus retains an articulated and moveable epipubic bone (Griffiths 1978). However, all this speculation could be verified by the opportunity to observe and undertake behavioural and physiological experiments on the developing and nursing platypus.

(e) *Differential developmental timing of epidermal sensory structures*

Although the histological details of the other epidermal structures found in the bill skin of the platypus were not investigated in detail in the present study, the timing of the appearance of these receptors was noted. Both the push-rod mechanoreceptor and the serous sensory gland were found to appear much later in development than the mucous gland electroreceptors. These receptors were most apparent in sections taken parallel to the surface of the epidermis and in high-power photography of the surface of the bill skin. These other sensory structures were first noted at 28 days p.h. This late appearance warrants discussion from two different aspects. First, the differential timing of appearance of the sensory receptors, and second, that the appearance of the second set of sensory receptors is coincident with the massive loss in numbers of the first set of sensory receptors to appear (see § 4b). Further to this, this death is coincident with a change in the gross morphometric development of the bill (Manger, Hall & Pettigrew, this issue).

The sensory structures in the bill of the platypus appear at two different times. Initially, at 10 days p.h., the primordia of the mucous gland electroreceptors appears. It is not until 28 days p.h. that the other sensory structures, the push-rod mechanoreceptor and serous sensory gland, appear. This differential timing of appearance of sensory structures in the sensory epithelium has correlates in other sensory systems. Vischer (1989*b*) noted that the three sensory structures found in the skin of *Eigenmannia*, mechanoreceptors, tuberous electroreceptors and ampullary electroreceptors, appeared at different times during development. The mechanoreceptors of *Eigenmannia* were found to appear very early in development, four days before the appearance of the tuberous electroreceptors, which in turn appeared one day before the ampullary electroreceptors. The sensory structures of the mammalian retina, rods and cones, are also seen to develop at different times. The cone photoreceptors appear significantly earlier than the rod photoreceptors (Robinson 1991).

The exact reason for the disparate appearance of the sensory receptors is unclear. However, it has been proposed for the retina that the cones are phylogenetically older structures than the rods (Reichenbach & Robinson 1995). This argument is based around Haeckel's (1905) biogenic law, that 'ontogeny recapitulates phylogeny'. Whether this argument applies to the platypus is a conclusion that cannot be made from the present study, or indeed any study of modern platypus. However, if mucous gland electroreceptors were phylogenetically older than the other sensory structures, then one speculation of interest can be made. This speculation would be that the stem monotreme would be in possession of an electroreceptive system. This is supported by the fact that all extant monotremes possess an electroreceptive system, despite having differing degrees of complexity (Andres & von During 1988; Andres *et al.* 1991; Manger & Hughes 1992; Manger & Pettigrew 1996; for a review, see Manger *et al.* (1996*b*)). This speculation may prove interesting for palaeontological observations of ancestral platypus body forms, natural history and habitat use (Archer *et al.* 1991).

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REFERENCES

Andres, K. H. & von During, M. 1988 Comparative anatomy of vertebrate electroreceptors. *Prog. Brain Res.* **74**, 113–131.

Andres, K. H., von During, M., Iggo, A. & Proske, U. 1991 The anatomy and fine structure of the echidna, *Tachyglossus aculeatus*, snout with respect to its different trigeminal sensory receptors, including the electroreceptors. *Anat. Embryol.* **184**, 371–393.

Archer, M., Hand, S. & Godthelp, H. 1991 *Riversleigh, the story of animals in ancient rainforests of inland Australia*, pp. 85–89. Sydney: Reed.

Burrell, H. 1927 *The platypus*. Sydney: Angus & Robertson.

Dreher, B. & Robinson, S. R. 1988 Development of the retinofugal pathway in birds and mammals: evidence for a common timetable. *Brain Behav. Evol.* **31**, 369–390.

Glücksmann, A. 1951 Cell deaths in normal vertebrate ontogeny. *Biol. Rev.* **26**, 59–86.

Gregory, J. E., Iggo, A., McIntyre, A. K. & Proske, U. 1988 Receptors in the bill of the platypus. *J. Physiol.* **400**, 349–366.

Griffiths, M. 1978 *The biology of monotremes*. New York: Academic Press.

Haeckel, E. 1905 *The evolution of man*. New York: Putnam's.

Hughes, R. L. & Hall, L. S. 1988 Structural adaptations of the newborn marsupial. In *The developing marsupial. Models for biomedical research* (ed. C. H. Tyndale-Biscoe & P. A. Janssens), pp. 8–27. Berlin and Heidelberg: Springer.

Hurle, J. M. 1988 Cell death in developing systems. *Meth. Achiev. Exp. Pathol.* **13**, 55–86.

Krubitzer, L. A., Manger, P. R., Pettigrew, J. D. & Calford, M. B. 1995 Organization of somatosensory cortex in monotremes: in search of the prototypical plan. *J. Comp. Neurol.* **351**, 261–306.

Manger, P. R. 1994 Platypus electroreception: neuroethology of a novel mammalian sensory system. PhD thesis, University of Queensland, Australia.

Manger, P. R. & Hughes, R. L. 1992 Ultrastructure and distribution of epidermal sensory receptors in the beak of the echidna, *Tachyglossus aculeatus*. *Brain Behav. Evol.* **40**, 287–296.

Manger, P. R. & Pettigrew, J. D. 1995 Electroreception and the feeding behaviour of platypus (*Ornithorhynchus anatinus*: Monotremata: Mammalia). *Phil. Trans. R. Soc. Lond.* B **347**, 359–381.

Manger, P. R. & Pettigrew, J. D. 1996 Ultrastructure, number, distribution and innervation of electroreceptors and mechanoreceptor organs in the bill skin of the platypus, *Ornithorhynchus anatinus*. *Brain Behav. Evol.* **48**, 27–54.

Manger, P. R., Pettigrew, J. D., Keast, J. R. & Bauer, A. 1995 Nerve terminals of mucous gland electroreceptors in the platypus (*Ornithorhynchus anatinus*). *Proc. R. Soc. Lond.* B **260**, 13–19.

Manger, P. R., Calford, M. B. & Pettigrew, J. D. 1996*a* Properties of electrosensory neurons in the cortex of the platypus (*Ornithorhynchus anatinus*): implications for processing of electrosensory stimuli. *Proc. R. Soc. Lond.* B **263**, 611–617.

Manger, P. R., Collins, R. & Pettigrew, J. D. 1996*b* Histological observations on presumed electroreceptors and mechanoreceptors in the beak skin of the long-beaked echidna, *Zaglossus bruinjii*. *Proc. R. Soc. Lond.* B **264**, 165–172.

Oppenheim, R. W. 1985 Naturally occurring cell death during neural development. *Trends Neurosci.* **8**, 487–493.

Oppenheim, R. W. 1991 Cell death during development of the nervous system. *A. Rev. Neurosci.* **14**, 453–501.

Reichenbach, A. & Robinson, S. R. 1995 Phylogenetic constraints on retinal organisation and development. *Prog. Ret. Brain Res.* **15**, 139–171.

Robinson, S. R. 1987 Ontogeny of the area centralis in the cat. *J. Comp. Neurol.* **255**, 50–67.

Robinson, S. R. 1991 Development of the mammalian retina. In *Neuroanatomy of the visual pathways and their development* (ed. B. Dreher & S. R. Robinson), pp. 69–128. Macmillan.

Saunders, J. W. 1966 Death in embryonic systems. *Science* **154**, 604–612.

Scheich, H., Langner, G., Tidemann, C., Coles, R. B. & Guppy, A. 1986 Electroreception and electrolocation in platypus. *Nature* **319**, 401–402.

Taylor, N. G., Manger, P. R., Pettigrew, J. D. & Hall, L. S. 1992 Electromyogenic potentials of a variety of platypus prey items: an amplitude and frequency analysis. In *Platypus and echidnas* (ed. M. L. Augee), pp. 216–224. Sydney: The Royal Zoological Society of New South Wales.

Vischer, H. A. 1989*a* The development of lateral-line receptors in *Eigenmannia* (Teleostei, Gymnotiformes). I. The mechanoreceptive lateral-line system. *Brain Behav. Evol.* **33**, 205–222.

Vischer, H. A. 1989*b* The development of lateral-line receptors in *Eigenmannia* (Teleostei, Gymnotiformes). II. The electroreceptive lateral-line system. *Brain Behav. Evol.* **33**, 223–236.

Vischer, H. A., Lannoo, M. J. & Heiligenberg, W. 1989 Development of the electrosensory nervous system in *Eigenmannia* (Gymnotiformes). I. The peripheral nervous system. *J. Comp. Neurol.* **290**, 16–40.

Young, R. W. 1984 Cell death during differentiation of the retina in the mouse. *J. Comp. Neurol.* **229**, 362–373.