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- Levins, R. 1965. Theory of fitness in a heterogeneous environment. V. Optimal genetic systems. *Genetics* 52:891-904.
- . 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton, N.J. 120 p.
- Lewontin, R. C. 1969. The meaning of stability. *Brookhaven Symp. Biol.* 22:13-24.
- MacArthur, R. H. 1969. Patterns of communities in the tropics. *Biol. J. Linnean Soc.* 1:19-30.
- Mayr, E. 1954. Change of genetic environment and evolution. P. 157-180 *in* J. Huxley, A. C. Hardy, and E. B. Ford [ed.], *Evolution as a process*. Allen & Unwin, London.
- . 1963. *Animal species and evolution*. Belknap, Cambridge, Mass. 797 p.
- Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Symp. Biol.* 22:82-95.
- Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with Protozoa. *Ecology* 50:362-371.
- van der Pijl, L., and C. H. Dodson. 1966. *Orchid flowers, their pollination and evolution*. Univ. Miami Press, Miami.
- Vetukhiv, M. 1954. Integration of the genotype in local populations of three species of *Drosophila*. *Evolution* 8:241-251.
- Wallace, B., and M. Vetukhiv. 1955. Adaptive organization of the gene pools of *Drosophila* populations. *Cold Spring Harbor Symp. Quant. Biol.* 20:303-310.
- Watkins, R., and L. P. S. Spangelo. 1968. Components of genetic variance in the cultivated strawberry. *Genetics* 59:93-103.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42:207-264.
- Wilson, E. O. 1958. Patchy distribution of ant species in New Guinea rain forests. *Psyche* 65:26-38.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. 6th Int. Congr. Genet., Proc. 1:356-366.

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ENDOTHERMY, SMALL SIZE, AND THE ORIGIN OF MAMMALIAN REPRODUCTION

These comments were stimulated by Long's (1972) recent note on the origin of lactation. My purpose is to suggest that the origin of mammalian reproduction may be viewed as the consequence of selection for two non-reproductive factors in the ancestors of mammals: (1) endothermy and (2) small body size. These two factors led to what I believe are the basic elements of the mammalian mode of reproduction. Viviparity, though usually considered to be the central element of mammalian reproduction, was in fact one of the last elements in a syndrome of reproductive adaptations to have evolved in mammals. The egg-laying monotremes possess the main

reproductive adaptations which set mammals so strikingly apart from *all* living reptiles. Viviparity was a natural, but secondary, consequence of an earlier shift in reproductive strategy. The origin of lactation, as discussed by Long, was one element of this shift.

If the typical reptilian reproductive adaptations are compared with those of egg-laying mammals, the main differences are:

Reptile	Mammal
1. Large egg with large energy content	1. Small egg with small energy content
2. Self-sufficient hatchling	2. Immature, dependent hatchling
3. Little or no parental care	3. Elaborate parental care

My thesis is that the origin of these mammalian adaptations was a consequence of selection for the improvement of endothermy and for smaller adult body size in the immediate ancestry of mammals. In developing this thesis I have drawn on a similar argument advanced by Dawson (1962) for the origin of altricial young in small birds.

Paleontologists are generally agreed that the cynodont therapsid ancestors of mammals possessed a useful degree of endothermy (e.g., Parrington 1967; Crompton 1968), and it is well documented that the earliest known mammals (morganucodontids and kuehneotheriids of the Late Triassic [Parrington 1971]) were comparable in size to the smallest living mammals. There is good evidence to suggest that early mammals were nocturnal (Jerison 1971), which indicates that they must have relied primarily on endogenous heat production to maintain an elevated body temperature. Because metabolic rate varies inversely with body size, the trend toward smaller size, which led from cat-sized Late Permian cynodonts to mouse- or shrew-sized Late Triassic mammals, involved a progressive increase in metabolic rate within the lineage. Hair probably originated in earlier therapsids as tactile sensory structures sparsely scattered over the body surface (Long 1972; Maderson 1972). However, with progressive increase in the surface/volume ratio in the line leading to mammals, the density of hair had to increase in order to provide increasingly critical insulation that was perhaps not required in the larger ancestors. It seems likely that the very small sizes attained by Late Triassic mammals could not have evolved without the prior development of a dense pelage.

Sharman (1970) has argued that the immediate common ancestor of marsupials and placentals most likely had an oviparous type of reproduction, somewhat like that of recent monotremes. This strongly suggests that *all* Late Triassic mammals, both therian and prototherian, still laid eggs. It is well known that relative egg weight in birds varies inversely with body weight; that is, small birds tend to lay relatively large eggs (Huxley 1927). Very small birds are able to produce disproportionately small eggs, however, by reducing the amount of yolk they deposit in them. As a consequence, the young of these birds have a short development time and hatch in an

immature (altricial) state. Witschi (1956) has suggested that the ability to produce a smaller egg was a key factor in the evolution of small body size in birds. I believe the same argument can be applied to early mammals.

The production of small-yolked eggs and very small young poses energetic problems for an endotherm because at small sizes metabolic rate increases rapidly with decrease in size. If the young were as endothermic as their parents, their metabolism would have to be far higher and their energy requirements relatively far greater. Small birds and mammals solve this problem by having immature, essentially ectothermic, young with relatively low metabolic rates (see Pearson 1948). Parental care provides shelter and heat to the young in order to maintain their body temperatures at near-endothermic levels. Only when the young approach mature size do their thermoregulatory mechanisms develop fully and they become fully endothermic. Prior to this time, a relatively large proportion of the food provided by the parents is converted into protoplasm because the high maintenance costs of endothermy have been avoided (Dawson 1962).

The conclusion I draw from the consideration of the problems of egg size and energetics in small endotherms is that selection acted in early mammals to evolve: (1) progressively smaller eggs (containing less nutrient for the embryo); (2) progressively more immature hatchlings; (3) adaptations (behavioral, physiological, and morphological) for creating a warm, humid environment, first for the eggs, then for the young; and (4) special adaptations for feeding the young.

The complex of adaptations leading to the development of mammary glands now becomes important. As emphasized by Long (1972), a variant of Darwin's theory relating the origin of lactation to the incubation of eggs and young offers the best framework within which to organize the known facts. I agree with Long that an abdominal incubation area evolved in endothermic therapsids, specifically in advanced cynodonts close to the ancestry of mammals. The formation of the incubation area was probably under the control of reproductive hormones, as is the brood patch of birds (Jones 1971). This brood area may have lain in a depression in the abdomen supported by the marsupial bones (Long 1972), but for reasons given below I doubt that a true pouch was developed in the earliest mammals. Rather, I believe that the eggs and young were sheltered from the environment in a burrow or nest. Cutaneous glands, evolved in association with hair, but seasonally hypertrophied as a result of hormonal activity, moistened the brood area to prevent desiccation of the eggs and young. In the early stages of evolution, the young would have been fed on food brought by the mother, though the glandular secretions may have been licked up to provide moisture. Even partial utilization of these secretions (assuming they had minimal but positive nutritive value) would have spared the mother from having to go on food-gathering forays quite so frequently and thus from having to expose herself so often to predation. As early mammals were probably nocturnal, the shift to maternal secretions for all food needs of the young would have allowed the mother to confine her forays from the nest to optimal hunt-

ing times and would have allowed her to forage more widely before returning home. An important factor selecting for utilization of maternal secretions as food for the young is the probable primitive mammalian pattern (inherited from reptilian ancestors) of male nonparticipation in care of the young. This is a major difference between birds and mammals: in living birds participation of the male is so widespread that Kendeigh (1952) and Skutch (1957) suggest that it represents the primitive avian condition.

It has been suggested that the main features of mammalian reproduction (i.e., intensive parental care of young, including suckling) had evolved in Early Triassic cynodonts (Brink 1957), which, as already noted, were many times the size of early mammals. That this was not the case is indicated by recent work on tooth replacement patterns in cynodonts (Hopson 1971, unpublished data). Known cynodonts show continuous replacement of teeth through all or most of their lives, and even the tiniest juvenile specimens, belonging to a variety of species, possess a functional dentition. This suggests that the cynodont young resembled modern reptiles in being fully capable of obtaining and processing food directly upon emerging from the egg. Therefore, there is no evidence for elaborate maternal care in cynodonts (though it is possible that the parent provided a certain amount of protection to the eggs or young and may even have incubated the eggs, activities which occur in some living reptiles). The earliest mammals, however, show a mammalian pattern of limited (diphyodont) tooth replacement (Parrington 1971; Hopson 1971). Assuming that the drastic limitation of tooth replacement is correlated with rapid growth rates and early dependence on maternal milk for nourishment, the diphyodonty of Late Triassic mammals suggests the presence of a truly mammalian level of parental care, including suckling of the young. This interpretation derives support from the fact that this pattern is present in both monotreme and therian mammals, whose time of divergence dates from the Late Triassic (Hopson and Crompton 1969).

The time of origin of the marsupium and its relation to the origin of mammary glands and epipubic (marsupial) bones is problematical. Long argues that mammary glands originated in association with a preexisting pouch and that the presence of marsupial bones is always associated with the presence of a pouch. Mammary glands and true sucking behavior occur both in monotremes (see Griffiths 1968) and therians and are most simply interpreted as primitive features inherited from a common ancestor. On the other hand, evidence for the occurrence of a pouch in this common ancestor is equivocal at best. The appearance of the pouch before the mammary glands in marsupial ontogeny, cited by Long as evidence for the greater antiquity of the pouch, is of doubtful value because ontogeny recapitulates phylogeny only when it is developmentally useful to do so. The pouch of echidnas is often cited as being nonhomologous with that of marsupials (see Griffiths 1968), and among the latter it is absent in many of the smaller members of the primitive families Didelphidae and Dasyuridae (Walker 1968). (It is also absent in the platypus, though secondary loss as a speciali-

zation for amphibious life cannot be ruled out.) These data suggest that the echidna pouch and that of marsupials had independent origins subsequent to the origin of mammary glands. Evidence is also equivocal on the primary functional association of the epipubic bones with the pouch. Epipubic bones are fully developed in pouchless male marsupials and monotremes and in the pouchless female platypus. In both orders they provide attachment for hypaxial musculature and in the monotremes for part of the gracilis muscle (Vaughn 1956). Vaughn argues that the epipubic bones are a retention (or functional replacement) of the anterior part of the puboischiadic plate of primitive therapsids whose primary function in advanced therapsids and early mammals was the maintenance of an anterior attachment area for the gracilis as the pubic portion of the pelvis rotated posteriorly to a more mammalian position. Such an explanation is consistent with the presence of marsupial bones in tritylodontid cynodonts (Fourie 1962) because these forms possess the most mammalian pelvis of any cynodont. Their retention in marsupials, in which the gracilis takes origin mainly from the pelvis, is interpreted by Vaughn (1956) and Lillegraven (1969) as the result of a possible secondary association with the pouch. This is especially likely if, as Long has suggested, the marsupial bones functioned earlier as supporting structures for a ventral incubatorium. They are probably present in males because their absence would require a different arrangement of abdominal muscles in males and females (Kean 1966).

Living monotremes lay eggs which are extremely small relative to adult body size, and the tiny hatchlings are virtual fetuses (Griffiths 1968). Though viviparous, marsupials produce similarly immature young. This extreme fetalization of the young of monotremes and marsupials may be a direct inheritance from their common Triassic ancestor, but I believe it is more likely to represent two independent but parallel intensifications of the ancestral trend to produce altricial young. This intensification is probably correlated with the evolution of: (1) increasingly smaller eggs and correspondingly shorter incubation times (leading in therians to viviparity); (2) special protective mechanisms (pouches or, in the platypus, a well-protected nest); and (3) very rich milk allowing rapid growth rates in the young. Elimination in the therians of a yolky shelled egg which required incubation removed an inconvenient step from the reproductive cycle. However, the fact that marsupials possess an inefficient yolk-sac placenta (though a few also possess an allantoic placenta) and a gestation period which cannot exceed the length of a single estrus cycle (Sharman 1965) means that the young of necessity are born extremely immature. The pouch and uniquely specialized mammary apparatus allow the young to complete their "embryonic" development outside of the mother's body (Lillegraven 1969).

Though derived from the same ancestral therian stock as marsupials, placental mammals evolved reproductive specializations, particularly those allowing a long intrauterine life, which ultimately proved more successful than the reproductive specialization of marsupials. Small placentals usually have short gestation periods and altricial young, as I assume their early

therian ancestors did. However, a complex allantoic placenta, with secretory properties permitting the suspension of estrus and prolongation of the gestation period, has allowed many placentals to produce large precocial young. This has usually occurred in larger mammals in which metabolic rates are much lower than in small forms. Thus, endothermic placental mammals, by evolving the means for allowing the embryo to reach an advanced state of development in utero have partially reconverged upon their ectothermic reptilian ancestors in which advanced young were produced from large-yolked eggs. However, available evidence indicates that production of advanced young is not primitive for mammals, but rather is a secondary specialization developed relatively late in mammalian history. The pathways by which placental viviparity evolved can only be understood in the context of reproductive strategies related to small size and endothermy in the earliest ancestors of all modern animals.

LITERATURE CITED

- Brink, A. S. 1957. Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. *Palaeontol. Afr.* 4:77-96.
- Crompton, A. W. 1968. The enigma of the evolution of mammals. *Optima* 18:137-151.
- Dawson, W. R. 1962. Evolution of temperature regulation in birds. P. 45-71 in J. P. Hannon and E. Viereck [ed.], *Comparative physiology of temperature regulation*. Arctic Aeromed. Lab., Fort Wainwright, Alaska.
- Fourie, S. 1962. Notes on a new tritylodontid from the Cave Sandstone of South Africa. *Navorsinge Nat. Mus. Bloemfontein* 2:7-19.
- Griffiths, M. 1968. Echidnas. *Int. Monogr. Pure Appl. Biol., Zool. Div.*, 38. 282 p.
- Hopson, J. A. 1971. Postcanine replacement in the gomphodont cynodont *Diademodon*, p. 1-21. In D. M. Kermack and K. A. Kermack [ed.], *Early mammals*. *Zool. J. Linnean Soc.* 50 (Suppl. 1).
- Hopson, J. A., and A. W. Crompton. 1969. Origin of mammals. P. 15-72 in T. Dobzhansky, M. K. Hecht, and W. C. Steere [ed.], *Evolutionary biology*. Vol. 3. Appleton-Century-Crofts, New York. 309 p.
- Huxley, J. S. 1927. On the relation between egg-weight and body-weight in birds. *J. Linnean Soc.* 36:457-466.
- Jerison, H. J. 1971. More on why birds and mammals have big brains. *Amer. Natur.* 105: 185-189.
- Jones, R. E. 1971. The incubation patch of birds. *Biol. Rev.* 46:315-339.
- Kean, R. I. 1966. Marsupials. *Tuatara* 14:105-120.
- Kendeigh, S. C. 1952. Parental care and its evolution in birds. *Illinois Biol. Monogr.* 22. 356 p.
- Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *Univ. Kansas Paleontol. Contrib. Article* 50 (Vertebrates 12). 122 p.
- Long, C. A. 1972. Two hypotheses on the origin of lactation. *Amer. Natur.* 106:141-144.
- Maderson, P. F. A. 1972. When? why? and how? some speculations on the evolution of the vertebrate integument. *Amer. Zool.* 12:159-171.
- Parrington, F. R. 1967. The origins of mammals. *Advance. Sci.* 24:1-9.
- . 1971. On the Upper Triassic mammals. *Roy. Soc. (London), Phil. Trans., B.* 261:231-272.
- Pearson, O. P. 1948. Metabolism of small mammals, with remarks on the lower limit of mammalian size. *Science* 108:44.

- Sharman, G. B. 1965. Marsupials and the evolution of viviparity. P. 1-28 in J. D. Carthy and C. L. Duddington [ed.], Viewpoints in biology. Vol. 4. Butterworth, London.
- . 1970. The biology of sex in marsupials. Australian J. Sci. 32:307-314.
- Skutch, A. F. 1957. The incubation patterns of birds. Ibis 99:69-93.
- Vaughn, P. P. 1956. The phylogenetic migrations of the ambiens muscle. J. Elisha Mitchell Sci. Soc. 72:243-262.
- Walker, E. P. 1968. Mammals of the world. 2d ed. Vol. 1. Johns Hopkins Press, Baltimore. 644 p.
- Witschi, E. 1956. Development of vertebrates. Saunders, Philadelphia. 588 p.

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CANNIBALISM AND KIN SELECTION IN *LABIDOMERA CLIVICOLLIS* (COLEOPTERA:CHRYSOMELIDAE)

Intraspecific predation is not a rare occurrence in nature. Analysis of the evolutionary consequences of such behavior in *Labidomera clivicollis* reveals features possibly capable of more general application.

Labidomera clivicollis females lay clutches of up to 60 eggs (usually 15 to 30). Females mate more than once, so that individuals in a clutch may be siblings or half-sibs. Most cannibalism in this species involves the eating of unhatched eggs by newly hatched larvae. Cannibalistic behavior was observed in the field, but exact rates cannot be given. An average of 17% of the eggs were cannibalized under optimum humidity conditions in the laboratory. Similarly, 3%-5% of the first instar larvae are eaten by other larvae in the same clutch.

Superficially, cannibalistic behavior may seem maladaptive, especially where, as in this case, there is little or no competition for food (Eickwort 1971). However, the development of a cannibalistic larva is considerably accelerated, especially in the early first instar, so it is likely that the probability of survival of such larvae is enhanced. Let us examine the situation in which one newly hatched larva eats another sibling or half-sib with the same initial fitness. Since these are prereproductive individuals, let the fitness of each be represented by pf , where p is the probability of survival to adulthood and f is the potential fecundity. Assume that the cannibal's probability of survival is increased by p' , so that its new fitness is $(p + p')f$. In the absence of competition for food, we can analyze this as an interaction between these two individuals alone, the cannibal and the larva eaten. According to Hamilton (1964), the inclusive fitness of an individual will be increased, and the "selfish" trait selected for, if $-k < 1/r$. In this equation k would represent the change in fitness of the larva eaten divided by