

The origin of eutherian mammals

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Palaeontologically recognizable eutherians originated no later than the Early Cretaceous in warm, probably moderately seasonal climates. Immediate ancestors were small, sharing many anatomical, physiological and reproductive features with small modern marsupials. Development of characteristically eutherian features involved interactions of body size, rates of metabolism, energetic costs of reproduction, anatomical/physiological processes of development and effects of each upon rates of population growth. In contrast to eutherians, marsupials have a narrow range of basal metabolic rates (lacking high rates), and show no direct links between rate of energy expenditure and gestation period, postnatal growth rate, fecundity or reproductive potential. Biological implications of this contrast are most pronounced at small body sizes. When resources are abundant, the relatively higher growth rates and earlier maturation of small eutherians (particularly those with high rates of metabolism) can lead to rapid population growth; among most marsupials, however, both pre- and postnatal constraints apparently preclude attainment of such high rates of reproduction. Also, only eutherians among the amniotes combine intimacy of placentation with prolonged active intra-uterine morphogenesis. Once established, that

combination permitted (and even favoured) increases in diversity of adaptation in such disparate aspects as elevated metabolic rate, increased pre- and postnatal growth rates, increased encephalization, greater longevity, increased gregariousness, greater karyotypic flexibility, and augmented variability in adult morphology. However, all such boosts in diversity were probably secondary and dependent upon prior innovation of trophoblastic/uterine wall immunological protection of foetal tissues during prolonged intra-uterine development. Increased metabolic rates followed thereafter, with synergisms that may have speeded evolution among early eutherians. Eutherian-style trophoblast probably originated in the Mesozoic. Dependent adaptations, variably expressed, evolved later in sundry descendant lineages. Reproductive differences between marsupials and eutherians are not biologically trivial; to the contrary, breakthroughs among eutherians assured their dominance: (1) in high intensity food habits; (2) at small body masses; and (3) in very cold climates.

KEY WORDS:—Adaptation – behaviour – body size – brain – chromosomes – development – energetics – Eutheria – evolution – life history – longevity – Marsupialia – play – reproduction.

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INTRODUCTION

Living mammals are ordered into three easily-defined major groups, the oviparous monotremes, the ovoviviparous marsupials (the 'pouched mammals'), and the viviparous eutherians ('placentals'). Our summary has two main purposes. The first is to establish an hypothesis that explains the origin, during Mesozoic time, of biological specializations peculiar to eutherians; we put emphasis on *why* such innovations should have come to be, focusing on conditions during the Early Cretaceous. The second is to evaluate biological consequences of the advent of unique eutherian features in terms of increased potential for diversity. The subjects are complex, drawing pertinent comparative information from various subdivisions of the biological sciences as well as from palaeontology; thus considerable background must be provided.

Surprisingly few general anatomical or physiological differences exist between

eutherians and marsupials. Therefore, unless one postulates inordinately high levels of parallel evolution between the two groups since their Mesozoic common ancestry (the "Bursalia" of Wilson & Hill, 1897), one must accept the premise that the highly-advanced level of many features seen in living eutherians and marsupials also must have existed in mammals of the Early Cretaceous. The origins of specializations peculiar to eutherians seem to have involved interacting influences of body size, rates of metabolism, energetic costs of reproduction, anatomical/physiological innovations in processes of reproduction, and the resulting effects of each upon potentials for population growth.

By far the most significant differences between eutherians and marsupials appear in the reproductive system (Eisenberg, 1980; see McNab, 1986b, Tyndale-Biscoe & Renfree, 1987). Special emphasis, therefore, is provided to procreation as it applies to comparative energetics and, ultimately, to life histories. We begin the essay, however, with general information on relative mammalian diversities and their comparative distributions through space and geological time.

DIVERSITY AND ZOOGEOGRAPHY, PRESENT AND PAST

Significant differences in taxonomic diversity and zoogeographic distribution are seen amongst the three major groups of extant mammals. Living monotremes (sometimes called "prototherians"; see Wyss, 1987) are represented by only three monotypic genera, restricted to the Australian zoogeographic realm. Living marsupials (sometimes called 'metatherians') are much more diverse, represented in the Americas (according to Kirsch & Calaby, 1977) by 15 genera (and about 78 species) and in the Australian realm by 59 genera (and about 171 species). Living eutherians are cosmopolitan (including the world's oceans) and the most diverse, represented (according to Anderson & Jones, 1984) by about 979 genera and 3943 species. For purposes of discussion, we use the taxonomic scheme presented by Anderson & Jones (1984).

Study of the fossil record highlights greater complexity (in terms of taxonomic diversity and zoogeographic distribution) than the rather simple picture provided above for living representatives. For example, in contrast to statements by Tyndale-Biscoe & Renfree (1987: 422), marsupials are known to have inhabited *all* continents during Tertiary time, at least for restricted intervals. Even though the Cenozoic fossil record of marsupials is woefully biased (geographically and temporally) on several continents, enough is known to state confidently that they formed more than a minor part of overall mammalian diversity only on the 'island continents' of Australia, South America, and possibly Antarctica. Entry to recent literature on this subject can be gained from the following selected references: Australia (Archer, 1981; Rich, 1982; Murray, 1984; Rich & van Tets, 1985), Antarctica (Woodburne, 1984; Woodburne & Zinsmeister, 1984), South America (Marshall, 1982; Marshall & Muizon, 1984; Reig, Kirsch & Marshall, 1985), North America (Fox, 1983; Krishtalka & Stucky, 1983), Europe (Crochet, 1980), northern Africa (Bown & Simons, 1984; Crochet, 1984; Mahboubi, Ameur, Crochet & Jaeger, 1984; Simons & Bown, 1984), and central Asia (see Benton, 1985; Russell, 1985).

Mesozoic marsupials are known only from North America (Clemens &

Lillegraven, 1986; Lillegraven & McKenna, 1986; Cifelli & Eaton, 1987) and South America (Muizon, Marshall & Sigé, 1984). Biases in the palaeontological record of the Late Cretaceous, however, are so great that one can discuss Cretaceous palaeobiographical issues only with great caution (see Lillegraven, Kraus & Bown, 1979, and Woodburne, 1984).

The palaeontological record of Cenozoic eutherians (see Broadhead, 1984) is much more complete on a worldwide basis than for the marsupials, with ordinal and familial diversities reaching their peaks in Eocene time (see Lillegraven, 1972, and Rose, 1984). The fossil record of monotremes, in contrast, is poorly known, but boasts a recently discovered extension of their known existence (as an ornithorhynchid-like form) into the middle Cretaceous of Australia (Archer, Flannery, Ritchie & Molnar, 1985).

PALAEONTOLOGICAL CONSTRAINTS TO DOCUMENTATION OF THE ORIGIN OF EUTHERIANS AND MARSUPIALS

The known fossil record provides little precision about times or places of the origins of eutherians or marsupials (for a useful timescale see Kent & Gradstein, 1985). Fossil remains representing related groups are extremely scattered and fragmentary (mainly incomplete dentitions), with severe gaps in geographical and temporal representation. The summary that follows is intended to be only the barest outline of palaeontological constraints to the problem at hand, and as a guide to pertinent recent literature.

Marsupials plus eutherians are referred to as 'therian' mammals. The subclass Theria, however, also has a rich diversity of extinct 'experimental' precursors that lived during Mesozoic time (see Cassiliano & Clemens, 1979; Kraus, 1979; Freeman, 1979; Kielan-Jaworowska, Eaton & Bown, 1979; Datta, 1981; Prothero, 1981; Chow & Rich, 1982; Fox, 1982, 1984, 1985; Kielan-Jaworowska, 1982; Sigogneau-Russell, 1983b; Dashzeveg & Kielan-Jaworowska, 1984; Sigogneau-Russell, Frank & Hemmerle, 1984; Yadagiri, 1984, 1985; Cifelli & Madsen, 1986; Clemens & Lillegraven, 1986). Therians share the phylogenetically unifying feature of having their principal molar cusps arranged in a triangle (see Kermack & Kermack, 1984; Mills, 1984; Crompton & Sun, 1985) and their origin goes back to the earliest known unequivocal mammals (Sigogneau-Russell, 1983b; Fraser, Walkden & Stewart, 1985; Buffetaut & Martin, 1985) in the Late Triassic, at least 210 million years ago.

Although traditional wisdom (e.g. Marshall, 1979; Crompton & Sun, 1985) holds that monotremes have been distinct phylogenetically from therians since the very origin of Mammalia, Kemp (1983) favoured a 'eupantotherian' (i.e. a paraphyletic grade ancestral to living therians) origin for the monotremes. Archer *et al.* (1985) have described a partial mandible of a middle Cretaceous mammal (*Steropodon*) from Australia that they consider to be a possible ornithorhynchid. Its lower molars show a cusp pattern characteristic of therian-style design, thereby suggesting that *Steropodon* had a special phylogenetic relationship with therians. Kielan-Jaworowska, Crompton & Jenkins (1987), however, suggested that the cusp pattern of *Steropodon* had not achieved the tribosphenic pattern characteristic of the most advanced therians, including marsupials and eutherians. Pridmore (1985) has shown that monotreme limb postures and their movements during locomotion are most similar to those seen

in generalized therians. Similarly, Presley (1981) suggested from evidence associated with braincase development that monotremes and standard therians may have had closer ancestry than generally is considered.

Despite continuing uncertainty about the phylogenetic position of monotremes, the marsupials and eutherians share a common ancestry more recently than with any other known major groups of mammals. Although the concept of a phylogenetic separation into 'therian' versus 'prototherian' (or 'atherian') monophyletic lineages at the beginning of the mammalian radiation was once supported, new knowledge about early forms shows that the early differentiation of mammals was more complex than previously considered (e.g. see Jenkins, Crompton & Downs, 1983; Kemp, 1983; Sigogneau-Russell, 1983a; Miao & Lillegraven, 1986). Although the therian lineage appears monophyletic, the so-called 'prototherians' almost surely do not represent a phylogenetically natural group.

The oldest fossils unequivocally identifiable as eutherians are known from Cretaceous rocks of central Asia (see Kielan-Jaworowska, 1984b), though probably the ages of enclosing strata are significantly younger than is generally stated (Lillegraven & McKenna, 1986). Unfortunately, the oldest specimens (considered on questionable evidence to represent late Early Cretaceous time) are named but not adequately described (*nomina nuda*; see Kielan-Jaworowska, Bown & Lillegraven, 1979: table 12-1). A series of new genera from southwestern Asia has been named by Nessov (1985a, b), though many questions exist in regard to their affinities. Peculiar, highly-specialized forms identified as "paratherians" (see Bonaparte, 1986) from the Late Cretaceous of South America serve to emphasize the extent of our ignorance of the palaeogeographic history of advanced Cretaceous therians; they were placed within the eutherian cohort Edentata by Mones (1987).

Specifying which fossils represent the oldest known marsupials is more contentious (see Kielan-Jaworowska, 1982, for review; Fox, 1971; Slaughter, 1981), but at least pertinent specimens are adequately described. Without pursuing complexities of the issue further, the oldest unquestionably-accepted fossil marsupials are from the early Late Cretaceous (Cenomanian) Dakota Formation of southern Utah (Cifelli & Eaton, 1987). The new species is identified as a questionable early stagodontid, suggesting that even as early as the Cenomanian important diversification from presumed didelphid ancestors had occurred.

Palaeontologists are forced by the very nature of fossils to identify extinct 'marsupials' and 'eutherians' on the basis of dental/skeletal features (especially molar cusp morphology and tooth formulae) that are associated with soft-part specializations in living species of the two groups (see Kielan-Jaworowska *et al.*, 1979). Without doubt, by use of these criteria, marsupials and eutherians were distinct and palaeontologically recognizable during Late Cretaceous time. Farther back in the geological record, however, dental/skeletal specializations diagnostic of living members of either group become less obvious (or non-existent), and identifications as 'marsupials' or 'eutherians' become tenuous (see Clemens & Lillegraven, 1986).

We know of no fossils that would qualify as suitable candidates for the last common ancestor of marsupials and eutherians. Further, in some cases uncertainty exists as to which dental/skeletal features should be *expected* in such an

organism. The continent(s) on which the phylogenetic separation(s) occurred is(are) unknown, and available palaeobiogeographic evidence is so limited as to allow postulation of virtually any distributional scenario. The event(s) probably occurred after the Jurassic, because the modern molar morphology (i.e. fully tribosphenic) shared by marsupials and eutherians is unknown prior to the Early Cretaceous (see Dashzeveg & Kielan-Jaworowska, 1984). Thus the last common ancestor of marsupials and eutherians existed at least 100 million years ago (probably in the Early Cretaceous) on uncertain spot(s) of the earth's dry surface.

SEASONALITY OF THE EARLY CRETACEOUS

Seasonality profoundly influences life-history factors and reproductive patterns among living mammals (see Bronson, 1985; Boyce, 1979, 1984). Would this also have been the case in Early Cretaceous times? As summarized by Lillegraven (1974) and Lillegraven *et al.* (1979), widespread epicontinental seaways allowed an unusually large number of exchange routes between warm, tropical and cooler, northern-polar marine water masses during the Early Cretaceous. Results were warm mean annual temperatures and relatively great equability of temperatures on a world scale (also see Barron & Washington, 1982; Hallam, 1985).

Warm temperatures and high equability, however, do not necessarily imply aseasonal environments. Geological evidence alluded to by Parrish, Ziegler & Scotese (1982) and Doyle, Jardiné & Doerenkamp (1982) strongly suggests that continents during Early Cretaceous time showed local climatic differentiation. Further, seasonality (in terms of rainfall and resulting food availability) would have been a reality, even in fully tropical areas (see Leigh, Rand & Windsor, 1982). Hallam (1985) specifically emphasized the probability of widespread seasonality (even monsoonal climates) across much of the continental world during Cretaceous time. As now, seasonality in the Early Cretaceous would have influenced intertwined life cycles of plants, insects, and mammals through altering periods of precipitation, growth, food availability, and accessibility to favourable habitats. Whether due to more uniformly warmer climates or to competition/predation from their various vertebrate contemporaries, however, Cretaceous mammals seemed not to respond to stresses of seasonality by increasing body size, as obtains today among many eutherian species (see Lindstedt & Boyce, 1985). Because of the generally warmer, more equable conditions then prevailing, the influence of seasonality on reproductive cycles during the Early Cretaceous probably was less important than in today's, much colder, temperate and high-latitude realms.

THE IMPORTANCE OF BEING SMALL

In our opinion the single most important biological observation derived from the fossil record of Mesozoic mammals is that they were of small body size (Hopson, 1973; McNab, 1978c; Lillegraven, 1979a). Even though an assortment of species achieved sizes comparable, for example, to modern wolverines (*c.* 10 kg), the great majority was shrew- to rat-sized (<400 g adult body mass). During Cenozoic time, in contrast, large (marsupials and eutherians) to gigantic

(eutherians only) mammals evolved repeatedly. Even in today's world, however, most species of mammals are small. Fleming (1979) showed that of the roughly 3900 species of extant mammals, an excess of 90% are less than 5 kg as adults; such a mass would encompass the vast majority of all known species of Mesozoic mammals. Body size has been important to physiological function, with many implications for overall mammalian adaptation, including 'reproductive strategy' (used throughout our paper in a non-teleological sense).

Ecological evolutionary advantages and disadvantages of small body size (<3 kg) in mammals were summarized by Bourlière (1975). Principal advantages according to Bourlière include: (1) ready concealment from predators and low energy expenditure needed for escape; (2) wide variety of potential foods; (3) wide variety of available microhabitats; (4) potentially high rates of population increases in response to favourable environmental conditions; and (5) high potential for rapid evolutionary change in adaptation to prevailing conditions through splitting into small, localized populations.

The principal disadvantages of small body size as expressed by Bourlière include: (1) life near the energetic limits of food gathering abilities (necessitated by high costs of endothermy relative to body energy reserves); (2) short lifespans (generally less than a year under field conditions); (3) energy expenditures for locomotion over significant distances are proportionately high (but see Altmann, 1987); and (4) energetic costs of reproduction are proportionally high (species having smaller adult body size generally have offspring with relatively greater masses at weaning; Lee & Cockburn, 1985: 60). Because Mesozoic mammals were predominantly small, and the earliest identifiable marsupials and eutherians were very small (i.e. <400 g), modifications to the above types of trade-offs should be of major concern in analyses of the phylogenetic separation of marsupial and eutherian lineages.

BIOLOGICAL NATURE OF THE LAST COMMON ANCESTOR

What were the principal features of biological consequence that existed in the last common ancestor between eutherians and marsupials? Although existence of most items on the list that follows cannot be 'proven' by direct examination of fossils, comparative studies of living representatives provide bases for highly probable interpretations. As discussed above, however, the fossil record provides direct information that nearly all Mesozoic mammals were of small body size. Because of the large number of mammalian life-history factors known to be related to body size, this knowledge is crucial to our developing story.

Females of the marsupial-eutherian common ancestor probably were ovoviviparous, giving birth to extremely altricial live young (see Portmann, 1962: 55) that 'hatched' intra-uterinely from thin, uncalcified shell membranes. Early embryogenesis followed patterns standard for noneutherian amniotes, but blastocysts (rather than discs; see Selwood, 1986a, b) were formed in response to greatly reduced yolk contents (see Krause & Cutts, 1984, 1985a). Ureters were placed medial to the adult derivatives (i.e. uterine/vaginal horns) of the embryonic Müllerian ducts. Placentation was choriovitelline, and was restricted to the last trimester of a short gestation period (probably shorter than a normal estrous period). Development of mammary tissue preparatory to lactation was minimal during pregnancy, and did not involve mammatrophic hormones of

placental origin (i.e. placental lactogens; see Forsyth & Hayden, 1977). Lactation (and extra-uterine development of the young) was prolonged. Evidences for most of these generalizations were summarized by Lillegraven (1969, 1975, 1979b, 1985). Rothchild (1981), on the basis of comparative endocrinology, independently suggested that the last common ancestor exhibited short gestation times, live birth, and presence of corpora lutea that were under autonomous control and were unresponsive to external stimuli.

The animals had invertebrate-based (probably mainly terrestrial and flying insects) diets, as indicated by fossil dentitions (see Kielan-Jaworowska *et al.*, 1979). The prey species probably varied with seasons in their availability and composition. Basal metabolic rates were relatively low (for mammals), as in modern small marsupials and some small eutherians (Schmidt-Nielsen, Bolis & Taylor, 1980; McNab, 1978a, b, 1986b). As is true today for small mammals in general (see Fleming, 1979), the Mesozoic species probably were nocturnal and short-lived; they probably were essentially solitary except for times of mating and the mother-infant bond. Rates of population turnover were high. Their brains had many primitive features (see Quiroga, 1980; Kielan-Jaworowska, 1986), including small relative size and the absence of a corpus callosum. Additional features considered primitive to the last common ancestor of eutherians and marsupials were summarized by Müller (1967, 1968a-c, 1969a-c, 1972a-c, 1973), Lillegraven (1969), Marshall (1979), Johnson, Kirsch & Switzer (1984), and Tyndale-Biscoe & Renfree (1987).

The features listed above are characteristic of most small species of extant marsupials, especially didelphids and dasyurids. These characteristics should be considered primitive (plesiomorphic) for marsupials (and for eutherians). In addition, however, living marsupials share unique specializations (apomorphic characters) that almost certainly were attained subsequent to their phylogenetic divergence from ancestral eutherians. Examples include (1) presence of end artery blood supply to the surface of most of the brain (Gillian, 1982; Johnson, Kirsch & Switzer, 1984), rather than anastomosing capillaries; (2) their peculiar mode of tooth replacement and dental formula (McKenna, 1975; Archer, 1978; Clemens & Lillegraven, 1986); (3) the pseudovaginal canal (Lillegraven, 1969: fig. 46), through which neonates pass at birth; and (4) anterior fusion of the Müllerian ducts (Tyndale-Biscoe & Renfree, 1987). Thus the metatherian-eutherian ancestor was *not* a 'marsupial' as we generally diagnose living members of the order; extant marsupials can be considered a fascinating amalgam of phylogenetically primitive and specialized mammalian features.

REPRODUCTION

Introduction

The following sections serve to compare and contrast reproduction in living marsupials versus eutherians, implying the kinds of evolutionary changes that must have occurred since their common ancestry. The most important factors are those with direct bearing on population biology, including (1) duration of gestation; (2) duration of lactation; (3) duration of parental care; (4) age of sexual maturation (earliest birth by an adult female); (5) litter size; (6) litter frequency (annual); (7) size of young at birth; and (8) size of young at weaning.

Because these characteristics determine reproduction in terms of speed (duration, 1–4), numbers of offspring (5, 6) and net investment (7, 8), insight can be gained to the relative ecological performance of each mode. When applying this information to the Mesozoic, *small* marsupials (i.e. <5 kg) must be compared to *small* eutherians of similar body mass.

There is no generally accepted definition of the term 'small mammal', and different references typically use different size criteria for this term. Thus, for ease of discussion, we define 'very small mammals' as those with less than 400 g body mass, 'small mammals' as less than 5 kg, and 'large mammals' as over 5 kg. Any deviations from this general terminological scheme are duly noted in the text.

Comparison of eutherian and marsupial reproductive biology must incorporate effects of body mass. Thus we use allometric analyses both to subtract and to evaluate the effects of body size (see Smith, 1980, 1984a, b) on diverse reproductive parameters. Although arguably not the most appropriate method, we have employed least squares regression throughout this paper (see objections by Harvey & Mace, 1982). Such methods almost universally have been employed in pertinent literature, and use of other analyses would unnecessarily complicate comparisons (also see Seim & Saether, 1983; Lee & Cockburn, 1985: 48). Furthermore, it is unlikely that use of other methods (e.g. major axis analysis) would affect qualitative patterns of results. Thompson (1987) compared marsupial and eutherian population biology within a taxonomically diverse sample, controlling both for body size and ecological roles. Species of marsupials and eutherians were paired by similarities of body mass and dietary habits, yielding comparative sets of data. Analyses of such matched data avoid inappropriate ecological comparisons (such as kangaroos with shrews, or small possums with small eutherian herbivores; see Martin & Harvey, 1985). Thus, unless otherwise stated, the following synopsis is based upon comparisons of a group of marsupials for which exist similar data on eutherians of equivalent body size and dietary habits (Thompson, 1987: appendix 1).

Prenatal comparisons

The interspecific range of variation in gestation periods (i.e. conception to birth) is similar among small marsupials and small eutherians. Among marsupials (range in female adult body mass of 7–25 000 g), gestation varies from 12 to 44 days (L. Collins, personal communication to S.D.T. 1985), and its duration is not closely correlated with adult body mass (Russell, 1982). Gestation periods among eutherians, however, increase markedly with increasing adult body size; at body masses greater than about 1000 g, eutherian gestation is substantially longer than that of species of marsupials of similar adult size (Fig. 1).

Marsupial and eutherian gestation periods do differ, however, in duration and extensiveness of active embryogenesis. Selwood (1980, 1981) has shown that while the marsupial embryo is still encapsulated by shell membranes and floating freely in uterine fluids, gestation is characterized by marked pauses in embryogenesis. Actual organogenesis lasts less than 11 days in all marsupials studied thus far (Renfree, 1980; Selwood, 1981; Tyndale-Biscoe & Renfree,

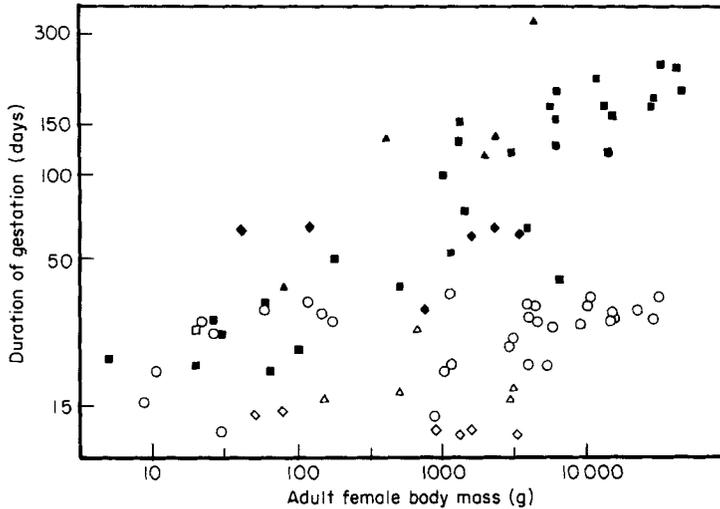


Figure 1. Duration of gestation as function of body mass in 42 species of marsupials compared with 42 species of ecologically similar eutherians (data from Thompson, 1987). Symbols: open, marsupials; solid, eutherians; triangles, folivores/nectarivores; open diamonds, Peramelidae and Didelphidae (Marsupialia); solid diamonds, eutherian omnivores/frugivores; open circles, Dasyuridae and Macropodidae (Marsupialia); solid squares, eutherian insectivores/carnivores and grazers.

1987), and in most is restricted to the last few days of gestation (see McCrady, 1938; Krause & Cutts, 1985b, c). Species of marsupials with relatively long gestations have longer and/or more frequent periods of embryogenic inactivity; an extreme of this may be the embryonic diapause characteristic of macropodids (Tyndale-Biscoe, 1977).

Although litter sizes of both small marsupials and small eutherians vary between 1 and 14, small marsupials (especially dasyurids and didelphids; Fig. 2A) usually have significantly larger litters than do their counterparts amongst small eutherians. This is not true, however, for the small, potoroine macropodids; their litter size is one, as in all other members of that specialized marsupial family. Despite their small litter size, potoroines have high rates of potential population growth because their aseasonal breeding plus short interbirth interval (due to small size and embryonic diapause) allow them to produce as many as three young per year. Comparably-sized eutherians typically can produce only one or two young per year. At larger adult body mass (>5 kg), litter size both of marsupials and eutherians converges on unity (Fig. 2B).

All marsupials give birth to tiny young, ranging in mass among species from 10 mg to just under one gram (Tyndale-Biscoe, 1973; Lee & Cockburn, 1985:51). In all species of marsupials, an individual neonate constitutes less than 0.2% of the mother's body mass (and <1% for the litter; Lee & Cockburn, 1985:53). Marsupials at the time of birth effectively are embryos, anatomically and physiologically (Block, 1964; Eisenberg, 1981: fig. 102). Eutherians, in contrast, are relatively much larger at birth, with individual neonates in small species comprising as little as 2–3% of the mother's body mass (and up to 50% for the litter). Because of their comparatively sustained high rates of intra-uterine morphogenesis, neonates of small species of eutherians also

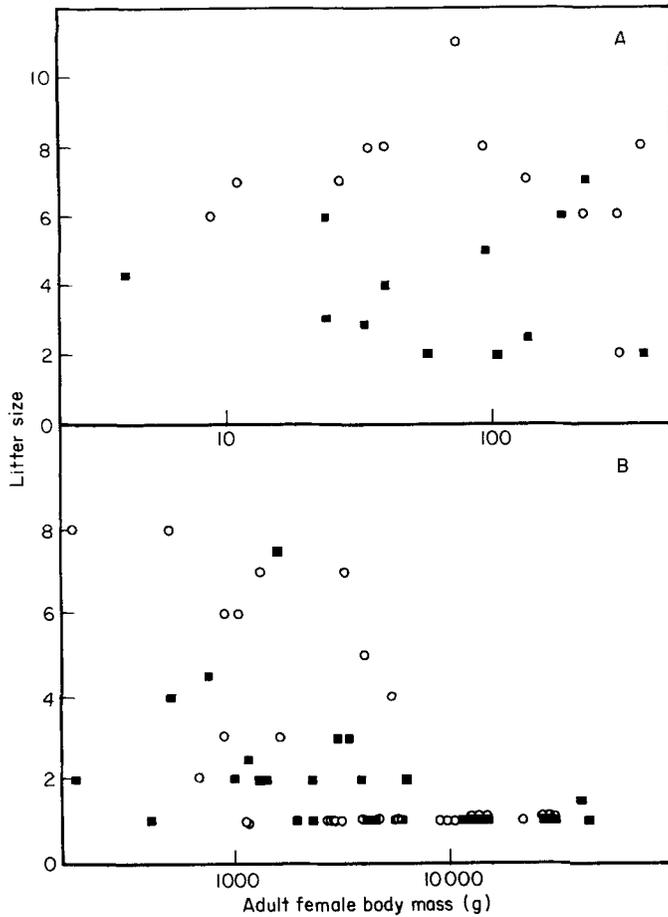


Figure 2. Litter size as function of body mass for marsupials and eutherians less than 400 g body mass (A) and greater than 400 g body mass (B; data from Thompson, 1987, $N = 84$). Symbols: open circles, marsupials; solid squares, eutherians.

are considerably more advanced anatomically, even though their gestation periods (see Millar, 1981) may be no longer, or even shorter, than those in marsupials of the same body mass.

Extensive prenatal morphogenesis as seen among all sizes of eutherians requires major transfer of energy to the developing foetus. In the absence of a significant yolk supply, nearly all products necessary for growth must be supplied by the mother, by way of a placenta. The placenta also serves in foeto-maternal exchanges of a wide variety of other materials needed for foetal life, including the elimination of foetal waste metabolites.

Because of high rates of the various exchanges required by the rapidly-growing and large eutherian foetus, the placenta must be extensively developed. Further, it requires a large surface area that involves intimate apposition of foetal and maternal tissues and their respective bloodstreams. Such profound intimacy of maternal and foetal tissues engenders potential for significant danger to the developing young from attack by the mother's haematopoietic system. The placenta, after all, is of foetal origin, developed under the partial influence

of the paternal genotype. The eutherian placenta, therefore, often is considered to represent a naturally occurring allograft.

The antigenic (immunogenic) nature of eutherian placental tissue is well established (e.g. Stern *et al.*, 1986; Contractor & Sooranna, 1986). Thus knowledge of mechanisms that thwart maternal immunological attack of potentially incompatible foetal tissues is crucial to a full understanding of the origin of the eutherian form of viviparity (see Crichton, 1984). Key physiological activities associated with protection of the developing young occur locally at the foeto-maternal interface (see reviews by Lala, Kearns & Colavincenzo, 1984, and Lala & Kearns, 1985). One aspect involves close interaction of cells of the trophoblast with cells of the endometrial wall of the uterus. Of particular interest are 'decidual cells' of the uterine lining. They seemingly derive by migration as descendants from maternal bone marrow precursors. "Besides playing a putative nutritive role during early placentation, decidual cells are considered to release chemical mediators such as prostaglandins; to have an endocrine function of secreting prolactin, estrogen, and progesterone; and to have an immunoregulatory role during semiallogeneic pregnancy" (Lala *et al.*, 1984: 515). Specifically, the decidual cells are thought to prevent proliferation of cytotoxic T-lymphocytes which could serve in recognition of class I major histocompatibility antigens on the trophoblastic surface. By restricting proliferation of cell-killing T-lymphocytes, the first stage in the classic and very complex syndrome of allograft rejection is abrogated.

Additionally, certain trophoblastic cells themselves have strong potentials for immunosuppression. For example, Stites & Siiteri (1983) have shown that trophoblastic cells secrete various steroids that concentrate in effective immunosuppressive doses at the foeto-maternal interface. As an indication of the bewildering complexity of interactions that exists at the foeto-maternal junction, there is evidence that cells of a human mother's uterine glands become phenotypically altered in response to antigenic influences of trophoblastic cells (Bulmer & Johnson, 1985). Immunological innovations in mammalian reproduction, though inordinately complex and quite incompletely understood, undoubtedly were critical to the evolution of the form of viviparity characteristic of eutherians.

At least two principal reasons probably exist why no species of marsupial has extended the embryogenetically active interval of its gestation. First, studies of marsupials provide little evidence of physiological sophistication adequate for prolonged protection of the genetically 'foreign' embryo (with paternally derived antigens) against the mother's immune system (see Moors, 1974, and Lillegraven, 1975, 1985). Although peramelid marsupials have intimate, eutherian-like chorioallantoic placentation, their gestation is not longer, and their stage of development at birth is only trivially more advanced than most non-peramelid marsupials (see Padykula & Taylor, 1982). Further, no marsupial extends the interval of intra-uterine active organogenesis beyond 10 days, and in most species that interval is considerably shorter. Intra-uterine 'hatching' of the embryo from maternally-derived shell membranes occurs near the beginning of organogenesis (see Tyndale-Biscoe & Renfree, 1987: fig. 7.15). Advent of organogenesis heralds a marked heightening of embryonic energy demands for rapid growth. Following expenditure of meagre yolk reserves, elevated needs for energy require placentation, an adaptation among marsupials

that must await 'hatching'. Close contact of genetically disparate foetal and maternal tissues (and especially their respective bloodstreams) is further deferred until after a period of free floating of the 'hatchlings' followed by an interval of loose appression of placental membranes to the uterine wall; these two intervals commonly last for several days.

Even under conditions of surgical grafting of immunologically foreign tissues to a mammalian host (in which the graft, through the very nature of the procedure, is put into close contact with the host's bloodstream), immunological rejection requires 7–10 days to effect. Thus we do not find convincing the claim by Rodger & Drake (1987) that marsupials exhibit immunological invulnerability of the placenta to the extent seen in eutherians. Although we agree with Tyndale-Biscoe & Renfree (1987:333) that immunological research completed to date on marsupials does not provide direct support for an hypothesis that their placental tissues *lack* immunosuppressive properties, we also point out that the same research does not clearly indicate that the marsupial tissues *have* consequential immunosuppressive properties.

A second reason for short gestation in marsupials is that their corpus luteum (CL) (except peramelids) is short-lived; the CL secretes progesterone, a key hormone to mammalian viviparity (Amoroso, Heap & Renfree, 1979). As stated by Rothchild (1981:190), in marsupials "Neither pregnancy, the uterus, nor the type of ovulation cycle affects the duration of the luteal phase proper." In eutherians, in contrast, the foetus, placenta, uterus, endocrine system and immune system form a physiologically cooperative functional unit that allows prolonged intervals of gestation (in large species) and degrees of foetal development (in all species) well beyond those seen in marsupials of comparable size.

Use of the term 'trophoblast'

Use of the term 'trophoblast' for early developmental tissues among therian mammals has suffered a tortured history, involving trivial semantics on the one hand and fascinating questions of genuine biological consequence (such as blastular homologies and evolutionary innovation) on the other. Some of the more important elements of the various controversies were reviewed by Lillegraven (1985). Recent appearance of discussions by Rodger, Fletcher & Tyndale-Biscoe (1985), Rodger & Drake (1987), and Tyndale-Biscoe & Renfree (1987), however, demands that at least part of the issue be re-opened.

Identification of homologous elements of the blastula among mammals represents the crux of one question—is 'trophoblast' a uniquely eutherian specialization? As reviewed by Lillegraven (1985), the unilaminar blastocyst of marsupials differs significantly only in its spherical shape (related to reduced yolk content) from the blastodisc of telolecithal monotremes and other non-eutherian amniotes. The cells of the unilaminar blastula of marsupials, monotremes, and other non-eutherian amniotes initially are pluripotent, and: "Only the slow processes of folding and fusion and resorption gradually divide continuous layers of cells into separate portions which are embryonic or extra-embryonic by accident of position" (McCrary, 1944:248). There is no sharply demarcated boundary between cells of the early blastula that are destined for embryonic versus extra-embryonic fates. Much of the unilaminar blastocyst of

non-eutherian amniotes eventually becomes incorporated into the embryo proper. Use of the term 'formative region' (or 'embryonal area') for the slightly thickened region on a marsupial late blastula is based upon the long-persisting misidentification of the early medullary plate as that part of the blastula which will form the entirety of the embryo proper.

In marked contrast to marsupials, monotremes and other non-eutherian amniotes, all eutherians studied to date exhibit segregation and early determination of cells that are destined for embryonic versus extra-embryonic fates. The latter are arrayed as an external sphere ("trophoblast" or "trophectoderm" as used by Lillegraven, 1985) that wholly encloses cells ('inner cell mass' or more loosely-aggregated equivalent cells) that form the embryo proper. Thus, presumptive cells of the embryo are isolated from their earliest stages of development from direct contact with maternal epithelium and uterine fluids.

Tyndale-Biscoe & Renfree (1987:406) reviewed early development in certain eutherian insectivores. Early cleavages in these animals result in an initial unilaminar blastocyst, bypassing a morular stage that is more common among the diversity of eutherians. Subsequent cleavages result in cells that migrate internally, surrounded by the main sphere of the blastula (trophoblast); the internal cells form the embryonic tissues plus various other extra-embryonic tissues, but the main blastular sphere forms only extra-embryonic tissues. Tyndale-Biscoe & Renfree argued that these insectivoran early developmental sequences closely resemble those of marsupials, and thereby support the homology of eutherian trophoblast (cells of their main unilaminar blastocyst) with the unilaminar blastocystic wall of marsupials. Further, Tyndale-Biscoe & Renfree (1987:406) stated: "The reason for drawing attention to these unusual patterns of development among eutherian species is to emphasize again that cladistic analyses based on generalizations may result in apparent distinctions between Eutherian [*sic*] and Metatheria that do not exist." Their major point was that "trophoblast" (*sensu* Moors, 1974, and Lillegraven 1969, 1975, 1979b, 1985) is not a phylogenetically neomorphic tissue unique to eutherians, but rather is common to all living therian mammals.

Statements by Tyndale-Biscoe & Renfree (1987:406) to the contrary notwithstanding, the above comparisons of early development of certain insectivorans with marsupials better serve to emphasize the fundamentally different developmental approaches between the two groups. The developmental pathways described for the insectivorans differ dramatically from those of marsupials and other non-eutherian amniotes. Marsupials follow the basic early developmental plan common to all known non-eutherian amniotes. Eutherians, in striking contrast, are unique in: (1) the early differentiation of presumptive extra-embryonic versus embryonic cells; and (2) in the early physical internalization of the latter within the former. Such phenomena are unknown among non-eutherian amniotes, and thus can serve as diagnostic specializations of the Eutheria. The developmental differences are not anatomically trivial, and their importances go beyond mere quibbling over Hubrecht's (1889) original intended use of the term "trophoblast".

Nevertheless, the functional significance of differences between early development of marsupials and eutherians, in absence of pertinent experimental studies of the former, remains speculative. We strongly suspect, however, that

immunological aspects associated with early, intimate and prolonged implantation common among eutherians are especially involved. As discussed earlier, maternally-derived shell membranes among marsupials are retained late into a short pregnancy; intimacy of foetal/maternal contact of circulatory systems is restricted to a few days. Eutherians, in contrast, lack shell membranes and typically initiate implantation of trophoblastic tissues into the uterine wall early in pregnancy; embryonic energy demands begin early and are sustained at high levels throughout pregnancy. Though the protective mechanisms are far from understood, it is well known that eutherian trophoblastic tissues (which are known to express class I major histocompatibility antigens of paternal origin) are capable of masking themselves from maternal immunological attack. Although Rodger *et al.* (1985) and Roger & Drake (1987) postulated that mechanisms to solve the problem of foetal 'grafts' evolved long before the phylogenetic divergence of marsupials and eutherians, we find their evidence for such a conclusion unconvincing.

Comparisons of durations of gestation versus lactation

Most morphological development in marsupials occurs during a prolonged interval of lactation (Fig. 3). The shortest lactation period for a small marsupial appears to be about 60–70 days; many species take well over 200 days (Russell, 1982; Thompson, 1987). Duration of lactation increases with adult size both for marsupials and eutherians. As judged by the great variability in relative lengths of gestation and lactation, eutherians possess high flexibility in apportioning development between the two phases (see Martin & MacLarnon, 1985). The ranges of variability ($N = 42$; data from Thompson, 1987) in the ratio of gestation length to lactation length are (1) marsupials 0.07–0.55 (mean = 0.17 ± 0.11 s.d.) and (2) eutherians 0.63–5.75 (mean = 2.00 ± 1.17). Despite the comparative disparities of durations of gestation and lactation,

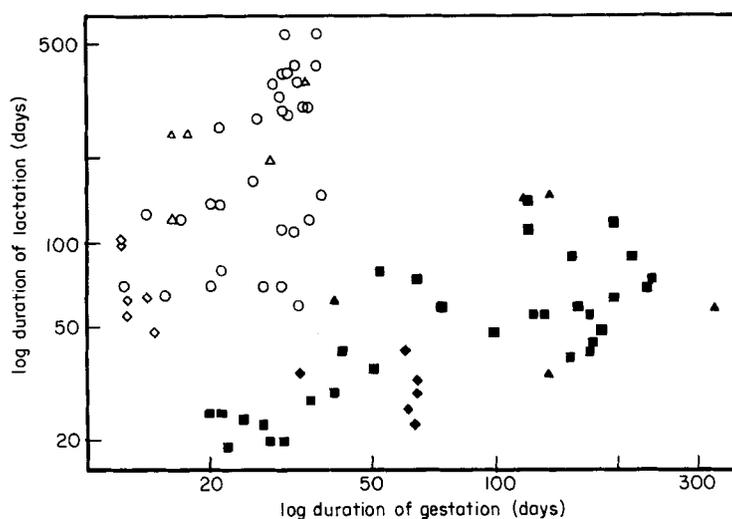


Figure 3. Duration of lactation as function of duration of gestation in marsupials and eutherians (data from Thompson, 1987, $N = 82$). Symbols (open, marsupials; solid, eutherians) as in Fig. 1.

marsupials and eutherians wean litters of similar total mass (Hayssen, Lacy & Parker, 1985; Lee & Cockburn, 1985:61). Marsupial postnatal growth rates are slower than eutherians (see Derrickson, 1986), and are spread over a longer period of parental care.

Duration of parental care

Data are too few to allow a thorough assessment of the *total* duration of parental care for some eutherians. For example, in many of the Carnivora, young are weaned onto food captured by the parents (e.g. regurgitation in canids), and subsequently must learn critical foraging techniques before achieving true nutritional independence. Nevertheless, the period from conception to weaning has become an accepted measure of the duration of parental care (Low, 1978; Hayssen *et al.*, 1985; Braithwaite & Lee, 1979; Lee & Cockburn, 1985; Thompson, 1987).

For any given body size, marsupials take about half again as long from conception to weaning of a litter as do eutherians (Lee & Cockburn, 1985:62; Thompson, 1987). The scaling coefficients for time from conception to weaning differ for marsupials and eutherians, with the differences being greater at body sizes in excess of 5 kg (Thompson, 1987). Longer parental care among marsupials may (1) increase probability of juvenile mortality associated with that dependence (e.g. separation from protection of mother); (2) increase probability of maternal mortality resulting from maternal care; and (3) limit the maximum number of litters per year (Thompson, 1987). Thus, the longer parental care of marsupials potentially increases the risk of reproductive failure due to mortality and decreases the ability to respond to early litter loss with a replacement litter (but see Read, 1985a). These general features of marsupial reproduction could represent marked disadvantages, relative to the faster reproduction of eutherians, in situations characterized by high and/or unpredictable, juvenile mortality. Unfortunately, there are virtually no records on juvenile survivorship and mortality among marsupials.

Long maternal care also may affect a mammal's ability to respond reproductively to climatic changes. When environments become more harsh (Kiltie, 1984) or unpredictable (*sensu* Low, 1978), prolonged nutritional dependence makes it difficult to adjust the time of weaning to occur within a particularly favourable season (or part thereof). Kiltie (1984), for example, suggested that many large (>100 kg) eutherians were unable to adjust their long periods of parental care to increasing seasonality at the end of the Pleistocene, thus contributing to their extinction. Such problems would be expected to be especially pronounced for large marsupials; the predicted (Thompson, 1987) interval of conception to weaning for a 100 kg marsupial is about 698 days, while that for a comparably-sized eutherian is only about 467 days. Thus it would be predicted that, for any worldwide climatic change associated with mammalian extinctions, the lower body size limit within marsupial megafaunal extinctions should be smaller than that of eutherians. Pleistocene extinctions in Australia were consistent with such a pattern (Martin & Klein, 1984).

The longer duration of parental care characteristic of marsupials might intuitively be expected to delay onset of sexual maturity. Measuring from the

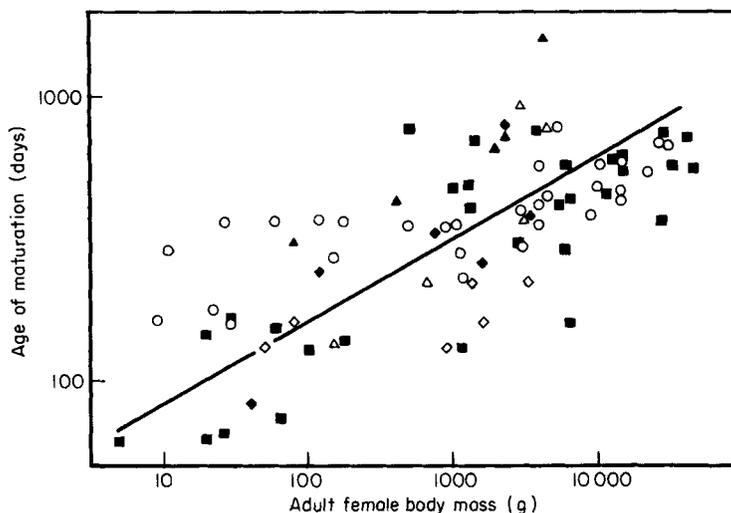


Figure 4. Age of maturation (birth to first birth by same individual as mature female) as function of body mass in marsupials and eutherians (data from Thompson, 1987, $N = 82$). Symbols (open, marsupials; solid, eutherians) as in Fig. 1. Solid line is reduced major axis regression for marsupials and eutherians combined.

day of birth, most very small female marsupials (<400 g) do, indeed, mature later than eutherians of the same mass (Fig. 4). However, many species of marsupials have shortened the interval from weaning to sexual maturity relative to that seen in most species of small eutherians (Fig. 5; Thompson, 1987). Thus, some populations of very small marsupials are capable of responding quickly with an additional litter to newly available resources (Morton, 1982; Lee, Wooley & Braithwaite, 1982; Read, 1985a, b).

Early maturation per se is less important for seasonally- than for aseasonally-breeding species. For example, species that breed during only a few months of each year may not reach sexual maturity until the following breeding season. For these species, developmental constraints on the earliest possible date of sexual maturity need not affect the actual date of first breeding. Thus,

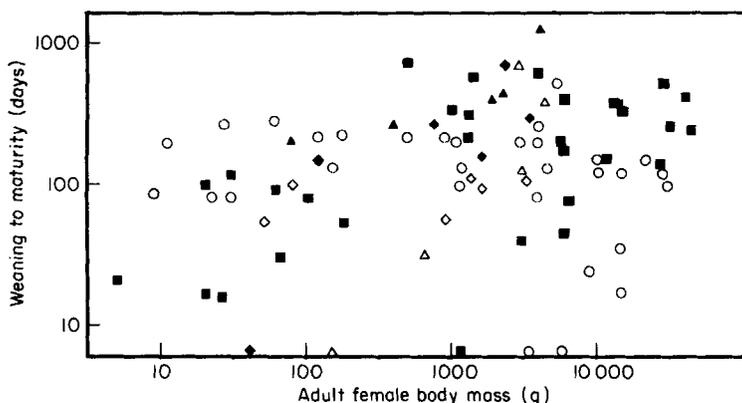


Figure 5. Period from weaning to maturity as function of body mass in marsupials and eutherians (data from Thompson, 1987, $N = 84$). Symbols (open, marsupials; solid, eutherians) as in Fig. 1.

compared either among species of seasonally breeding very small mammals, or among larger mammals with longer parental care and slower growth to adult size, the longer parental care of marsupials may not result in a difference in age of first mating from that seen in eutherians. Aseasonal, opportunistically breeding marsupials that mature at or soon after weaning, however, tend to mature later than their eutherian counterparts. Thus very small, aseasonally reproducing marsupials tend to have lower potential rates of population growth (because of their delayed maturation) than similar-sized eutherians of comparable breeding habits (Thompson, 1987).

Basic similarities and differences of reproduction in marsupials versus eutherians can be summarized via comparison of two pairs of species, with each pair of similar body size, food habits, and habitat: pair 1, *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae) compared with *Onychomys torridus* (Rodentia: Cricetidae); and pair 2, *Macropus robustus* (Marsupialia: Macropodidae) compared with *Gazella thompsoni* (Artiodactyla: Bovidae; Fig. 6). The pairs typify differences between marsupials and eutherians in rates of development at small and large body sizes; the impact of seasonality in breeding must be superimposed upon these comparisons.

Energetics and mammalian population biology

In addition to comparisons of duration of reproduction in marsupial and eutherian females, the physiological correlates of these different durations and the production of litters must be considered.

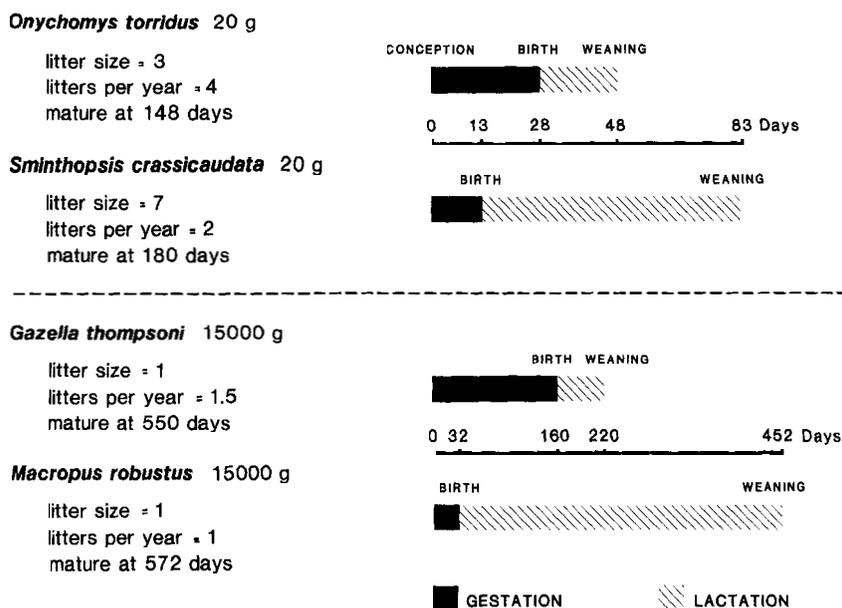


Figure 6. Comparisons of reproductive parameters between matched pairs of ecologically similar species of marsupials and eutherians. Upper comparative pair is between two small, desert-dwelling insectivores, *Onychomys torridus* (Eutheria, Cricetidae) and *Sminthopsis crassicaudata* (Marsupialia, Dasyuridae). Lower comparative pair is between two larger, open-country grazers, *Gazella thompsoni* (Eutheria, Bovidae) and *Macropus robustus* (Marsupialia, Macropodidae). Illustrated is the general feature among marsupials of comparatively long (both in relative and absolute terms) intervals of lactation.

All mammals are endothermic, regulating body temperature principally by internal generation of heat. Endothermy permits activity and reproduction to be relatively independent of environmental conditions, at least in comparison with ectotherms. But endothermy has one overwhelming limitation: it requires exceedingly high rates of energy expenditure (see Else & Hulbert, 1985), which means that thermal independence has a necessary reliance on constantly available trophic resources.

Energy expenditure in endotherms can be estimated in many ways. The best measure might be mean daily expenditure in the field, which would vary with body mass, temperature, season and many other factors. Unfortunately, few such estimates exist for mammals. The most available estimate of energy expenditure is the 'basal' rate, which is measured in the laboratory when the animal is post-absorptive, inactive and at ambient temperatures over which rate of metabolism shows independence. Because field energy expenditures in eutherians are positively correlated with basal rates of metabolism (McNab, 1980), basal rate may be used as an index of, but is not equal to, field expenditures.

The single most important factor setting basal rates (and, by implication, field expenditures) in eutherians is body mass; total basal rate is roughly proportional to body mass raised to the three-quarters power, $m^{0.75}$ (Kleiber, 1932, 1961; McNab, 1983a; Else & Hulbert, 1985). Because total rates are proportional to total body mass raised to a power less than 1.0, mass-specific rates are proportional to mass raised to a negative power ($m^{-0.25}$); mass-specific rates thus decrease with an increase in mass.

Data from most eutherians do not fall precisely on the mathematically expected Kleiberian standard curve; much variation in basal rate exists. At masses greater than 100 g, for example, eutherians that feed on grass, seeds or vertebrates have basal rates that are slightly greater than expected from the Kleiber relation. In contrast, those that feed on fruit, leaves or invertebrates have low basal rates compared to Kleiber (McNab, 1986a); such depression in basal rate associated with these food habits is accentuated at large masses. Frugivorous and folivorous eutherians have especially low basal rates (in association with small muscle masses; McNab, 1978a) if they are arboreal and sedentary. The influence on metabolic rates of food habits is independent of taxonomic relationships among eutherians.

Climate also influences basal rates of eutherians, independent of body mass, and in complex interaction with food habits. For example, marine mammals, most of which are vertebrate-eating, have even higher basal rates than terrestrial vertebrate-eaters (Scholander, Hock, Walters & Irving, 1950; McNab, 1986a). Terrestrial mesic species that feed on seeds or invertebrates have higher rates than desert species with similar food habits (McNab & Morrison, 1963; Hulbert & Dawson, 1974; Shkolnik & Schmidt-Nielsen, 1976; McNab, 1979a). Burrowing species, on the other hand, have lower basal rates than other species, irrespective of food habits (McNab, 1979b). Influences of climate on basal rate in eutherians are secondary in magnitude to those of mass and food habits.

As a result of complex interactions in eutherians among basal rate, food habits and body mass, equally complex relations exist between temperature regulation and food habits. A few examples follow. At very small masses, most eutherians

regulate body temperature precisely, and do not enter daily torpor. Those eutherians that have basal rates falling below a 'boundary' curve (that describes minimal rates required for continuous endothermy; see McNab, 1983a), normally feed on flying insects, mast crops in deserts, or on other foods that are seasonally available. Although most larger species do not have basal rates so low as to impair thermoregulation, if they feed on soil invertebrates, leaves of trees, fruit, or a mixture of these foods, they normally have low body temperatures (unless they have thick fur coats compensatory for low rates of metabolism). Finally, some eutherians facultatively enter seasonal torpor (hibernation or aestivation), usually in relation to a seasonally restricted food or water supply. This form of torpor, however, does not issue from thermoregulatory incompetence associated with low rates of metabolism.

Marsupials scale basal rate of metabolism with respect to body mass in a manner similar to that found in eutherians (i.e. total rates are proportional to $m^{0.75}$: see MacMillan & Nelson, 1969; and Dawson & Hulbert, 1970). But basal rates of eutherians and marsupials differ in three principal ways. First, no marsupial has a basal rate greater than that expected from Kleiber's standard curve, and the marsupial average is approximately 30% lower than the standard curve (MacMillan & Nelson, 1969; Dawson & Hulbert, 1970; McNab, 1978b, 1986b). Implications of this are that: (1) no very small marsupial follows the boundary curve; (2) all very small marsupials enter daily torpor; and (3) larger marsupials that feed on grass and meat have low basal rates, even though comparably-sized eutherians with these habits have high basal rates (McNab, 1978b, 1983a, 1986b). Secondly, the lowest basal rates relative to those expected from mass are found in eutherians, mainly because marsupials with food habits leading to low basal rates rarely attain the mass of the largest eutherians having similar food habits. Finally, the first and second points combine to mean that marsupials have a much narrower range in basal rate than eutherians, after the influence of body mass is subtracted (Fig. 7). On average, however, eutherians and marsupials have similar basal rates (McNab, 1986b), at least at masses greater than 150 g.

As discussed above, rate of energy expenditure in eutherians varies both with body mass and type of food used. In marsupials, energy expenditure also varies with mass, but to a lesser extent than in eutherians in relation to food habits. Do such variations and differences in ranges of rates of expenditure have effects of biological consequence beyond those associated with temperature regulation? Indeed, major consequences for eutherians exist in reproduction and, as discussed below, on important elements of population biology.

Evaluation of duration of reproductive phases and aspects of fecundity can be facilitated by use of an index that integrates these parameters in a biologically relevant fashion. One such index, a fundamental parameter of population biology, is the exponential constant, r , that describes the rate at which a population grows when resources are abundant:

$$N_t = N_0 e^{rt}, \quad (1)$$

where N_t is the number of individuals in the population at time t and N_0 is the original number of individuals in the population. The parameter r is approximated (if and only if r is not zero) by the relation:

$$r \approx \ln R_0/T, \quad (2)$$

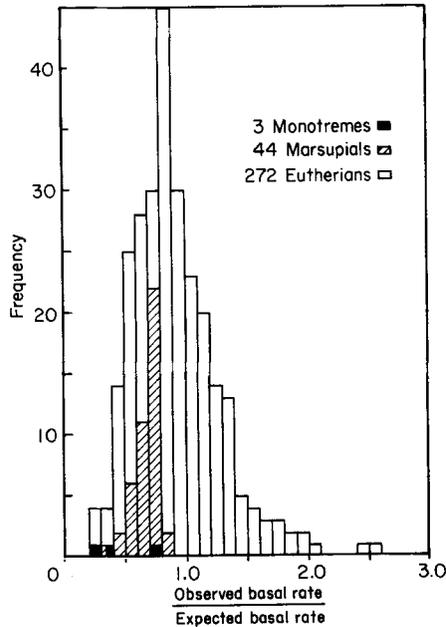


Figure 7. Frequency distribution of observed basal metabolic rates in mammals compared to those rates expected from the Kleiber function (i.e. $m^{0.75}$).

where R_0 is the net rate of reproduction (i.e. annual fecundity) and T is generation time (i.e. the mean period between conception and age of first reproduction of that offspring). Because the parameters R_0 and T vary with environmental conditions, r is maximal only when R_0 is maximal and T is minimal. When r is maximal, it is called the maximal intrinsic population growth constant, r_{\max} (also referred to as the intrinsic rate of natural increase; see Cole, 1954; Hennemann, 1983, 1984). Of the two factors setting the value of r , variation in T is the more important; R_0 is present only as a logarithm. As an aside, empirically determined values of r_{\max} (see McNab, 1980) are not necessarily the same as estimated values of r_{\max} (see Hennemann, 1983). Because both forms are discussed below, we specify estimated values by use of an asterisk (i.e. r_{\max}^*).

Such a parameter as r_{\max} gives a reasonable comparative measure of capacities of marsupials and eutherians to respond numerically to increased resource availability (Birch, 1948; Cole, 1954; McNab, 1980; Hennemann, 1983, 1984). The magnitude of r_{\max} also provides an integrated measure of population parameters that incorporates trade-offs among variables, such as between litter size and numbers of litters per year. Thompson (1987) compared an estimated r_{\max}^* among pairs of ecologically similar species of marsupials and eutherians. Although several outliers were noted (see also Lee & Cockburn, 1985: 62), Thompson concluded that, as overall groups, values of r_{\max}^* for the Marsupialia and Eutheria were statistically indistinguishable. However, small marsupials (<400 g) as well as very large marsupials (>5 kg) have values of r_{\max}^* much lower than eutherians of comparable mass.

Certain intermediate sized marsupials (*c.* 1–4 kg) may attain high values of r_{\max}^* . For example, didelphid, peramelid, and potoroine marsupials have much higher values for r_{\max}^* than are observed in other species of comparably sized marsupials and many eutherians. However, eutherian ecological counterparts of didelphids and peramelids also have relatively high values for r_{\max}^* (Thompson, 1987: fig. 2). Didelphids and peramelids achieve their characteristically high values for r_{\max}^* via a combination of increased litter sizes, greater litter frequencies, and shortened intervals from conception to weaning.

Both parameters of r (i.e. R_0 and T) vary in eutherians with basal rate of metabolism, independent of influence of body mass. Annual fecundity (the product of litter size and number of litters per year) varies directly with rate of metabolism (McNab, 1986b: fig. 5). For example, if the basal rate increases by about 50% in eutherians weighing 24–69 g, the annual fecundity increases by about 40%; at a mass of 1.4–3.3 kg, a 50% reduction in basal rate corresponds approximately to a 50% reduction in annual fecundity.

Generation time decreases in eutherians with an increase in basal rate. Generation time can be approximated by the sum of the periods from (1) conception to birth (prenatal period) and (2) birth to age of first reproduction (postnatal period). The duration of gestation increases with body mass (Fig. 1), and is longer in precocial than in altricial species (Martin & MacLarnon, 1985). In addition, gestation period, independent of direct influences of body mass and of body mass on rate of metabolism, decreases upon increase in rate of metabolism in eutherians (McNab, 1986b: fig. 1). This correlation probably occurs because the intra-uterine growth rate increases with an increase in rate of maternal metabolism; a high rate of metabolism in a pregnant female means high rates of molecular synthesis, placental transfer, and embryogenesis.

Postnatal growth rates can be characterized by an exponential growth constant, which may be described by logistic, Gompertzian, or Bertalanfian transformation (Ricklefs, 1967). Growth constants vary inversely with body mass (McNab, 1980; Zullinger, Ricklefs, Redford & Mace, 1984), and vary directly with rate of metabolism, independent of influence of body mass (McNab, 1986b: fig. 2). Thus, eutherians which have high basal rates also have high postnatal growth rates, just as they have high intra-uterine growth rates. Postnatal growth rates may depend upon rates of metabolism both of the lactating mother and the suckling young, whereas during the prenatal period, hormones of the pregnant female may set the rate of metabolism of foetal young. Suckling eutherians, irrespective of mass, tend to have much higher basal rates than expected from the Kleiber relation (McNab, 1983a), which both assures effective endothermy at small masses and high growth rates during adolescence. High growth rates reduce the period over which young depend upon their mother for sustenance (Lee & Cockburn, 1985:61), and reduce the period required for attainment of the age of first reproduction. High rates of metabolism in lactating mothers presumably permit, or perhaps reflect, high rates of milk synthesis (Glazier, 1985).

A dependency exists in eutherians between r_{\max} and basal metabolic rates. That is because of the heightened effects on fecundity and generation time (through faster pre- and postnatal growth) of increased basal rates. Such dependency between r_{\max} and metabolic rates is reflected (1) by inference in the correlation of r_{\max} with body mass (Fenchel, 1974), when both the mass-specific

basal rates and r_{\max} are proportional to $m^{-0.25}$; and (2) in the direct correlation of r_{\max} with basal rate independent of influence of body mass (Hennemann, 1983). Because a high r_{\max} may permit a population that is low in numbers to increase rapidly when resources are not limiting, the living eutherians most noted for high population fluctuations, as expected, have high basal rates compared to the Kleiber relation (McNab, 1980). These species most notably include microtine rodents and lagomorphs.

This analysis of the relation of reproduction in eutherians to energetics suggests several conclusions. First, at a given body mass, the principal means by which r_{\max} can be increased is through an increase in rate of metabolism; but this will occur only if food habits permit an increase in metabolic rate. Secondly, eutherians have basal rates as high as are ecologically possible, to maximize their ability to exploit available resources (as reflected in a high r_{\max}). Finally, some eutherians have low basal rates, because they use food resources that will not permit high rates of metabolism. That is, low rates found in eutherians are imposed by the food and environment, and do not reflect a phylogenetically immutable 'intrinsic' property of the species.

Marsupials differ markedly from eutherians in the degree of connection between reproduction and energetics. Marsupials, unlike eutherians, show little direct linkage of fecundity, gestation period, or postnatal growth rate to rate of energy expenditure (McNab, 1986b). For example, fecundity in marsupials shows appreciable variation independent of body mass, but it is not related to variation in rate of metabolism independent of influence of body mass (McNab, 1986b: fig. 5). Similarly, although gestation periods in some marsupials equal the shortest periods found in small eutherians, marsupial gestation periods show little variation with adult body mass (Fig. 1) and no variation with maternal basal rate independent of effect of body mass (McNab, 1986b: fig. 1). The postnatal growth constant in marsupials does not vary with rate of metabolism independent of influence of body mass (McNab, 1986b: fig. 2).

The comparative independence of marsupial reproduction from metabolism may be responsible for the lengthy time from conception to weaning in most species. And this, in turn, is probably responsible for the longer generation time (later maturation; Fig. 4), fewer litters per year (Thompson, 1987), and lower r_{\max} 's of large and small marsupials. Many small marsupials compensate for the effect of longer development on litter frequency with an increase in litter size (Thompson, 1987), thus bringing fecundity up to near eutherian levels. Even this near parity in fecundity, however, is not sufficient to overcome the effect of later maturation on marsupial r . Thus, the absence of strong coupling between r_{\max} and rate of metabolism has marked biological consequences for the lives of marsupials.

The combined influences of food habits and reproductive output account for much of the residual variation in eutherian basal metabolic rate (independent of the influence of body mass). Eutherians have great residual variation in basal rate (Fig. 7) because (1) selection for an increased rate of reproduction has been accomplished by increasing fecundity and decreasing generation time (both facilitated by increases in basal rate of metabolism); and (2) some food habits have imposed a low basal rate, irrespective of consequences upon reproductive rate. In most cases, the principal advantage to eutherians of a high rate of metabolism is found in a high r_{\max} . Marsupials, in contrast, have a strikingly

small residual variation in basal rate (Fig. 7) aside from the influence of body mass, except for selective depression of basal rate by a few food habits.

The entire basis for connection of reproduction to energetics in eutherians (and the virtual absence of such a connection in marsupials) is unclear. One factor probably is important during *prenatal* life. Because of development of trophoblastic tissues (see Lillegraven, 1985) and a physiologically sophisticated placenta, eutherians can have high rates of exchange (of gases, nutrients, hormones, metabolites and wastes) between a rapidly growing foetus and its mother without risking allograft rejection by the mother of foetal-derived tissues. Intimacy of placentation and rates of exchange must heighten as rates of metabolism of the eutherian mother and its foetus increase (and as pregnancy progresses through time), thereby permitting increased rates of prenatal development. As discussed earlier, however, marsupials have restricted rates and, especially, durations of active exchange between mother and embryo (never developing prenatal young to what is generally considered a foetal level). Assuming for the moment that a cause of restriction of embryonic-maternal exchanges among marsupials is, indeed, due to limited trophoblastic protection against allograft rejection (and their consequent maintenance of intact shell membranes late into a short pregnancy), high maternal and embryonic rates of metabolism would offer little opportunity for increased rates and magnitudes of placental exchange; the threat of immunological rejection would increase exponentially as pregnancy continues and as elaborate intimacy of placentation develops.

The reason why fecundity and *postnatal* growth rates are not more closely coupled to basal metabolic rates in marsupials is more obscure (but see discussion of certain peramelids and didelphids, below).

Energetics of mammalian reproduction

With the above background on marsupial energetics and its relation to population biology, now we can consider differences in energetic investment of marsupial versus eutherian reproduction. Two commonly used indices for comparison of energetic costs associated with reproduction are: (1) *parental* (or more accurately, *maternal*) *investment*—the amount of energy expended for production of an individual young or a litter; and (2) *parental effort*—the additional energy spent on reproduction relative to expenditures for routine maintenance during non-reproductive intervals.

Both indices are related intimately to rates of energy expenditure, and both commonly are estimated by comparisons of body mass of the mother to that of her offspring (see Russell, 1982, Lee & Cockburn, 1985:61). Rates of food consumption and/or analysis by indirect calorimetry (Randolph, Randolph, Mattingly & Foster, 1977; McClure & Randolph, 1980; Mattingly & McClure, 1985), however, provide more accurate representations of energy expenditures because they permit estimation of energy allocated to maternal respiration, neonatal respiration, and net production (=growth). The eutherian commitment to gestation, coupled with the inverse correlation between metabolic rate and gestation length (McNab, 1986b: fig. 1), may explain why marsupial and eutherian net investments are similar (Lee & Cockburn,

1985:61); nevertheless, eutherians make their investment in less than two-thirds the time required by marsupials.

Gestation appears energetically more efficient in terms of nutrient transfer than lactation (Randolph *et al.*, 1977; McClure & Randolph, 1980; Mattingly & McClure, 1983, 1985). Whether this increased efficiency is related to biochemical (e.g. milk synthesis and subsequent digestion) or thermoregulatory (see McClure & Randolph, 1980) components of lactation is unclear. Actual investment, in terms of energy spent to wean an individual young or a litter, increases with the duration of lactation because (1) thermoregulatory costs of nursing young are high (Randolph *et al.*, 1977; McClure & Randolph, 1980; Mattingly & McClure, 1985); and (2) activity costs for growing young are greater in extra-uterine environments than within the uterus (Mattingly & McClure, 1985).

The total maternal energetic expenditure toward respiration by her infants is a function of duration of lactation combined with the infants' rate of metabolism (low prior to onset of endogenous thermoregulation but very high thereafter; see Poczopko, 1979; McClure & Randolph, 1980; McNab, 1983a). Infant respiration comprises a significant fraction of maternal energy allocated to reproduction (Randolph *et al.*, 1977; McClure & Randolph, 1980; Thompson & Nicoll, 1986). Such thermoregulatory costs via lactation seem to favour prolonged intra-uterine rather than extra-uterine development. The marsupial commitment to extended lactation (Fig. 3) suggests that they allocate a larger proportion of reproductive energy to infant respiration than do most eutherians.

Three developmental patterns among mammals minimize energy allocated to respiration by infants: (1) extending gestation, (2) deferring onset of endogenous thermoregulation (McClure & Randolph, 1980), and (3) shortening lactation. Reproductive constraints in marsupials leave only delayed thermoregulation and shortened lactation as viable options. Development of thermoregulation has been studied in three marsupials, the quokka (*Setonix brachyurus*: Macropodidae; see Loh & Shield, 1977), a bandicoot (*Isodon macrourus*: Peramelidae; see Gemmell & Johnston, 1985), and *Didelphis virginiana* (see Walker & Berger, 1980). All three species appear to delay onset of thermoregulation, and their infants do not attain the high levels of metabolism characteristic of baby eutherians (McNab, 1986a, b; see also McClure & Rudolph, 1980).

Peramelids and didelphids have shorter times from conception to weaning than seen in other, comparably sized marsupials (Lee & Cockburn, 1985:61; Thompson, 1987), apparently contributing to their relatively greater values of r_{\max}^* . Peramelids and didelphids not only have comparatively short periods of gestation, but also have relatively shortened durations of lactation. The shorter lactation periods may be related to increased maternal rates of metabolism during lactation. For example, two didelphids (*Monodelphis domestica* and *D. virginiana*) have non-reproductive basal rates of metabolism, respectively, of 64 and 76% of the expected Kleiberian value for mammals. During lactation, however, their resting metabolic rates, respectively, are 97 (Thompson & Nicoll, 1986) and 87% of Kleiber (Fleming, Harder & Wukie, 1981, as recalculated in McNab, 1986b). An implication is that at least some marsupials (to date known only within the Didelphidae) are able to reap benefits of high metabolic rates during reproduction, thereby speeding development, shortening the time from conception to weaning, and increasing the potential number of litters per year.

These marsupials are not metabolically unique, however, as all eutherians with low non-reproductive basal rates of metabolism studied thus far also raise their metabolic rates during reproduction (Thompson & Nicoll, 1986).

Low (1978) and Parker (1977) suggested that marsupials have low initial parental effort while eutherians have high initial efforts. To test these generalizations, Thompson & Nicoll (1986) used respirometry to compare schedules of reproductive investment of a marsupial against two species of eutherians that have low standard rates of metabolism. The compared species were found to have similar investment schedules, involving low initial energy costs that gradually increase until weaning. In addition, the total energetic cost of producing a single young was remarkably similar for the compared species of marsupials and eutherians (differing in body mass, litter size, and basal rates of metabolism). Marsupials, however, may be less efficient in that they channel a smaller proportion of the total energy expenditure (for reproduction) into growth and development of the young (i.e. by committing more energy to respiration by offspring; Nicoll & Thompson, 1987); this may contribute to the comparatively long time required for marsupial young to achieve nutritional independence.

HYPOTHESIS FOR THE ORIGIN OF EUTHERIAN MAMMALS

All preceding discussion must be considered background, necessary to the hypothesis developed in the present section. Perhaps the most significant single biological difference between eutherians and other amniotes is that development in the former exhibits “. . . the unique combination of 1) intimate apposition of fetal and maternal tissues and circulatory systems (necessary to satisfy prolonged high embryonic energy demands); with 2) sustained, active morphogenesis (through which the fetus runs an ever increasing risk of rejection during gestation by the mother's immune system)” (Lillegraven, 1985:298). Such a combination in small mammals allows relative abbreviation (see Vogel, 1981; Forsyth & Hayden, 1977) of the energetically costly (see Pond, 1983) period of lactation and, in concert with elevated metabolic rates, enhances fecundity and potential for rapid population increase (higher r_{\max}). Once operational, the potential adaptive advantages of these characteristically eutherian features are apparent, especially in species of small body size. But by what sequence of steps, staying within a framework of reasonable evolutionary theory, did such specializations come to be? We argue that reproductive innovation came first, followed closely by selection for higher rates of metabolism.

As implied in Fig. 8, the first (and undoubtedly most difficult) evolutionary step involved the functionally related intra-uterine developmental changes of (1) earlier shedding and eventual loss of shell membranes; (2) advent of eutherian-style trophoblastic tissues (and restriction of presumptive embryonic cells to an “inner cell mass”; see Potter & Morris, 1985); and (3) earlier initiation of extensive and intimate placentation. The actual processes that were involved within development of these three innovative and by necessity essentially simultaneous changes are wholly unknown. That they occurred subsequent to phylogenetic separation from the last common ancestor with marsupials, however, is clear; the features are unique to eutherians, and in combination provide suitable criteria by which the living Eutheria can be diagnosed.

GEOLOGIC INTERVALS	TAXONOMY	FEATURES, EVENTS, & CONSEQUENCES	
? Early Cretaceous ?	Eutheria	<p>Step 1 - simultaneous "experiments" in forming:</p> <p>A. trophoblastic tissues -</p> <ul style="list-style-type: none"> • allowed extension of intrauterine active morphogenesis via heightened immunological protection (initially slight) • resulted in: <ul style="list-style-type: none"> reduction of duration of lactation relative to duration of gestation somewhat quicker reproduction less energetic drain on mother more rapid population growth <p>B. mammatrophic hormones -</p> <ul style="list-style-type: none"> prepared mammary glands for nourishment of larger neonates 	
Early Cretaceous & Late Jurassic	pre-Eutheria	<p>Common ancestors of modern therians -</p> <ul style="list-style-type: none"> tiny, with short lifespan <p>Warm, moderately seasonal climate</p>	<p>Essentially "marsupial" in reproductive mode (standard amniote style of formation of EEM, live birth of extremely altricial young) plus relatively low metabolic rate</p>

Figure 8. Hypothesized first step in the origin of eutherian mammals. Although both marsupials and eutherians were derived from the 'common ancestor', only the eutherian descendant lineage is shown. The origin of true marsupials also involved new specializations, but developmentally did not involve differentiation of inner cell mass versus trophoblastic tissues. See text for further explanation. EEM = extraembryonic membranes.

Once even earliest stages of the above-listed changes occurred, the lineage(s) could be considered eutherian mammals; a crucial milestone in eutherian evolution had been reached. As suggested in Fig. 8, the principal change of adaptive consequence was increased duration of active intra-uterine morphogenesis. Such was allowed by enhanced protection of foetal-derived tissues against attack from the maternal immunological system (see Lala *et al.*, 1984); protection was by way of physiological activities within phylogenetically neomorphic trophoblastic tissues in cooperation with immunologically specialized cells of the endometrial wall.

Prolonged internal gestation also depended upon gradual development of endocrinological adaptations associated with increasingly sophisticated forms of placentation (see Porter, Heap & Flint, 1982). Initial selection for development of such adaptations probably directly involved relative shortening of energetically expensive (see Sampson & Jansen, 1984:46) lactation. The relative shortening of lactation allowed more rapid reproduction at no more cost to the mother (and probably at *less* cost; see Millar, 1977, McNab, 1978b), and with potential for heightened fecundity. As discussed by Forsyth & Hayden (1977), however, the greater anatomical maturity (and energy requirements) of eutherian neonates required concomitant evolution of endocrinological enhancement of mammatogenesis during pregnancy, such that copious milk secretions would be available soon after birth; this appears to be another important trophoblastic function among disparate lineages of eutherians.

Innovations summarized above formed the inception of the eutherian mode of reproduction. Additionally, they provided foundations upon which selection for

elevated metabolic rates (see Fig. 9) could act, by way of increasing prenatal and postnatal growth rates, shortening the interval of high maternal energetic drain, and further increasing fecundity. As discussed earlier, no marsupial studied to date has high adult basal metabolic rates; all are below the 'expected' Kleiberian value (for mammals in general; see Hayssen & Lacy, 1985) at any given body size. We argue that marsupials, because of their phylogenetic retention of commitments to development via prolonged lactation, have little 'reason' to maintain energetically costly, high rates of metabolism. Elevated metabolic rates in small eutherians, as seen in above discussions, appear most advantageous (adaptively and energetically) in enhancing rapid and extended intra-uterine morphogenesis (comparatively less costly) and thereby shortening the relative interval of lactation (more costly). These benefits would be ineffective within constraints of the style of reproduction characteristic of *most* marsupials, although some didelphids may shorten lactation by elevation of maternal metabolism during the nursing period (Thompson & Nicoll, 1986).

We see the most important evolutionary processes of eutherian origins as having occurred in two, probably closely-sequential steps: (a) trophoblastic innovation linked with physiological sophistication of pituitary/placental/uterine/mammary gland interactions; quickly followed by (b) increases in adult metabolic rate. The two steps, once established, would have been adaptively synergistic. We suspect, as a result, that evolutionary rates would have been very high among lineages of early eutherians. We emphasize, however, that the initial sequence of the above evolutionary steps logically follows only (a) to (b); additional increases in fecundity/ r_{\max} (aided by heightened metabolic rates) would have depended on specializations in placentation, not vice versa. Thus, competitive benefits resulting from increased metabolic rates (such as increased fecundity and potential for more rapid population growth) were secondary, depending for their origin upon initial reproductive innovations that allowed the strictly-eutherian combination of intimacy in placentation plus rapid, sustained morphogenesis *in utero*. Assuming sympatry of species with similar ecological requirements, the 'fast-living' species with higher metabolic rates (and resulting greater r_{\max}) in most cases would be expected to swamp out their contemporaries, as long as foods used permit high metabolic rates (McNab, 1980: table 1). Rates of population growth would have been greatest at times when the influences of seasonal retardation of reproductive cycles were minimal.

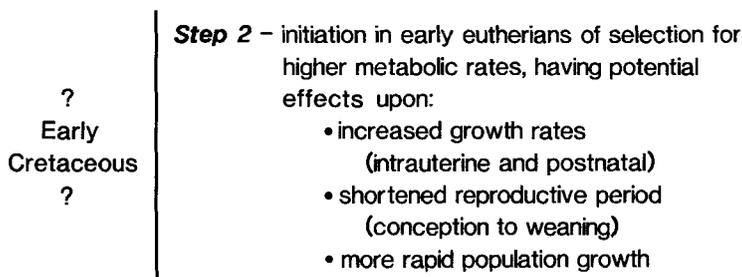


Figure 9. Hypothesized second step in the origin of eutherian mammals, presumably quickly following Step 1 (see Fig. 8). The animals involved still were of small body size, and refinements of trends begun in Step 1 probably continued simultaneously, and at rapid rates. See text for further explanation.

ADDITIONAL EVOLUTIONARY IMPLICATIONS TO BEING AN EARLY EUTHERIAN

Introduction

The eutherian style of reproduction, which involves rapid and prolonged intra-uterine development, appears to have evolutionary implications far beyond enhanced potential for rapid growth of populations. Though mechanisms in most cases are poorly understood, eutherian reproduction is linked with enhanced diversity in relative brain size/complexity, longevity, gregariousness and, perhaps, chromosomal plus morphological evolution. We defend this supposition in the following sections.

Brain development

As stated by Hofman (1982:94), because brain size (and most importantly for mammals the cerebral cortex) “. . . is almost completely determined by its neural elements (number of cells, size of cells and number of connective fibers), any size increase can be translated in terms of its basic elements.” Thus, because comparative brain size (and relative proportions of its parts) can be related to numbers of neuronal elements and their connections, biological relevance in terms of brain function can be tied thereto (see Welker, 1976).

Looking across the diversity within mammals, gross brain mass (approximating volume and mass) scales to an exponent of about 0.75 of body mass (Hofman, 1982; Martin & Harvey, 1985). Variations in brain mass exist, however, as much as a factor of five to either side of the average value for any given body mass (Martin, 1981), associated in part with patterns of life histories (Harvey & Bennett, 1983). Neuronal and glial packing is less dense in brains of large mammals than in brains of small species (see Jerison, 1973: fig. 3.3). Similarly, sizes of individual neurological cell bodies are greater in mammals of large body size than in small species. Nevertheless, on an absolute basis, larger brains have vastly more neurons and glia, and exponentially larger numbers of interneuronal associations (see Welker, 1976). Kalat (1983:312) stated: “Through an increase in the number of neurons or the number of their synaptic connections, the brain becomes capable of making a larger number of associations, processing more information, holding it longer, and more accurately keeping track of both similarities and distinctions among many experiences.” A positive link between proliferation of patterns of association neurons and “intelligences” (see Jerison, 1985) seems inevitable.

Precious few studies on neurological development of marsupial brains have been conducted. Work to date, however, shows most processes to be in common with those known for eutherians. In both groups, for example, gliogenesis, maturation of neurons, and development of synaptic connections within the brain continues far into postnatal life (Lund, 1978; Renfree, Holt, Green, Carr & Cheek, 1982). Minor glial proliferation even occurs in adults of some eutherians (Jacobson, 1978).

An important difference, however, is seen between eutherians and marsupials in the relationship between time of birth and embryonic differentiation of neurons (neuronogenesis) from the ventricular wall of the primitive brain (see Purves & Lichtman, 1985, for general features). Although some highly restricted

postnatal brain neuronogenesis is known among eutherians (Jacobson, 1978), virtually all brain neurons originate in that group prior to birth. Postnatal life in eutherian brains is characterized by development of interneuronal connections and synaptogenesis (Jones, 1981), neuronal maturation (Berry, Bradley & Borges, 1978), organization of neuronal tracts (Ebbesson, 1984), and neuronal death (Oppenheim, 1981; Zamenhof & van Marthens, 1979). As discussed by Hall & Oxberry (1977), spontaneous and evoked electrical activity of the brain begins early in developmental stages following the main period of neuronal multiplication.

Marsupials, in contrast, continue the process of neuronogenesis in certain parts of the brain well beyond the time of birth (Morest, 1970; Cavalcante & Rocha-Miranda, 1978). As an example, neuronogenesis in the superior colliculus and caudal pretectum of the midbrain of *Didelphis* continues for nearly two weeks into postnatal life (Cavalcante, Rocha-Miranda & Linden, 1984).

The term encephalization (including cerebralization, the increase in volume and complexity of the cerebral cortex), of course, implies more than proliferative neuronogenesis. It also involves proliferation of glial cells and growth in size to adult proportions of all brain cell bodies and their cytoplasmic extensions. The process of brain growth in eutherians and marsupials involves both intra-uterine and postnatal periods. Further, effective increase in adult eutherian brain size is positively correlated with the amount of time available for active *prenatal* morphogenesis (Müller, 1969a, 1972b). Species of eutherian mammals born in precocial states have larger adult brains, relative to body size, than species born in altricial states, and the gestation period of the former tends to be longer (Zeloff & Boyce, 1980). Under the assumptions and statistical procedures employed by Martin & MacLarnon (1985:222; see Zeloff & Boyce, 1986), "... a typical precocial mammal has a gestation period almost four times longer than a typical altricial mammal of the same body size." Also, eutherians (such as man; see Zeloff & Boyce, 1982; Sacher, 1982) that combine extraordinarily high levels of encephalization with birth at altricial body states have unusually long periods of gestation in comparison with less encephalized species of the same body mass.

Thus, in eutherian mammals, the intra-uterine environment and extended durations of pregnancy (less any early intervals of morphogenetic quiescence) appear to be crucial to development of large adult brain size. In contrast, no correlation of biological consequence exists among species of marsupials between duration of active morphogenesis during pregnancy and relative extensiveness of adult cerebralization. Marsupial species of larger body size have among the lowest ratios of brain mass to maternal body mass seen within therian mammals (see Lee & Cockburn, 1985: fig. 3.13; Nelson & Stephan, 1982). Recall that extended gestation (see Tyndale-Biscoe, 1984: 439) in association with sustained intra-uterine morphogenesis is unknown among marsupials.

As discussed by Johnson (1977) and Meyer (1981), gross proportions of major brain parts are similar between marsupials and eutherians. Many species of eutherians also have low levels of encephalization, especially at small body sizes. For example, no significant difference exists between eutherians and marsupials in average values for ratios of adult body mass to brain mass for species with body mass less than about 100 g (see Lee & Cockburn, 1985: fig. 3.13). For animals in excess of 1 kg, however, the relative brain size of marsupials falls

progressively below that of eutherians. Metabolically costly (see Hofman, 1983, and Armstrong, 1983, 1985), relatively large brains do not exist in mammals of very small body size.

As emphasized by Riska & Atchley (1985), selection on the genotype that controls brain growth probably acts at two quite separate developmental levels, 'hyperplastic', and 'hypertrophic'. Genes emphasizing hyperplastic development are associated with embryonic stages, and largely control increases in specific brain cell numbers. Genes controlling hypertrophic growth, in contrast, become active later in development, affecting changes in brain cell size, functional maturity and structural reorganization. Also, experimental enrichment of experience in growing and adult rodents is known to result in enlargement of cortical mass and individual neurons, together with increases in numbers of glial cells (see Rosenzweig, 1979). Synaptic sizes and numbers can be increased by raising animals in complex environments, with associated improvements in performances in maze tests (Greenough & Juraska, 1979).

The intra-uterine environment experienced by embryonic eutherians would appear to approach the ideal for allowing extensive hyperplastic neuronogenesis; external stimuli are at a minimum, and trophoblastic tissues (functionally cooperating with the mother's body) provide oxygen and all needed nutrients, eliminate metabolic wastes, provide ionic controls for physiological activities, and perhaps synthesize substances promoting embryonic growth (see Tarlatzis, Sanyal, Biggers & Naftolin, 1984). Complex physiological functions that in other amniotes must be done by the developing organism itself are minimized. Developmental hyperplastic emphasis, therefore, can be placed upon establishment of rudiments of large, complexly structured brains (see Martin & Harvey, 1985). Maternal malnutrition during early stages of foetal development has been shown to have serious consequences on brain development and function in a diversity of eutherians (Cheek, 1975; Hall & Oxberry, 1977). Conversely, Zamenhof & van Marthens (1979) have shown that neonatal brain mass (and total DNA, correlated with numbers of neurons) in rats can be increased through experimental supernutrition of the pregnant mother.

Pond (1977: 193) argued: "Whether the early embryonic development takes place in an egg, in a nest or pouch, or within the mother is shown to be of minor importance in determining other features of the anatomy and growth processes." However, neonatal marsupials, which are true embryos on several generally accepted anatomical and physiological criteria (see Block, 1964), must gain all energy for continued growth from milk, suckled through their own muscular activity. Oxygenation must be accomplished via muscularly-controlled functional lungs (Farber, Fisher & Sant'Ambrogio, 1984), plus perhaps some cutaneous respiration. A mesonephric kidney eliminates nitrogenous wastes.

Little is known about the metabolic processes by which tiny newborn marsupials convert nutrients from serous milk to molecular forms useful in cellular growth. Much of the anabolic activity, however, must be coordinated by the neonatal liver (see Block, 1964, and McCrady, 1938), in contrast to analogous extra-embryonic (placental) metabolic activities existing at comparable anatomical stages among prenatal eutherians. Postnatal growth rates in marsupials (see Case, 1978, and Cutts, Krause & Leeson, 1978) decline sharply from prenatal levels, and are much slower (see Loudon, Rothwell & Stock, 1985) than growth observed in correlative morphogenetic stages in

eutherians. Achievement of endothermy in marsupials (see Walker & Berger, 1980) is much delayed in postnatal marsupials relative to even the most altricial eutherians (Morrison & Petajan, 1962; Case, 1978; Russell, 1982). Thus, contrary to Pond's (1977) assertion quoted in the preceding paragraph, processes of marsupial external development may well have consequential differences from those occurring within the eutherian uterus.

Krous, Jordan, Wen & Farber (1985) demonstrated that branches of the vagus nerve in opossum pouch young become functional prior to myelination at a stage much less anatomically mature than is characteristic of early vagus function in eutherians. Perhaps because of such requirements for similarly early somatic neurological independence of function, conditions in marsupials are less favourable for potentially extensive hyperplastic brain development than in eutherians, especially as adult body sizes increase. As shown by Müller (1972–1973), the cerebral cortex of marsupials develops more slowly, in lesser volume, and to lesser degrees of complexity than in eutherians. Hofman (1982: table 1 and fig. 2), using quite a different approach to evaluation of evolutionary progression of the cerebral cortex, demonstrated that *Didelphis* has the smallest relative brain size among the 19 mammalian species he studied (18 were eutherians, representing eight orders).

Müller showed that the interspecific rate of intra-uterine brain growth in marsupials is quite uniform, using the time of first appearance of endoderm as a reference starting marker. Similarly, Sacher's & Staffeldt's (1974) allometric analysis (employing 91 species of eutherians of 12 orders) showed a remarkably stable relationship between the cube root of neonatal brain mass and gestation time. In comparison, variation in allometric relationships between neonatal body mass and gestation times was observed to be several-fold greater. Sacher & Staffeldt (1974) concluded that intra-uterine growth of the brain, which is the slowest-growing organ of the mammalian body, is the single most important determinant of the duration of gestation. The brain must grow at its own intrinsic rate (see Passingham, 1985), and the sophistication of brain development at birth must be appropriate to the level of body structure characteristic of the species at the time of birth. We add that extensive hyperplastic neural development is most efficiently done within the intra-uterine environment.

As discussed in an earlier section of the present paper, gestation periods in eutherians can be shortened through increased maternal metabolic rates. Intra-uterine rates of neural development, however, are rather stable and, once begun, appear to be difficult to speed up, interrupt, or even slow down. Sacher & Staffeldt (1974:606) stated: "The disadvantage of a reduced rate of fetal growth in homoiotherms must be severe, for in the ecological situations that require postponement of birth, this requirement is almost always met by means of delayed implantation or delayed fertilization. It can be inferred that reduced growth rate is not resorted to because it is a suboptimal method for achieving delay of birth." Miller (1981) noted the relatively constant nature of eutherian foetal bodily growth rates, and Sacher & Staffeldt (1974) put particular emphasis on eutherian high stability in rates of prenatal neural growth.

Thus, as recognized by Portmann (1962) and Müller (1969a) and as approached above using more recent studies from several different perspectives, the intra-uterine environment appears crucial to development of advanced

levels of encephalization among mammals. Nevertheless, selection for relatively large brains probably was not an important factor in the origin or early evolution of eutherians, but developed later in several distinct lineages. The fossil record, incomplete as it is, suggests that extensive eutherian cerebralization occurred first in the early Cenozoic (Jerison, 1973), with steps in that direction initiated in the Late Cretaceous (Kielan-Jaworowska, 1984a, 1986). Larger brains in certain lineages of eutherians would seem to be an almost inevitable, adaptively useful byproduct of prolonging internal gestation in concert with sustained morphogenesis. Gradual extensions in the duration of embryonic neuronal hyperplasia, and all the adaptive implications derivable therefrom, became possibilities. Although determination of cause versus effect in evaluation of brain evolution usually is enigmatic, the conclusions seem reasonable (and consistent with the fossil record) that advanced cerebralization (Fig. 10) in mammals was secondary to, and probably dependent on, the evolution of the style of prolonged, active intra-uterine morphogenesis characteristic of eutherians.

Longevity

A feature developed in association with increased cerebralization in several descendant lineages of eutherians is increased longevity. Hofman (1983) suggested that mammalian longevity is a complex phenomenon, dependent upon two opposing primary components: (1) basal metabolic rate, and (2) evolutionary degree of encephalization beyond what is expected in a species from an allometric basis for any given body mass.

Mammalian maximum potential life span was found by Hofman (1983) and McNab (1983b) to vary as a reciprocal of the basal metabolic rate; that is, 'faster-living' species generally die sooner. Countering that tendency, however, is the fascinating observation that mammals can be expected to live longer in direct proportion to phylogenetically advanced size increases in those parts of the cerebral cortex that presumably are involved in higher-order brain activities—beyond those associated with body size and primary sensorimotor function. Calder (1985:163) has shown that, within limits of available data,

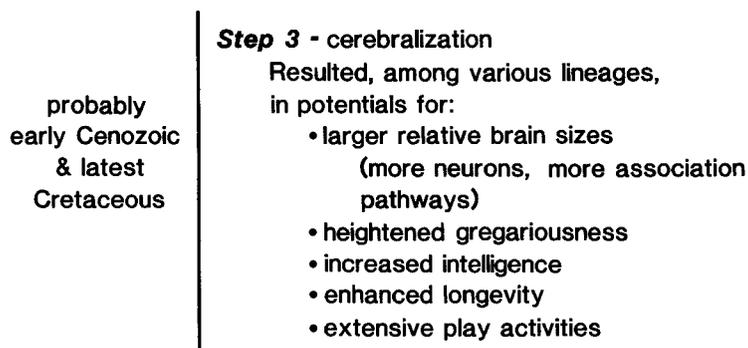


Figure 10. Potential secondary effects (see Figs 8, 9) among certain lineages of Cenozoic eutherians of increasing the time of intrauterine active morphogenesis of the foetus. The size and complexity of the brain (most importantly the cerebral hemispheres) depends in mammals upon the duration of prenatal development that involves active morphogenesis. See text for further explanation.

“... for a given size, marsupial longevity tends to be brief compared to eutherian mammals.” This is in spite of their generally low rates of metabolism. As discussed above, enhanced encephalization among mammals seems to have been dependent upon prior establishment of the eutherian style of reproduction. Any derivative benefits by way of increased longevity, therefore, may have had the same dependence of origin.

Gregariousness

Knowledge of social organization among marsupials was summarized in the excellent review by Russell (1984). Although vast informational gaps concerning social patterns exist within the Marsupialia, the generalization that most members do not engage in group living is correct. The incidence of polygyny and monogamy is less than in eutherians (see Zeveloff & Boyce, 1980) and, as in most mammals, mating is promiscuous and male parental care is of little import. Even territoriality among marsupials is a comparative rarity (Lee & Cockburn, 1985:44,160). The highest levels of gregariousness observed among living marsupials occur in the Macropodidae (which, incidentally, also are specialized in having among the largest body sizes and highest levels of neocortical development in the order). Russell (1984: 146) stated: “Most marsupials do not have a life history pattern which favours selection of the increased relative brain size which would be necessary for the evolution of complex social organization.” Although we disagree that relative brain size need be large among mammals to allow “complex social organization”, life-history patterns certainly are closely intertwined with levels of gregariousness.

Several possible contributing factors to low levels of group living in marsupials were considered by Russell. She focused, however, on the unifying nature of their reproduction as being most important. She stated (1984: 148): “... to a large extent, the marsupial pattern of reproduction and, in particular, the pattern of parental care based on the pouch have rendered inoperable one of the driving forces in selection for non-promiscuous mating systems and long-term male-female bonds.” We have argued that reproduction in the small mammals that comprised the last common ancestor of marsupials and eutherians was characterized by emphases on temporally extended lactation and postnatal morphogenesis (i.e. as in modern marsupials). Thus, if Russell’s suggested connection between style of reproduction and limitations on gregariousness is correct, it may be that the dominance of essentially solitary existence among most marsupials adaptively parallels a phylogenetically ancient aspect of therian mammal behaviour. With obvious exceptions (e.g. bats and naked mole rats), selection among small mammals (marsupials and eutherians alike) in most cases has not favoured heightened gregariousness.

Play

The phenomenon of extensive ‘play’ often is considered to be associated with heightened social complexity among mammals. Burghardt (1984) provided an interesting summary of the general interdependence among metabolic energetics, dietary habits and extent of brain development upon expression, presumed functions and origins of mammalian play. The roles or importances of

play to mammalian behaviour in most cases are uncertain. Nevertheless, play is not an obvious feature among juveniles of most species of marsupials. Though at this point only an hypothesis ripe for testing, it may be true that purported social and motor benefits derivable from extensive play activities (as commonly are seen among eutherians) may be serendipitous bonuses made possible by origin of the peculiar eutherian form of reproduction, as linked with brain development and high rates of metabolism.

Chromosomes and evolution

Significant differences exist between chromosomal complements of marsupials and eutherians in terms of ranges of diversity. In the following section, we attempt to set such differences into evolutionary contexts. At the moment, however, conclusions regarding the underlying bases for these differences cannot be firmly established. Nevertheless, the following section, while especially speculative, is provided to summarize the present status of the subject and to propose hypotheses suitable for further testing. Despite uncertainties, it appears unlikely to us that the vast karyological differences observed between marsupials and eutherians are devoid of biological consequence.

The taxonomic distinctness of most named species of vertebrates was recognized initially on the basis of morphological differences (e.g. tail lengths, cranial structure, coloration, etc.) from their contemporaries. Thus 'taxonomic distance' within the Linnean hierarchy and extensiveness of comparative morphological differences are to some degree related. Such a relationship was applied as an underlying principle to the study of mammalian karyotype evolution by Wilson, Bush, Case & King (1975), Bush, Case, Wilson & Patton (1977), and Bengtsson (1980). These authors showed that relative interspecific 'taxonomic distance' (determined traditionally by comparative morphology) is generally correlated with karyotypic diversity, as measured by diploid and chromosome arm numbers. This relationship between the amount (or rate) of karyotypic change within any single group and its expressed range of taxonomic diversity led some authors (e.g. Wilson, Sarich & Maxon, 1974; Wilson, White, Carlson & Cherry, 1977) to suggest a causal relationship between chromosomal rearrangements and morphological evolution. The latter was viewed to result from adaptive changes in gene regulation brought about by structural chromosomal rearrangements shifting linkage relationships. Although initially appealing, for several reasons this simplistic view is no longer held by most investigators (for critiques, see Charlesworth, Lande & Slatkin, 1982; John, 1983; Larson, Prager & Wilson, 1984). For one, there are simply too many examples of morphologically cryptic species that differ almost solely by karyotype (the remarkable example of the Indian and Chinese muntjacs, in which $2n$ ranges from 6 to 42, is but one obvious case (Shi, Ye & Duax, 1980)). Secondly, there exist examples of morphological diversification that are devoid of obvious karyotypic differentiation (e.g. the 120 or so species of homosequential picture wing *Drosophila* of Hawaii (Carson, 1981)). Moreover, most karyotypic mutations have no visible phenotypic effects (see Lande, 1979, for review). Rather, taxonomic and karyotypic diversity probably co-vary only as a function of the underlying genetic or population conditions which promote general differentiation.

Gross karyological morphology is altered in mammals by mutations that generate a structural rearrangement of existing gene order (or linkage relationships), or by mutations affecting the amount and position of specific underlying sequences. Among the former are the classical cytological rearrangements of fusions, fissions, translocations, inversions, and so forth; among the latter are amplification of repeated sequences associated with heterochromatin additions (or deletions), transposable elements shifting position among non-homologous chromosomes, and the activation or deactivation of specific gene loci, such as ribosomal sites (see Lewin, 1980, for general review). There are numerous examples among the Mammalia for structural rearrangements of all types, and different taxa exhibit wide variance in the types of rearrangements observed (see Patton & Sherwood, 1983, as a general review for rodents; Baker, Haiduk, Robbins, *et al.*, 1982, for bats). Less is known about the second class of cytological mutations, although it is clear that heterochromatin variation is extensive in many mammalian groups, such that cellular DNA content can vary by a factor of two to three (see Sherwood & Patton, 1982).

Imai, Maruyama & Crozier (1983) presented evidence that most mammalian karyotypic evolution at a gross level has occurred through a combination of centric fissions and pericentric inversions; the long-term, statistical result has been a general tendency toward increased haploid numbers (n) and increased chromosomal arm numbers. They also recognized, however, that evolutionary "back eddies" of centric fusion also have occurred, opposite in direction from the general statistical trend.

As reviewed by Sharman (1973), Hayman & Martin (1974), Hayman (1977) and Rofe & Hayman (1985), the diploid number among marsupials is low, varying from 10 to 32. The range of $2n$ variation is much larger among the Eutheria (see Matthey, 1973, Hsu & Benirschke, 1967–1977; and Gardner, 1971), varying from 6 to 92 (*contra* Tyndale-Biscoe & Renfree, 1987: table 10.1). According to interpretations cited above by Imai *et al.* (1983), the characteristically low diploid number (and its low range of variation) of marsupials would approximate a primitive condition among therian mammals. Presaging such a conclusion, Reig, Gardner, Bianchi & Patton (1977) suggested that the low diploid number of 14 was primitive not only for American didelphid marsupials, but for "metatherian" mammals in general; increased diploid numbers among marsupials occurred mainly via centromeric fissions, but at very low (bradytelic) rates.

Studying Australian species, Rofe & Hayman (1985) also suggested karyological bradytely, with $2n = 14$ as a primitive number for marsupials, and with independent evolutionary chromosomal increases in various lineages by way of centric fissions. Further, Rofe & Hayman (1985) observed identical or near-identical autosomal patterns of G-banding among representatives of taxonomically disparate families of marsupials. On this basis, they argued for existence of high-level conservation of homologous segments of equivalent chromosomes among marsupials since the metatherian-eutherian phyletic separation. Thus karyological evolution of positions of banded sequences has been slow among most marsupials (although higher levels of repatternings were reported among certain phalangeroids). Rofe & Hayman (1985:49) stressed, however, that although the absolute amount of syntenic linkage groups would

be high in mammals with low chromosome numbers (such as marsupials), various cytological (and populational; see Hayman & Martin, 1974:51–52) mechanisms nevertheless exist to aid release of genetic variability; therefore, “The conserved complement should not be thought of as a limitation to evolutionary innovation.”

Other studies have stressed the comparatively low rates of karyological change among marsupials (e.g. Wilson *et al.*, 1975; Imai *et al.*, 1983; Casartelli, Rogatto & Ferrari, 1986) relative to eutherians. Wilson *et al.* (1975) showed that the calculated rate of karyotypic evolution (changes per million years) in eutherians has been several-fold that estimated for marsupials and other non-eutherian vertebrates. Bush, Case, Wilson & Patton (1977), using different assumptions and modes of calculation, found similarly large discrepancies between rates of change in marsupials versus eutherians. Imai *et al.* (1983) developed yet another means for estimating comparative rates of karyotypic evolution among mammals, and found that marsupials have had markedly the slowest rates (changes per million years) of any extant therians in terms of (1) karyonumber changes (2) chromosome number changes and (3) chromosomal arm number changes. According to summary statistics presented in their table 2, the estimated eutherian mean (combining all orders) for karyonumber changes per million years is roughly four times the estimated mean for marsupials. Finally, although Bengtsson (1980) studied only eutherians, he showed that high rates of karyotype evolution have occurred commonly and independently within many (though certainly not all) lineages, especially in species of small body size and within genera exhibiting high taxonomic (= morphologic) diversity.

As quantified earlier, there are fewer extant species of marsupials than eutherians, thus raising the possibility that observed differences between the two groups result from artefact of available sample sizes (see Lee & Cockburn, 1985:78). In light of the fact that the origin of marsupials was at least as ancient as that of eutherians, however, at least equal time for the evolution of karyotypic diversity has been available for marsupials, found in company of eutherians on all continents during Cenozoic time (*contra* Tyndale-Biscoe & Renfree, 1987:422). Few doubt, therefore, that the comparative marked conservatism in marsupial karyotypic evolution is a genuine phenomenon, probably with biological meaning. Further, because only members of the Eutheria among vertebrates (exclusive of birds, which generally have not figured into calculations of evolutionary rates in karyotype) show evidence of inordinately rapid rates of karyotypic change, we suggest that fundamentally different consequences of mode of karyotypic evolution may exist between marsupials as a group and many lineages of eutherians.

Documentation that differences exist in karyotypic diversity between marsupials and eutherians is, however, far simpler than determining the reasons behind the observation, or the significance to overall evolutionary diversification within and between each group. As presented by Larson *et al.* (1984), rates of chromosomal evolution (E) may be viewed as a product of two rates given by the equation, $E = MF$, where M = mutation rate producing chromosomal rearrangements and F = fixation rates for these rearrangements. Differences in chromosomal diversity within and among lineages can thus result from differences in the absolute rate for either, or both, M and F .

Certain types of rearrangements might be predominant within a given lineage both because of the existence of chromosomal 'hot-spots' (specific sites on chromosomes where break-points occur repeatedly and at probabilities greater than chance; e.g. Aurias, Prieur, Dutrillaux & Lejune, 1978), and because of meiotic mechanisms maintaining balanced gamete formation. Nevertheless, general chromosomal mutation rates are not known to vary greatly among a wide variety of animal taxa (see White, 1973, and Lande, 1979, for reviews), although the rate of incorporation of rearrangements into population karyotypes can vary greatly depending both upon the organism and the type of rearrangement in question (e.g. see Stone, 1949). The differences between marsupials and eutherians in overall karyotypic diversity probably do not result from fundamental differences in the population conditions enhancing fixation of novel rearrangements (*contra* Bush *et al.*, 1977), or from fundamental differences in meiotic capabilities. Rather, these differences likely reside in either, or both, (1) the architectural designs of the chromosomes characteristic of either group, (2) fitness differentials that determine the probability of incorporation of mutations into the underlying karyotype.

Sequences of nucleotides housed on enormously elongated strands of nuclear DNA in the form of chromosomes provide the principal control of protein synthesis and embryogenesis for all eukaryotes. Various forms of microscopy, plus a diverse and rapidly growing arsenal of recombinant DNA techniques, now allow recognition and mapping, within and among species, of particular segments of chromosomes that are structurally unique, identifiable through biochemical (and sometimes functional) correlation and are interpreted as phylogenetically homologous sequences (see Roderick, Lalley, Davisson *et al.*, 1984).

Some unique nucleotide sequences are regularly repeated as 'families', either on the same chromosome (in tandem positions, or scattered variously along the length of the chromosome; see Dutta, 1984) or on other chromosomes of the species' genome (see Brown, 1984). Homologous repeated families of chromosomal segments often can be identified in other species (see Ohno, 1973), but particular species commonly show diagnostic variations in the sequence. Good correlation exists within species of higher organisms between highly repeated DNA sequences and regions of heterochromatin in the chromosomes (see Lewin, 1980, for general review; Dennis & Peacock, 1984), thus suggesting a general reliability of various histochemical banding techniques to the identification of homologous chromosomal segments. Many identified chromosomal sequences appear to have been ancient in origin, conserved in some cases essentially unchanged since Precambrian time (see Bishop, 1983). Certainly, the mammalian X-chromosome is a linear sequence of genes highly conserved across both metatherian and eutherian taxa (Pathak & Stock, 1974; Ohno, 1984), and certain autosomal linkage groups are widespread among a diverse group of eutherians (such as *Mus* and humans; Lalley, Minna & Francke, 1978). This structural stability and taxonomic ubiquity exhibited by many of these gene units suggest that the contained information is of vital functional importance to the organism itself (Bishop, 1983).

As discussed by Trosko, Chang & Wade (1984), the origin of heritable variability (mutations) derives both from alterations in the genes themselves (i.e. point changes in arrangement of nucleotide base pairs, gene repetition, intra- or

interchromosomal additions) and from gross chromosomal rearrangements. Experimental procedures that do not damage the DNA show that induced chromosomal rearrangements often affect fidelity of replication of normal DNA and chromosomal replication, abilities to repair damaged DNA and normal chromosomal segregation at meiosis (see Trosko *et al.*, 1984). Most of these processes, of course, are crucial during ontogenesis, and all are needed for the very processes that sustain life. Thus the position of genes relative to the length of the chromosome in many cases really does seem to matter. Relatedly, selection against deleterious 'position effects' probably explains in large part the marked stability of syntenic genes and genetic linkage groups (see Stallings, Munk, Longmire *et al.*, 1985, and Roderick *et al.*, 1984) conserved among many mammals on sex chromosomes and autosomes alike.

Nadeau & Taylor (1984:818) accepted the idea that chromosomal rearrangements (especially translocations and inversions) have been the principal mechanisms during genomic evolution of disrupting linkage groups. Nevertheless, they challenged the concept that conservation of autosomal linkages can be ". . . regarded as evidence that certain autosomal segments are protected from chromosome rearrangements because of regulatory or functional interactions between the loci involved." Rather, Nadeau & Taylor suggested the simpler interpretation that conserved chromosomal segments are mere relics, undisrupted (through chance alone) by chromosomal rearrangements. They specified that independent evidence for active protection of autosomal linkages would be needed to show functional importances for conserved linkage groups. Such independent evidence is lacking, not because it has been unsuccessfully sought, but because our knowledge of the architecture of chromosomes and their underlying DNA sequences is still far too meagre to permit an investigation of the question.

It can be argued, however, that the existence of karyotypic uniformity, as within the Marsupialia, provides indirect evidence for active linkage conservation through evolutionary time. This is the interpretation provided by Reig *et al.* (1977:209–210) who advanced a "metatherian supergene" hypothesis: "According to this scheme, the relative constancy observed in didelphid karyotypes may be a reflection of a rather rigid pattern of gene coadaptation by internal balance . . . which is believed to be the result of the stabilization of definite sets of linked genes established through the action of epistatic selection . . . early in the evolution of the family." "The mechanisms of genic regulation may lie in the sequential structuring of families of repetitious and non-repetitious DNA within the chromosomes. Therefore, most chromosomal rearrangements would modify these sequential patterns and disrupt the regulatory systems."

As suggested by Reig *et al.* (1977), one prediction of the 'supergene' hypothesis as applied to mammalian evolution is that rates of chromosomal and morphological changes should be correlated positively. Among mammals, as noted above, there is a general relationship between karyotypic diversity and taxonomic diversity. And as applied within the Marsupialia, didelphids have low karyotypic and morphological diversity. Phalangeroids, in contrast to other superfamilies of marsupials, not only have the greatest range of karyotypic diversity (see Rofe & Hayman, 1985: table 1), but also show the greatest range of bodily morphological variation. Looking more broadly within therian

mammals, Lee & Cockburn (1985:39–43) stressed that extant marsupials are known to fill only 15 of the 83 ‘macroniches’ (of Eisenberg, 1981) used today by eutherians; the much greater range of karyotypic diversity among eutherians was stressed above. The comparatively more prolific extent of speciation within eutherians (see Lee & Cockburn, 1985:78) in itself is an indication of higher magnitude of morphological variation (though speciation is not necessarily accompanied by morphological change).

Clearly, however, the ‘supergene’ hypothesis (in terms of causally linking bodily morphological change with karyotypic alterations) cannot be applied with any degree of generalization among the eutherians. The case of the sibling species of muntjac with diploid numbers of 6 and 42 was given above, and the cytological literature is replete with examples of similarly extensive chromosomal differences among closely related species. Moreover, karyological variation also can be great within many species of eutherians. As pointed out by Hsu & Benirschke (1977:iii), for example, karyotypes tend to be so polytypic within muroid rodents (the most speciose group of extant mammals; see also Patton & Sherwood, 1983) that often a single karyotype is inadequate to characterize a species.

While recognizing the general inapplicability of the ‘supergene’ hypothesis to eutherians, might it remain as an appropriate and ultimately testable hypothesis as applied to the Marsupialia? Might there be varieties of gene interactions among marsupials that are strong enough for selection to actively preclude more frequent interruptions of chromosomally-bound genes? Rofe & Hayman (1985:47) approached the second question in the negative by stating: “It is not possible to identify similar reproductive and ecological factors that would explain the marsupial data. The diversity of life forms and reproductive biology found among the marsupials that have retained $2n = 14$ basic complement is considerable, ranging from small, short-lived, rodent-like animals (among the Dasyuroidea) with large litter numbers to large, longer-lived animals with smaller litter numbers (among the Vombatoidea).” We suggest, however, that one unifying biological factor seen among the marsupials may have been overlooked within such an argument.

As discussed earlier, all marsupials restrict most of their active prenatal morphogenesis (and essentially all prenatal organogenesis) to the latter stages of intra-uterine life, generally to the last few days of an otherwise highly variable interval following fertilization. Lillegraven (1975), in congruence with the “metatherian supergene” hypotheses of Reig *et al.* (1977), suggested that an extensive genetic synteny existing within marsupials (presaging the banding data of Rofe & Hayman, 1985) might be related to a necessity for maintaining rigid developmental precision during a short interval of embryogenesis. The very immature neonates must be fully prepared for external life, and must be capable of independent travel to, and affixing onto, a nipple. Although that idea was rejected by Lee & Cockburn (1985:81) on the basis of lack of confirmatory evidence, neither are there directly contradictory data. Moreover, there are additional considerations on related aspects that should be kept in mind.

For example, certain blocks of DNA (given the pejorative term ‘cellular oncogenes’) are known to be present and highly conserved structurally in normal chromosomes. They are taxonomically widespread among mammals and, although most of their functions are not known with certainty, are thought

to have important roles in normal development and growth (Bishop, 1983). As emphasized by Stallings *et al.* (1985:161), oncogenes “. . . would appear to be excellent candidates for gene loci that, if altered, would affect survival.” They argued that blocks of DNA involved in functions of development would be expected to be highly regulated (also see Alberch, 1980), and therefore especially sensitive to changes in gene expression wrought by chromosomal rearrangements. Indeed, such appears to be the case for certain tumours of man in which known oncogene loci have been disrupted by chromosomal mutations of various kinds (see Rowley, 1983). Although we know of no research on marsupials that attempts to link control of early development with particular gene loci, it seems that marsupials, by the very nature of their mode of reproduction, would be excellent candidates for such studies among mammals.

While openly admitting the present lack of evidence for (or against) the hypothesized link between maintenance of close synteny and control of embryogenesis, early morphogenetic development among marsupials does, indeed, show comparatively little variability. Such uniformity, presumably under genetic control, implies significant resistance to variation. Selective maintenance of relatively tight genetic linkage groups (by way of evolutionary maintenance of karyotypic conservatism) is one way of controlling genetic potential for developmental variation. In absence of evidence to the contrary, we suggest that the concept of ‘metatherian supergenes’ is consistent with general knowledge about marsupials; focused research on the early developmental biology of marsupials may provide a solid foundation upon which to test the hypothesis.

In contrast to the situation in marsupials, comparative study of early development among eutherians shows spectacular variation in early morphogenetic sequences. It is reasonable to assume that such flexibility in development is allowed in part because the design of eutherian neonates is not constrained by the necessity of establishing independent means of travel to a nipple following an extremely short period of active morphogenesis. Genetic linkages by way of ‘supergenes’ would be expected to be less important within the eutherian framework of reproduction, involving greater anatomical maturity of neonates. As a corollary, the potential for more rapid karyotypic changes among eutherians may have been secondary evolutionary phenomena, enhanced by prior attainment of their unique style of early development.

ARE MARSUPIALS INFERIOR MAMMALS?

Many discussions have been published over the past two decades about the relative quality of adaptations as seen in marsupials versus eutherians. Unfortunately, semantical confusion and spurious preconceptions have partially obscured the genuine (and more fascinating) biological issues involved. The following quotation (Renfree, 1980:281) provides an appropriate vehicle for discussion of comparative diversification of marsupials versus eutherians: “. . . because they [marsupials] display as wide a range of physiological, morphological, and ecological adaptations as the eutherians, it must be concluded that the marsupial represents an alternative pattern to the already wide range of vertebrate reproductive strategies.”

As reviewed in earlier sections of the present study, the first phrase of

Renfree's quotation is strikingly incorrect; eutherians, in all three specified categories, show significantly greater total ranges of diversification than do marsupials. Nevertheless, as discussed by Lee & Cockburn (1985:76), only the relative investment in offspring at birth absolutely distinguishes all marsupials from all eutherians. Virtually all other differences are of degree, with overlap in expression of characters in most cases between the two groups. Indeed, marsupials have survived since the late Mesozoic and, at least on the island continents, have prospered in sympatry with eutherians. Marsupial species of Neotropical arboreal omnivores have been especially successful in this regard, but, as noted by McNab (1986b), have done so in a niche in which all mammals must operate at low levels of energy expenditure.

Lee & Cockburn (1985:44), in considering the implications of being a "marsupial", suggested that discussion of general adaptive advantages of "marsupialness" versus "eutherianness" is a sterile subject. In light of the entire thrust of the present paper, we heartily disagree. Quite to the contrary, we have pointed out how the common denominator of innovations within the eutherian form of reproduction has opened new corridors for evolution of diversity within the infraclass. The end result, in many lineages of eutherians, has been expression of characters (many of which have clear adaptive significance) beyond the range exhibited by marsupials.

Although we agree with the second part of Renfree's (1980) quotation that the marsupial form of reproduction is an "alternative" mode within the great diversity expressed among vertebrates, we add that such a form of development also seems to present certain local constraints (*sensu* Smith, Burian, Kauffman *et al.* 1985:267) to rates and ranges of mammalian evolution, many elements of which have adaptive consequences. The form of reproduction, whether marsupial or eutherian, really does matter to the processes of evolution, and hardly can be considered a biologically trivial difference. Whether major steps of ontogenesis are mediated by development in a pouch or in a uterus appear to have important evolutionary and, in some cases, adaptive ramifications.

Despite the documented reality of greater ranges of physiological, morphological and ecological diversification amongst eutherians, we feel that introduction of the pejorative and highly subjective term 'inferior' in reference to marsupials (e.g. Kirsch, 1977; Parker, 1977; Gould, 1977; Renfree, 1981; Hayssen *et al.*, 1985; Lee & Cockburn, 1985; Tyndale-Biscoe & Renfree, 1987) diminishes the otherwise fascinating interdisciplinary subject of the origin of mammalian diversity. We do not recommend (nor have we ever done so) use of the term 'inferior' in regard to marsupials, any more than we would suggest that salamanders or soil fungi are somehow 'inferior' to man. Indeed, most marsupials, as is true for salamanders (see Pough, 1980) and soil fungi, are admirably adapted to their local environments.

Marsupials do, however, retain many primitive or conservative features from their Mesozoic ancestry. These provide important clues to extents and directions of evolution among therian mammals over the last 100 million years. One impediment to fruitful thought on the subject, we suggest, is that the terms 'primitive' or 'plesiomorphic' (in a phylogenetic sense) often have been equated with 'inferior' (in an adaptive sense). Contrariwise, the words 'advanced' or 'apomorphic' (phylogenetically) often have been equated with 'superior' (adaptively). Such correlations in terminology are not necessarily true. For

example, although the characteristically low basal metabolic rate of marsupials (relative to many eutherians) certainly is primitive (relative to tetrapods generally; Else & Hulbert, 1985), low metabolic rates are not necessarily adaptively inferior (witness the large and successful array of functionally specialized species of marsupials *and* eutherians which have low basal metabolic rates). In fact, the lowest basal rates, relative to a mass standard, are found in eutherians (Fig. 7). Low metabolic rates in many cases seem to be fully adaptive; 'primitiveness' (in a phylogenetic sense) and 'adaptiveness' (in an ecological sense) are not mutually exclusive features.

Nevertheless, eutherians stand out as an evolutionary breakthrough as a result of special connections made between energetics and development, and therefore between energetics and r_{\max} . Wherever eutherians use seeds, grass or vertebrates as food, marsupials are at a competitive disadvantage. To the extent that reproductive rates alone can affect competitive interactions, this might explain, in part, (1) the ultimate replacement of marsupial carnivores by eutherian carnivores in South America, and (2) why marsupial carnivores and grazers survive in insular Australia, Tasmania and New Guinea. But when eutherians feed on foods requiring a low rate of energy expenditure (such as invertebrates, fruit or leaves), they have little potential advantage over marsupials because eutherians cannot exploit a coupling of reproduction to energetics (McNab, 1986b).

Furthermore, coupling of energetics with reproduction in eutherians seems to allow use of the boundary curve for endothermy, thereby evading need for daily torpor. Thus, the energetics of eutherians may have facilitated their more successful colonization of cold temperate and polar environments, which marsupials generally have not done (McNab, 1986b). Again, a marked coupling of reproduction to energetics apparently occurred early in the evolution of eutherians; we expect, therefore, that the Mesozoic therian ancestors of marsupials and eutherians were characterized by low rates of metabolism and, coupled to a small size, a propensity to enter torpor.

Whatever the causes of differences between marsupials and eutherians in coupling reproduction to energetics, only eutherians can take full advantage of those food resources (such as grass, meat and seeds) that permit high rates of metabolism by channelling more energy into reproduction. This increase in reproductive output gave eutherians a competitive advantage over all other mammals, therian and non-therian, whenever high intensity resources were used. With this breakthrough, dominance of eutherians usually was assured: (1) in high-intensity food habits; (2) at small body masses; and (3) in very cold climates.

We stress that eutherians taken as a group have enjoyed greater rates and ranges of morphological and physiological evolution than have marsupials. If such modifications prove selectively advantageous under local conditions, species of eutherians generally would be expected to outdistance their marsupial sympatriots in terms of niche occupation, especially if selection favours high intensity habits. If, on the other hand, such features do not provide local selective advantages, little or no difference in survival would be expected between sympatric species of the two groups.

As reviewed above, marsupials are known as fossils from the Cenozoic of all continents. Assuming that the fossil record, with all its various biases, can be

used for even gross comparisons of niche occupation, the features characteristic of marsupials have fared less successfully overall through the Cenozoic than have those characteristic of many lineages of eutherians. Written from the perspective of reproductive physiologists, Tyndale-Biscoe & Renfree (1987:422; based upon Storr, 1958) suggested that the lesser species diversity and geographic distribution of marsupials relative to eutherians “. . . is not because they are marsupials but because they evolved on small and isolated land masses of South America and Australia-New Guinea, whereas the dominant orders of Eutheria evolved in the more competitive areas of the world continent.” Such an explanation is untenable when the known fossil record is considered.

Rather than being a scientifically sterile endeavour, we suggest that comparisons of observable differences between marsupials and eutherians provide a unique framework for (1) recognizing specific elements of mammalian change and/or adaptation, and (2) evaluating relative importances of particular modifications during the evolution of therian mammals. Quantification of differences between marsupials and eutherians can be used to stimulate development of biologically relevant constraints to testable models of the sequence and mode of mammalian evolution. Furthermore, we believe that many otherwise excellent studies of patterns of eutherian life histories (e.g. Sacher & Staffeldt, 1974; Millar, 1977, 1981; Bengtsson, 1980; Zeveloff & Boyce, 1980; Martin, 1981; Armstrong, 1983; Stearns, 1983; Martin & MacClarnon, 1985) would have benefited in terms of general utility and breadth through inclusion of data derived from comparisons with marsupials.

We stand in basic agreement with the following quotation by Tyndale-Biscoe & Renfree (1987:423): “We hope that the perception of marsupials as mammals that took an alternative path in the evolution of those special features of mammalian reproduction—intrauterine development, lactation and maternal care—will prevail, rather than the perception of them as some irrelevant relic of the past. We hope for this, not from a misplaced chauvinism but because we believe that marsupials have much to offer in the quest for understanding of mammalian reproduction.” We add, however, that this alternative path was not without cost in terms of attainment of range of overall diversity.

SUMMARY

Modern marsupials and eutherians share a common ancestry from a rich diversity of therian mammals that lived during Late Jurassic and Early Cretaceous time. The last common ancestor of marsupials and eutherians is palaeontologically unknown, but must have lived at least 100 million years ago. Although the continent(s) on which the phylogenetic separation between marsupials and eutherians occurred is unknown, the oldest generally accepted, recognizable fossils of (1) marsupials are from the early Late Cretaceous of North America, and (2) eutherians from the (with some uncertainty) late Early Cretaceous of Asia. The marsupial-eutherian common ancestor lived under warmer and globally more equable climatic conditions than exist today. The influence of climatic seasonality upon reproductive cycles of mammals during the Early Cretaceous probably was less than exists across temperate and high-latitude areas of the present earth. Although descendant lineages of marsupials existed on *all* continents during various parts of the Cenozoic, they achieved

important diversity only on the 'island continents' of Australia, South America and possibly Antarctica.

The last common ancestor of marsupials and eutherians was of small body size. This ancestor also probably had early embryogenetic development in the form standard for noneutherian amniotes, choriovitelline placentation, a short interval of active intra-uterine morphogenesis, extremely altricial neonates, a lengthy period of lactation, and ureters placed medial to adult derivatives of the Müllerian ducts. It showed low encephalization, mainly solitary behaviour and lacked high metabolic rates. Thus, the last common ancestor of marsupials and eutherians is viewed to have been a highly advanced mammal, similar in most respects to living, small didelphid or dasyurid marsupials; it lacked, however, several of the peculiar specializations which characterize living marsupials.

The first step in the origin of eutherians involved modifications in the process of early embryogenesis, differentiating morular cells into tissues of an inner cell mass versus trophoblast. This is diagnostic for the Eutheria and, because of activities by the trophoblast (in conjunction with specialized cells of the uterine wall) in enhancing foetal immunological protection, allowed development of the unique combination among mammals of intimate placentation plus sustained, active morphogenesis of a foetus. New mammogenic hormones (derived from trophoblastic tissues) provided a copious milk supply at birth to nourish the larger and more mature neonate. Such modifications were of selective advantage because they allowed (1) shifting of energetic investment from less efficient lactation to more efficient gestation; and (2) shortening of overall duration of reproduction, and thereby allowed the animals to increase populations more quickly upon advent of favourable local environmental conditions.

A second evolutionary step, origin of elevated adult metabolic rates, occurred in early eutherians *after* advent of more extensive intra-uterine morphogenesis. Where food habits allowed, heightened metabolic rates resulted in more rapid growth rates, both pre- and postnatally. Thus early eutherians developed linkage between metabolic energetics and rates of reproduction. The combination of more mature neonates plus abbreviated lactation also reduced expenditure of maternal energy needed to sustain respiration by the litter. Marsupials, because of their prenatal restriction to development of extremely immature neonates (combined with their consequent requirement for extended lactation), were put at selective disadvantage in terms of potential rates of population growth when in competition with eutherian sympatriots that had higher metabolic rates. Effects of such constraints were most significant among mammals of small body size which lived under conditions of limited seasonality, the prevailing global situation until after the end of the Mesozoic.

Advent of eutherian specializations in reproduction had secondary evolutionary effects far beyond enhanced potential for rapid population growth. Eutherian reproductive specializations also allowed increased diversity in brain size/complexity, longevity, gregariousness, and, perhaps, chromosomal plus bodily morphological diversification. The comparatively stimulus-protected uterine environment, in combination with manifold physiological activities by the eutherian placental/maternal complex, provided ideal conditions for extensive hyperplastic neuronogenesis, a prerequisite for development of slow-growing, relatively large brains.

The fossil record suggests that unusually large brain sizes (generally

correlated today with heightened intelligences) did not occur until the Cenozoic. In light of stability in rates of brain ontogenesis among modern mammals, and the dependence upon an intra-uterine environment for initial differentiation of neurons, we argue that large brains (with their common correlates of enhanced potentials for intelligence, group living, and longevity) could not develop until after evolution of the eutherian style of reproduction. Selection for markedly increased encephalization was only a secondary phenomenon, however, restricted to a limited number of Cenozoic lineages of eutherians.

Marsupials and eutherians have had equal time since their phylogenetic divergence to develop karyotypic and somatic morphological diversity. Nevertheless, marsupials show a much lower range of chromosome numbers, and exhibit marked intragroup conservatism in karyological features. Eutherians, in contrast, provide many examples of rapid karyotypic change. Positive correlation exists among the marsupials between 'taxonomic distance' (almost universally based upon degrees of organismal morphological differences) and chromosomal features, thus suggesting linkage between adaptations of the body and karyotypic modification. Eutherians, in contrast, have such flexibility of karyotypic features that reliable generalizations cannot be made in relation to correlations between chromosomal and gross bodily morphological features. Eutherians also exhibit much the greater range of general bodily morphological diversification. Thus, we suggest that fundamental differences in the genetics of evolution may exist between marsupials and eutherians.

Differences in mode of reproduction between marsupials and eutherians hardly can be considered biologically trivial. To the contrary, the differences have important implications to processes of evolution. The mode of reproduction characteristic of marsupials presents important local constraints to diversification. Eutherians, with crucial reproductive innovations uniquely linked with metabolic energetics, have enjoyed greater rates and ranges of evolutionary change. Analyses of similarities and differences between marsupials and eutherians provide unique frameworks for (1) recognition of specific elements of mammalian diversification and/or adaptation, and (2) evaluation of relative importances of particular modifications through evolutionary time.

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