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Ontogeny of a Macroevolutionary phenotype: The External Cheek Pouches of Geomyoid Rodents

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#### ONTOGENY OF A MACROEVOLUTIONARY PHENOTYPE: THE EXTERNAL CHEEK POUCHES OF GEOMYOID RODENTS

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There is currently much interest among developmental and evolutionary biologists in the ontogenetic bases of morphological transformations during evolution (Alberch et al., 1979; Maderson et al., 1979; Presley, 1984). This is particularly true of macroevolutionary traits, which differ from their primitive homologues to the extent that the transformation from one to the other is difficult to explain (e.g., the evolution of the mammalian middle ear ossicles from the reptilian postdentary and quadrate bones). Such derived character states are often used to delineate higher taxa (groups of organisms above the species level). The debate that was made controversial by Goldschmidt (1940) over whether the evolutionary processes that produce macroevolutionary patterns differ from those that produce microevolutionary patterns (e.g., geographic variation in pelage color) has continued, in modified form, to the present (Bock, 1979; Gould, 1979; Charlesworth et al., 1982).

Geomyoid rodents (families Geomyidae [pocket gophers] and Heteromyidae [kangaroo rats and their allies]) are distinguished from other Rodentia in having fur-lined cheek pouches that open outside the mouth (Fig. 1). By contrast, the internal cheek pouches found in certain squirrels (family Sciuridae) and in New and Old World mice (Cricetidae and Muridae, respectively) open into the oral cavity and are lined with buccal

epithelium. Both kinds of pouches are used to store food temporarily (e.g., seeds) that is collected during foraging bouts. External cheek pouches are a macroevolutionary trait, the origin of which has been the subject of some discussion. Previous workers have hypothesized that external pouches evolved from a fold in the facial epithelium (Chiasson, 1954; Lackey, 1967; Long, 1976) or from internal pouches (evaginated buccal epithelia), either by the development of a secondary, external opening followed by loss of the internal opening or by a "developmental inversion" (Long, 1976), the exact mechanism for which is uncertain. In this paper, we demonstrate that external pouches are derived during ontogeny from the buccal epithelium, but in a simpler manner than has been previously hypothesized. We argue, on the basis of the developmental data, that the external pouch evolved from an internal pouch (i.e., that the common ancestors of living geomyoids possessed internal pouches as adults) and that this transformation can be explained by a small developmental change with a major phenotypic effect.

#### MATERIALS AND METHODS

We studied the cheek pouches in developmental series of a pocket gopher (*Thomomys bottae*) and three species of kangaroo rat (*Dipodomys merriami*, *D. elephantinus*, and *D. panamintinus*), which were obtained from pregnant females collected in California's Mojave Desert. We examined 60 individuals, 24 of which were sectioned for histological analysis. We also sectioned

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FIG. 1. Photograph of neonatal (approximately 30 days of age) *Dipodomys elephantinus*, showing the position of the external pouch, which is similar to that in adults. Arrows point to the anterior opening lateral to the mouth, and the dashed line shows the extent of pouch development beneath the skin.

three embryos each of the least chipmunk (*Eutamias minimus* [family Sciuridae]), which has internal pouches, and the house mouse (*Mus domesticus*, family Muridae), which lacks pouches of either kind.

Individuals were assigned to stages on the basis of external features, using Theiler's (1972) standard for the house mouse. They were then fixed in formalin and embedded in paraffin using standard histological procedures (Humason, 1979). Most of the specimens that were examined histologically were sectioned in the transverse plane (i.e., vertically across the snout), and embryos showing early pouch development were sectioned in frontal and sagittal planes to provide an accurate three-dimensional picture of the developing pouch.

#### RESULTS

External cheek pouch development is divisible into three continuous steps, which are summarized in Figure 2.

i) *Buccal evagination.*—The earliest sign of cheek pouch development is a ventro-lateral evagination of oral epithelium into the facial mesenchyme, which is first observed in stage 19 or 20 individuals (the equivalent of age 11.5 or 12 postconception in the house

mouse). The evaginated region extends caudally 60–90  $\mu\text{m}$  from the corner of the mouth (Figs. 2B, 3).

ii) *Pouch externalization and growth.*—The evaginated epithelia are closely apposed posteriorly but are fully separated anteriorly (Fig. 3), where they expand rapidly in the medial, dorsal, and ventral directions. Externalization of the evaginated epithelium (the presumptive pouch) from the oral cavity coincides with the appearance of the snout. The snout develops by a thickening of the facial epithelium, including the lips, which form medial to the evaginated corner of the mouth, resulting in the origin of the presumptive pouch's external opening (Figs. 2C, D and 4). The epithelium of the mouth opening participates in the evagination, leading to the transformation of what initially appeared to be the corner of the mouth into the external pouch opening, as the true corner of the mouth forms medial to it. Comparison of such individuals (see Fig. 2C) with older individuals (including adults) reveals that externalization of the external pouch is complete at this time. The continuity of the anterior pouch and buccal epithelia persists in adults but is greatly modified by the normal growth and development of the face. Thus, the developing external pouch "escapes" the mouth cavity without requiring any novel developmental events.

Concurrent with its early development, the pouch grows rapidly into the facial mesenchyme between the face and the buccal cavity. This growth occurs at the pouch's ventral, dorsal, and posterior margins by a solid plate of epithelial cells (Fig. 4). The anterior growth of the snout is accompanied by a change in the orientation of the pouch from ventro-lateral to vertical (Figs. 3, 4). This change in shape probably results from a compressive force on the pouch generated by the growing snout, to which the pouch is connected dorsally and ventrally.

iii) *Differentiation of hair follicles.*—In the gopher, hair follicles appear in the pouch and ventral neck region during the same time period (between 23 and 31 days postpartum), indicating that the induction of the pouch epithelium to develop hair occurs either directly by the mesoderm of the face, or by a wave-like cellular communication initiated anteriorly between the pouch and facial epithelia. Two observations argue in favor of the latter mechanism: the timing of hair-follicle development in the external pouch occurs in an anterior to posterior sequence; and the posterior regions of internal pouches occupy a similar position, relative to the facial mesoderm, as external pouches, yet lack fur.

#### DISCUSSION

Cheek pouches are thought to have evolved independently in geomyoids, sciurids, and cricetids (i.e., the absence of a cheek pouch is the primitive condition among rodents) (Chiasson, 1954; Ryan, 1986). The external and internal pouch are alternative derived states, which have evolved independently in these three taxa; in each case, the pouch develops by an evagination of the buccal epithelium. The evaginating pouch rudiment is absent from embryos of the house mouse; in the chipmunk (examined by us) and hamster (Hardy et al., 1986), it originates from the buccal epithelium of the anterior mouth cavity. The evolutionary history of a character is not always directly reflected in its

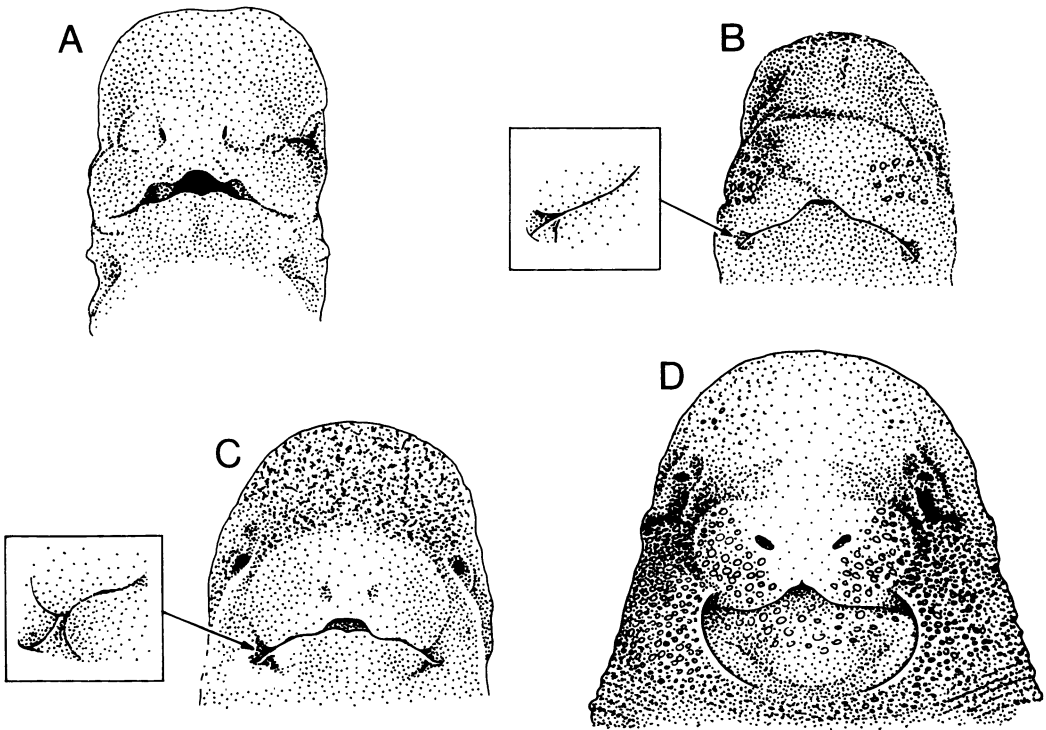


FIG. 2. Four stages in the development of the geomyoid external pouch. Stages (Theiler, 1972) and ages given for A–C are those for development in the house mouse. A) Evagination of the buccal epithelium commences but is not yet evident externally (stage 19–20, age 11.5–12 days postconception). B) The buccal evagination appears externally as a lateral extension of the mouth (see inset; stage 21, age 13 days postconception). C) Externalization of the pouch coincides with the development of the snout. The inset shows that the corner of the mouth develops medial to the evagination. The evagination is still oriented laterally; see also Figure 3 (stage 22, age 14 days postconception). D) The morphogenesis of the pouch is now complete. Its orientation is now vertical, as in adults (perinatal pocket gopher; approximately 19 days of age).

ontogeny, but the fact that the development of external pouches is initially very similar to that of internal pouches suggests that the external pouch was derived during phylogeny from an internal pouch. Because internal pouches are not found in living geomyoids, the change responsible for pouch externalization can only be inferred from the ontogeny of internal pouches in other rodents. In all three taxa, the epithelial evagination is continuous with the epithelium of the corner of the mouth, yet only in geomyoids does the corner of the mouth itself participate in the evagination. Thus, externalization appears to have resulted from an anterior shift in the location of the evagination to include the lip epithelium, or from a change in the direction of the evagination. We hypothesize that the external pouch is a threshold character, a discontinuous character produced by continuous variation in its developmental control parameters (e.g., the location and extent of the epithelial evagination; see also Alberch [1980 Fig. 9]). Despite some unavoidable uncertainty in the details, it is evident that a small change in the pattern of epithelial evagination is a sufficient developmental mechanism to explain the evolution of an external pouch from an internal pouch.

This study provides an example of how a seemingly

small change in the pattern of evagination, which is a ubiquitous epithelial behavior early in mammalian development (Goedbloed, 1964), can produce a large phenotypic change in adults (externalization of the pouch). The origin of an external pouch may have been a fortuitous outcome of variation in the location or direction of the buccal evagination. The likely selective advantage of an external pouch over an internal pouch is that it conserves body water that would otherwise be lost when seeds are passed through the mouth and later cached (Long, 1976). That water conservation was important early in the evolution of these granivorous rodents is supported by studies of their comparative physiology (MacMillen and Hinds, 1983). External cheek pouches are also typically larger in size than internal pouches (an exception involves the similarly large internal pouches of the Asian cricetid *Phodopus sungorus* [Vorontsov, 1979]). Although the large size of external pouches is probably adaptive (due to increased foraging efficiency and reduced risk of predation), we see pouch expansion as a secondary adaptive modification following its externalization.

Furring of the pouch epithelium also contributes to the water-conserving function of the external pouch, and therefore is also adaptive. However, an important



FIG. 3. Transverse section across the snout of *Dipodomys panamintinus* (Theiler [1972] stage 22, age 14 days postconception in the house mouse), showing continuity of buccal cavity (BC) and the presumptive anterior opening (AP) of the pouch rudiment. (HF: hair follicle; MC: Meckel's cartilage; MN: mandible; NC: nasal cavity; NS: nasal septum; T: tongue.)



FIG. 4. Transverse section across the snout of *Thomomys bottae* (Theiler [1972] stage 23, age 15 days postconception in the house mouse) immediately anterior to the corner of the mouth showing: 1) the change in the size and shape of the pouch (compare with Fig. 3), 2) the persistent continuity of the pouch and buccal epithelia across the developing lips, and 3) the solid plate of pouch epithelial cells (EC) growing into the facial mesenchyme.

distinction to be made is whether furred pouches evolved from external pouches with a buccal epithelium or were a direct result of pouch externalization due to an inductive interaction resulting from the novel juxtaposition of the pouch and facial epithelia. Neither hypothesis can be ruled out at present, but we favor the latter for two reasons: 1) the inductive interaction appears to come from the face, since follicle development in the pouch epithelium occurs in an anterior-to-posterior wave that is initiated where the pouch and facial epithelia are in contact; and 2) previous experiments have clearly shown that epithelia, even differentiated epithelia, exposed to novel inductive environments can form alternative structures. For example, differentiating avian corneal epithelium forms scales or feathers when grafted to the mesenchyme beneath scaled or feathered ectoderm (Coulombre and Coulombre, 1971), and developing vibrissa follicles in fetal mouse skin undergo glandular morphogenesis when exposed to excess Vitamin A (Hardy, 1968). Tissue recombinations of buccal and facial epithelia with their alternate mesenchymes have not yet been carried out.

Microevolutionary theory holds that evolution proceeds by the accumulation of small additive changes

in the genome and their translation into phenotypic variants, upon which natural selection operates (Huxley, 1944). Developmental and evolutionary biologists have argued that this model of evolution must be modified to incorporate development (Maderson et al., 1979; Hall, 1983). An important part of the debate concerning whether current microevolutionary theory is sufficient to account for macroevolutionary patterns in morphology surrounds the issue of whether one or a few attributes of the developmental process can account for major evolutionary changes (Charlesworth, 1982; Gould, 1982). Although discontinuous variants are adequately explained by quantitative-genetic theory as threshold characters, there is currently doubt among some microevolutionists as to whether such characters are responsible for the origin of higher taxa (Charlesworth et al., 1982 p. 488). We do not equate the origin of the external pouch with the origin of the Geomyoidea, because this implies an understanding of the relationship between morphological evolution and speciation not addressed by our data. However, our data are consistent with the hypothesis that external pouches arose without the existence of an intermediate

form with both internal and external openings. The hypothesis of such an intermediate form is unnecessary, considering the simplicity of the threshold model we propose. Based on our understanding of pouch development, we cannot see how a single evagination (such as gives rise to either an external or an internal pouch) could give rise to a pouch with both external and internal openings.

This study demonstrates the potential contribution of developmental research to understanding the nature and origin of morphological gaps and points to the role development can play in generating discontinuous characters. We have shown how a simple and continuous developmental pathway produces an external pouch from an internal pouch rudiment, for which there was a plausible selective advantage (or at least for which there was no disadvantage). In these respects, our findings are consistent with important aspects of microevolutionary theory. Unfortunately, the remaining difficult questions concerning how the external pouch (and threshold characters in general) persist and become fixed in a population (e.g., did they exist for a period in a polymorphic state?; did they arise in an isolated deme and become fixed through inbreeding?) cannot be answered with the data presented here. Nonetheless, the recognition of developmental phenomena such as those operating in the development and evolution of external cheek pouches provides an important step toward bridging the traditional dichotomy between microevolution and macroevolution.

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