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A ROLE FOR AGGREGATION PHEROMONES IN THE EVOLUTION OF MAMMALLIKE REPTILE LACTATION

Current theory concerning the origin and evolution of lactation is modified only slightly from that proposed by Darwin in 1859 (see Long 1969). Long (1972) summarized the major phases as: (1) evolution in mammallike reptiles of a vascularized incubation area, following attainment of homeothermy; (2) preadaptive utilization of cutaneous secretions from such a richly vascularized area for adherence of eggs, or, more likely, for essential moisture; (3) evolution of the marsupium; (4) utilization of the secretion as food and drink, perhaps first by absorption through the yolk sac and eventually in direct lapping by the offspring; (5) evolution of suckling behavior, "improvement" of the secretion to something approaching milk, and elongation of nipples. We propose here the addition of a new hypothesis to this scenario which incorporates the use of mother-young aggregation pheromones as an intermediate step in the evolution of lactation.

At some point before or during this sequence parental care ceased to be directed solely toward the eggs and began to involve the young after hatching. Lactation is generally believed to have preceded viviparity since monotremes exhibit lactation yet are oviparous (Sharman 1965; Eisenberg 1977; Pond 1977), hence, the animals involved in the scenario presented here were probably oviparous. Further, several investigators have argued that such an adaptation probably first appeared at a therapsid grade, presumably in cynodonts, the direct ancestors of all mammals (Brink 1957; Olson 1959; Van Valen 1960; Lillegraven 1975). At this point in the evolution of therapsid care of neonates, young were very probably still relatively precocial (Case 1978). One requirement for such precocial offspring to benefit from parental care is a set of ethological mechanisms by which young could aggregate and orient toward the mother, maintaining proximity with her. We propose that chemical signaling, probably mediated by vomeronasal organ olfaction, probably played an important role in such orientation. Considering the almost universal use of chemical signaling among animals (see Shorey 1976) it would seem unlikely that therapsids did not employ pheromonal communication (Duvall 1983; Duvall et al. 1983). We are inclined to agree with Maderson and Chiu (in press) that it is time to reevaluate the role of chemoreception in the history of terrestrial vertebrates; it now seems likely that olfaction was the primary sensory modality in early tetrapod evolution.

The vomeronasal organ is present at some point in the development or life history of every extant tetrapod species examined thus far for this character (Parsons 1971) and is regarded as a homologous feature throughout tetrapod evolution (Bertmar 1981; Duvall 1983; Duvall et al. 1983). Since virtually all mammals have vomeronasal organs and the structure appears homologous through tetrapod evolution, it follows that therapsids also had vomeronasal organs. There is also strong morphological evidence for vomeronasal organs of

therapsids opening into the nasal chamber (Cluver 1971; King 1981) or the oral cavity by way of nasopalatine canals passing through the incisive foramina of the secondary palate (Duvall 1983; Duvall et al. 1983).

Pheromone-mediated mother-young aggregation has been documented in a variety of mammals, and chemical signal mediated aggregation is exceedingly common in vertebrates (Shorey 1976; Duvall 1983). For example, Mykytowycz and Ward (1971) have demonstrated a mother-young aggregation pheromone in wild rabbits. Similarly, in marsupials the young manage to find the pouch relying on olfaction (the only developed sensory system at birth) to do so (Griffiths et al. 1969; Griffiths 1978). Hunsaker and Shupe (1977) suggest that it is specifically vomeronasal olfaction which mediates this migration to the pouch. Eutherian mammals have also been shown to require functional olfactory systems to locate and attach to their mother's nipples (Kovach and Kling 1967; Hofer et al. 1976). Furthermore, release of a pup aggregation pheromone in parturient female rats has been found to be dependent on oxytocin (Singh and Hofer 1978), the neurohypophysial hormone known to cause milk let-down from mammary glands (see Norris 1980).

It is probable that olfactory orientation toward pheromones on the mother's venter is as old in an evolutionary sense as any ventral exudates with nutritional value. It seems likely that mother-young aggregation, mediated by venter-exuded pheromones, preceded and facilitated the derivation of a relatively more complex exudate such as milk. Presumably, it was the integumentary tissues that produced the aggregation factors which were modified by evolution to produce a nutrient secretion.

Consideration of this possibility provides an ethological and morphological interactive mechanism of preadaptation (or exaptation; see Gould and Vrba 1982) for perhaps the largest and least explained transition in the evolutionary sequence provided by Long (1972). Specifically, once some glandular secretion which provides moisture to the eggs is present, eventually the young themselves utilize the secretion by direct lapping. We believe that this large step and the subsequent steps regarding evolution of suckling behavior, improvement of the secretion to something approaching milk, and elongation of nipples, can be explained more satisfactorily when mother-young pheromonal communication is considered.

Tongue or lip movements often facilitate introduction of chemicals into the vomeronasal organs of extant tetrapods such as squamate reptiles (Meredith and Burghardt 1978; Duvall 1979; Halpern and Kubie 1980; Gillingham and Clark 1981) and mammals (Negus 1958; Eisenberg and Kleiman 1972; Estes 1972; Poduschka 1977). If young therapsids introduced aggregation chemical signals from the mother's venter into their vomeronasal organs via an oral or even a nasal route, it is likely that tongue and lip movement and/or some type of nuzzling of the venter facilitated chemical signal detection in therapsid young as well. Thus, once some pheromonal secretion was present on the mother's venter and the young were licking and/or mouthing the area in some way, such behavior would influence the continued evolution of the glands providing the secretions, the apparatus for ingesting secretions, and would itself be affected by the changing morphologies. Central to our argument is the concept that behavioral events can

provide potent selective pressures to alter an animal's morphology (Colbert 1958; Schaeffer 1968; cf. Gans 1979). Some such ethological-morphological system of coevolution could lead to what we now observe as suckling and lactation in extant mammals.

As noted by Darwin (1872), "The development of the mammary glands would have been of no service, and could not have been effected through natural selection, unless the young at the same time were able to partake of the secretion. There is no greater difficulty in understanding how young mammals have instinctively learned to suck the breast, than in understanding how unhatched chickens have learned to break the egg shell" (p. 213). We believe that our hypothesized role for chemical signaling in the derivation of lactation provides added parsimony to any explanation for the evolution of the mosaic of morphological and behavioral characters required for mammalian lactation.

In conclusion, we propose a modification of Long's (1972) argument to take into account an exaptive function of mother-young aggregation pheromones and interactions in therapsids. Specifically, we hypothesize the: (1) evolution in mammal-like reptiles of a vascularized incubation area following attainment of homeothermy; (2) preadaptive utilization of cutaneous secretions from such a richly vascularized area for adherence by eggs, or, more likely for essential moisture; (3) cooptation of cutaneous secretions from the richly vascularized area as pheromones for mother-young aggregation, probably introduced into the vomeronasal organ via an oral route; (4) cooptation of the pheromonal secretions for food and drink through ingestion during lingual and/or labial contact; and (5) a coevolution of ingestion efficiency, nutritive/moisture supplying qualities of the secretions, and delivery efficiency (i.e., nipple formation).

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