

Cambridge University Press

978-0-521-10630-6 - Comparative Physiology: Primitive Mammals

Edited by Knut Schmidt-Nielsen, Liana Bolis and C. Richard Taylor

Excerpt

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# 1

## Biology of the earliest mammals

A. W. CROMPTON

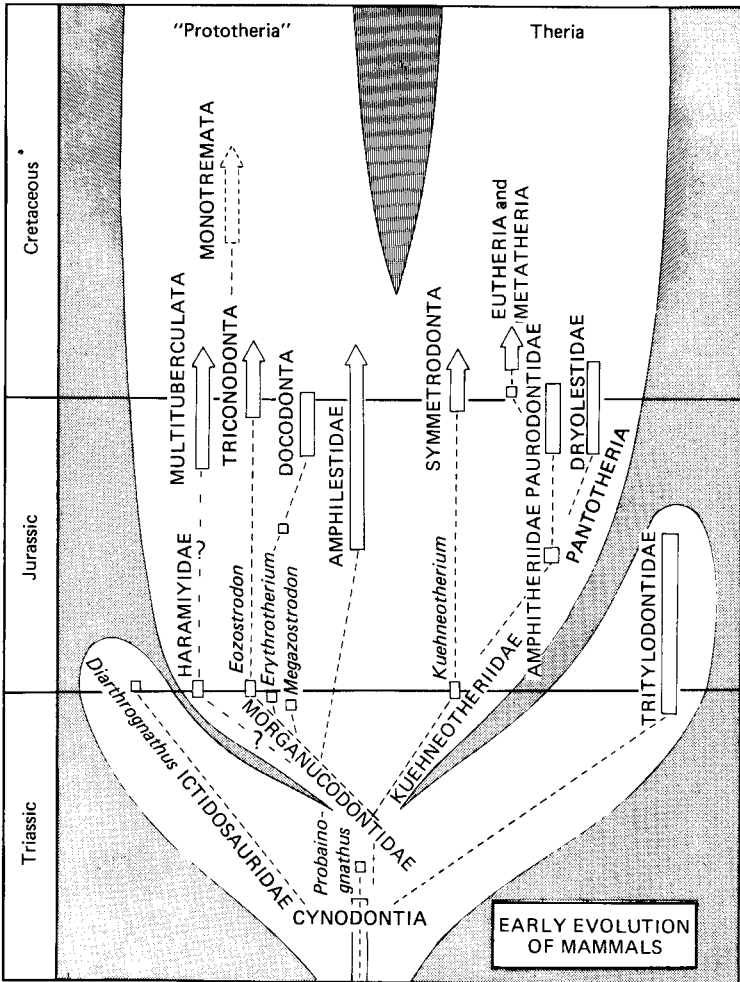
In a volume on “primitive mammals,” it is appropriate to review our knowledge of the earliest known mammals and to speculate on some aspects of their biology. This is necessary because it is difficult to distinguish clearly between advanced and conservative features in those living mammals often designated as “primitive” – the monotremes, didelphoid and dasyurid marsupials, edentates, and, among the insectivores, the tenrecs, solenodons, and hedgehogs.

As a result of a series of remarkable discoveries, starting with Walter Kühne’s finds in England shortly before the outbreak of World War II (see Parrington, 1971 for review), a fairly good record of the earliest mammals dating from the late Triassic, about 180 million years ago, is now available. Intensive searching and improved collecting techniques have provided a reasonable documentation of the first 100 million years of mammalian evolution. Recent discoveries in South America, in addition to the classic finds in southern and eastern Africa, have helped to document the transition from advanced mammal-like reptiles to the earliest mammals. It is against this background that I wish to review some aspects of the biology of the earliest mammals.

If we view the radiation of advanced mammal-like reptiles and early mammals (Figure 1), we find a clear separation between the mammalian and mammal-like reptile radiations. The most mammalian of the mammal-like reptiles are the cynodonts. It is from a single group of cynodont, or at the most from a group of closely related cynodonts, that mammals appear to have arisen (Crompton and Jenkins, in press). Representatives of the transitional forms have not as yet been discovered, but fossil forms slightly older and younger than this hypothetical group are now fairly well known. One way to determine the features that probably characterized these transitional stages is to compare the earliest mammals with the most advanced mammal-like reptiles. Clearly, many of the features possessed by mammals evolved earlier

within the mammal-like reptiles before this point was reached, such as secondary bony palate and double occipital condyle. However, new innovations were introduced at this stage and clearly separated mammals from the mammal-like reptiles and opened up a new adaptive zone. The earliest mammals were represented by two groups (Figure 1): one that appears to be related to therian mammals (marsupials and placentals and several extinct groups), the Kuehneotheriidae, and another that appears to be related to nontherian

Figure 1. Phylogenetic relationships of the principal groups of Mesozoic mammals and their suggested relationships to the most advanced group of mammal-like reptiles, the cynodonts. There is a clear separation between cynodonts and mammals, and it is suggested that this reflects the acquisition of numerous new features which are basic to the adaptive radiation of mammals at the transition between reptiles and mammals.

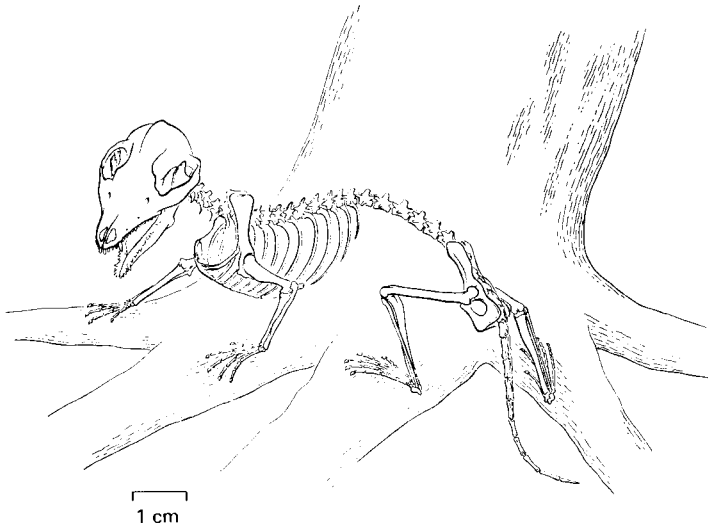


mammals (monotremes and several extinct groups), the Morganucodontidae. We know the Morganucodontidae much better than the Kuehneotheriidae.

The morganucodontids were rather small, about 20 to 30g in weight. Adaptions of the postcranial skeleton seems to suggest that they were adapted for foraging in a terrestrial and/or arboreal environment or on the interface between these two environments (Jenkins and Parrington, 1976). The first stages of the division of the vertebral column (Figure 2) into thoracic and lumbar regions with a transitional or anticlinal vertebra between these two divisions is present in these forms. This indicates that dorsoventral flexure of the vertebral column, a feature typical of mammals, was already present in these early forms. This feature is not present in the known mammal-like reptiles, in which lateral undulations of the vertebral column took place during locomotion (Jenkins, 1971). Jenkins (1974) has shown that dorsoventral flexure is a useful adaptation, not only for cursorial locomotion but also for locomotion in small arboreal animals such as tree shrews. Structural modifications of the foot, which permitted the hallux to secure an active grip by opposing the remaining digits, were present in these early mammals. This feature is found in many arboreal mammals, such as the tree shrew and didelphoid marsupials. Jenkins and Parrington (1976) have listed numerous other features of the skeletons of early mammals which clearly separate them from the advanced mammal-like reptiles.

The dentition (Figure 3A, B) consists of relatively small incisors (I) and canines (C), but relatively large premolars (PM) and molars (M). This is in contrast to those mammal-like reptiles that appear to be closely related to mammals such as *Probainognathus* (Crompton, 1972a) where the canines

Figure 2. Reconstruction of the skeleton of a late Triassic morganucodontid, one of the earliest known mammals. (After Jenkins and Parrington, 1976.)



tend to be large and the teeth behind relatively much smaller (Figure 4A). The early mammal postcanine teeth and especially the molars possess matching shearing surfaces (Figure 3C, D), and during occlusion only one side of the jaw was actively used at any one time (Crompton, 1974). This pattern of jaw movement required a high degree of musculature control so that the shearing surfaces could be brought precisely together when major forces were generated between the teeth. This represents a clear departure from the condition in the reptiles thought to be ancestral to or closely related to the first mammals. These forms did not occlude their teeth; the teeth bypassed one another so that a vertical space separated matching upper and lower teeth when the jaws are closed (Figure 4B); tearing rather than shearing characterized mastication (Crompton, 1972b).<sup>\*</sup> Precise dental occlusion in the early mammals permitted a more effective breakdown of food in the mouth. The structure of the tall shearing molars and premolars, the potential for large gape, together with the small size of the animals suggests that they fed principally on arthropods and other invertebrates, but could also have taken young reptiles, amphibians, and birds. This was also true of the other group of early mammals, the Kuehneotheriidae.

In the mammal-like reptiles ancestral to mammals new teeth erupt between older ones (Figure 5C, D), and tooth replacement seems to have continued throughout life (Osborn and Crompton, 1973). In early mammals the molars occlude with two teeth in the matching upper or lower jaw. Consequently, alternate tooth replacement would disrupt occlusal relationships. For this reason, in all mammals, including the earliest, the molars tend to be added sequentially so that precise occlusal relationships will not be disturbed (Figure 5A, B).

In the earliest mammals and in the majority of living mammals, the postcanine row is divided into premolars and molars (Figure 3). The premolars replace the milk molars, and the molars are added sequentially, from front to back, and not replaced (Figure 5B). This limited replacement and division of the postcanine row into premolars and molars indicates a growth pattern different from that of the mammal-like reptiles. Living mammals suckle when they are young and do not require teeth during early growth stages for the processing of food. Consequently, a substantial part of total skull and body growth can take place before the complete eruption of the first set of deciduous teeth (Ewer, 1963; Hopson, 1973; Pound, 1977). A single replacement of the milk teeth and the addition of three or four molar teeth is all that is required to accommodate for the remaining growth after weaning. This is in contrast to reptiles or the mammal-like reptiles where hatchlings require a set of functional teeth to process food by mastication as soon as they leave the egg. Because teeth crowns, once formed, cannot enlarge,

<sup>\*</sup> Precise dental occlusion was present in some specialized mammal-like reptiles that were not related to later mammals. However, the jaw movements and occlusion in these forms were fundamentally different from those of the early mammals.

Figure 3. Dentition of a late Triassic morganucodontid, *Eozostrodon*. (A) Snout and jaw in external view. (B) Lower jaw in medial view. (C) Matching shearing surfaces on the internal surface of the uppers and external surface of the lowers. (D) Matching shearing surfaces on the anterior surface of upper and a posterior surface of the lower molars, illustrating how the lowers move in a dorsomedial direction across the uppers during occlusion to shear the foods.

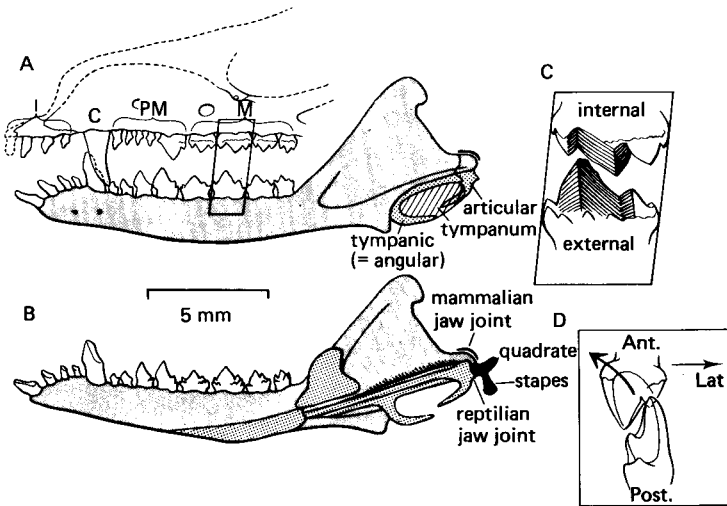
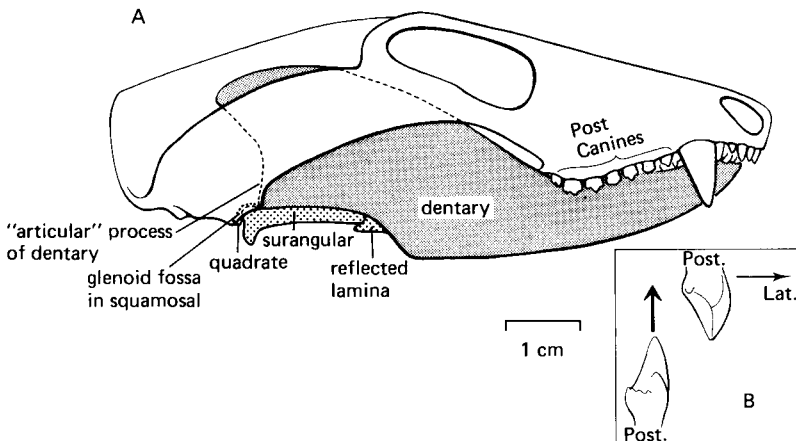


Figure 4. (A) Skull of *Probainognathus*, an advanced mammal-like reptile. (B) Posterior view of opposing upper and lower postcanine teeth to illustrate how, during the closing of the jaw, a space separates the teeth. Therefore, the teeth are capable of tearing, rather than shearing food.



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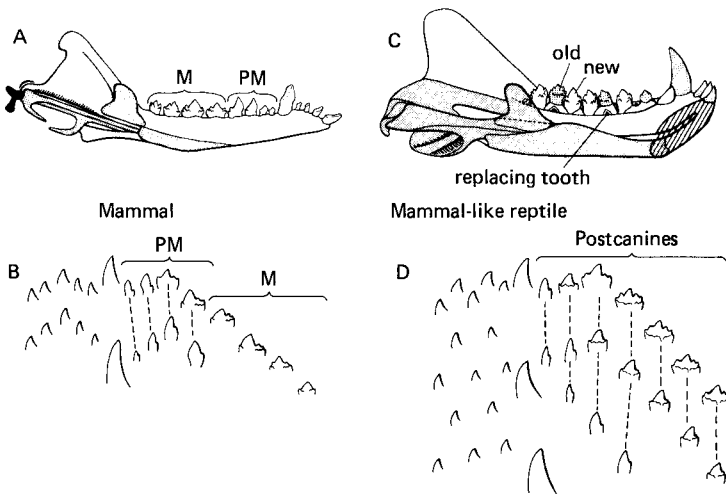
A. W. Crompton

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numerous replacements are necessary to accommodate the extensive growth range from hatchlings to adult. In mammal-like reptiles there may be at least six generations of teeth at any one tooth position (Osborn, 1973; Osborn and Crompton, 1973). The eruption and replacement pattern of the earliest mammals, therefore, suggests that maternal care and lactation were features of these forms but not of their immediate ancestors. A lack of replacement of the molars in the earliest and living mammals is accompanied by a clear termination of growth in the adult form. This is in contrast to their reptilian ancestors where a gradual, rather than an abrupt, termination of growth appears to have taken place.

The other group of early mammals, the Kuehneotheriidae, were slightly smaller than the Morganucodontidae. They appear to have had a mammalian tooth replacement pattern, indicating that lactation and maternal care characterized their early development. The Morganucodontidae appear to have been ancestral to several extinct orders as well as to the monotremes (Figure 1). It is, therefore, possible that reproduction in this group of early mammals was similar to that of living monotremes. Here the hatchling, or neonatus, is poorly developed, and the nutrition for growth and development is derived principally from milk. Prior to birth, nutrition for the limited amount of growth that takes place is derived either from yolk or from

Figure 5. Tooth succession in an advanced mammal-like reptile (c,d) and an early mammal (A,B). In a mammal-like reptile, the postcanine tooth row is not divided into molars and premolars. Replacement continues throughout life, with new teeth erupting alternately between older teeth. The diagram (d) shows the successive teeth which are added at each tooth position during growth. In mammals, the tooth row is divided into premolars and molars. The premolars replace milk molars, and the molars are added sequentially and not replaced.



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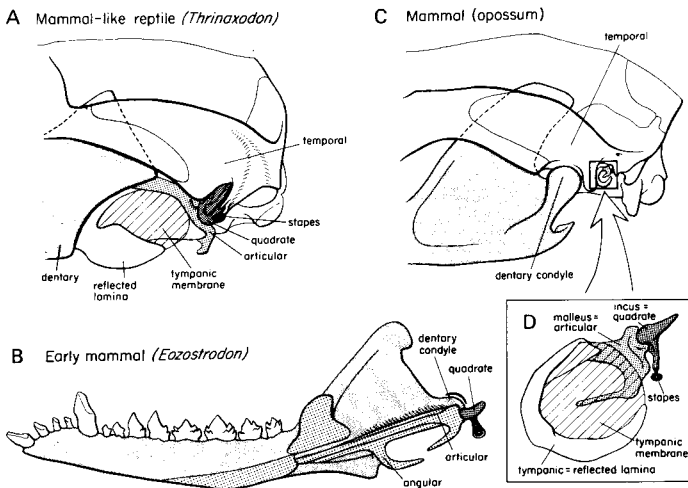
## Biology of the earliest mammals

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uterine secretions absorbed by the yolk sac. In marsupials, the young, at birth, are at about the same stage of development as the monotreme hatchling, and here also nutrition, for most of the growth and development, is supported by milk. It is relatively easy to derive the marsupial reproductive pattern from that of monotremes. Both the marsupials and the eutherians arose from a common stock which can be traced back to the other group of early mammals—the Kuehneotheriidae. This suggests that the birth, or hatching, of immature young and the heavy reliance on milk for growth and development probably also characterized this group of early mammals. Eutherian mammals increased the amount of nutrition derived from the uterine wall, and accordingly decreased the amount of growth dependent on nutrition derived from the milk.

A clearly defined feature that separates mammal-like reptiles from the earliest mammals is the jaw articulation (Crompton and Parker, 1978). In mammals an articulation exists between the dentary bone and the temporal bone, or the squamosal (Figure 6C); in mammal-like reptiles, it lies between the quadrate and articular bones (Figure 6A). Once the mammalian jaw articulation was established in early mammals (Figure 6B), the bones, which previously formed the reptilian jaw joint, separated from the lower jaw and

Figure 6. Jaw articulation of an advanced mammal-like reptile (A) an early mammal (B), and a living mammal, the opossum (C). In reptiles, the jaw articulation lies between the articular bone of the lower jaw and the quadrate attached to the skull. In early mammals a new articulation is established between the dentary bone and the temporal bone and lies alongside the old reptilian jaw joint between the quadrate and the articular. In modern mammals the old reptilian jaw joint bones have lost their contact with the lower jaw and are isolated in the middle ear, and they are involved in conducting vibrations from the middle ear to the inner ear (D). The malleus is the same as the articular, and the incus is the same as the quadrate.





were isolated in the middle ear and became specialized for the transmission of vibrations from the tympanic membrane to the inner ear (Figure 6D). It has recently been suggested that the freeing of the reptilian jaw joint bones from a suspensory function improved their ability to conduct sound (Allin, 1975; Crompton and Parker, 1978). This view seems to be substantiated by changes in the cochlea housing. This is a feature that clearly separates the most advanced mammal-like reptiles from the earliest mammals. In the mammal-like reptiles, the cochlea housing is relatively small and is not visible on the ventral surface of the skull, in contrast to the condition in the earliest mammals where the cochlea housing is relatively very large and forms a dominant feature of the ventral surface of the skull. The improvement of the efficiency of the middle ear appears to have been correlated with a refinement and enlargement of the cochlea. This organ is designed to distinguish between different sound frequencies transmitted by the middle ear, and its enlargement presumably reflects an improvement in auditory acuity.

We are not yet in the position to determine the exact brain size of the earliest mammals, but the braincase volume of these forms relative to body size appears to have been three to four times larger than that of cynodont mammal-like reptiles such as *Probainognathus*, which were closely related to the first mammals. This enlargement of the brain was in part due to the enormous increase in cranial space anterior to the pituitary fossa as a result of the vertical suppression of the interorbital septum. Jerison (1973) has suggested that this rapid increase may be correlated with the ability of the earliest mammals to process more sensory information than their ancestors, especially from the nasal capsule and inner ear. We can observe a refinement of the structure of the ear, but a similar morphological refinement of the nasal capsule is difficult to document. This will require the discovery of ossified ethmoturbinals in early mammals. Jerison (1973) has argued that the increase in brain size and improvement of the auditory and olfactory senses were correlated with the invasion of a nocturnal environment by the earliest mammals. This is not a new idea, and the structure of the earliest mammals is not inconsistent with this view.

The fauna found contemporaneously with the earliest mammals tends to support the view that the earliest mammals were nocturnal (Crompton and Jenkins, 1978). The dominant terrestrial forms found together with the earliest mammals are a wide variety of saurischian dinosaurs (herbivores and carnivores) and ornithischian dinosaurs (herbivores). Even the smallest of these is several orders of magnitude larger than the early mammals (Santa Luca, et al., 1976). Another well-represented reptile group is the thecodonts, which were principally large to medium-sized carnivores (this is the group that gave rise to the first crocodiles some time in the middle to late Triassic times).

Some specialized survivors of the earlier vast radiation of mammal-like



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reptiles are found together with the earliest mammals. They were either insectivores cum carnivores or small herbivores, and were small to medium sized, although considerably larger than the Triassic mammals. Robinson (1967a, 1967b, 1973) has shown that the latter half of the Triassic was characterized by an adaptive radiation of lizards, some of them smaller than the earliest mammals, some about the same size, and many quite a bit larger. As a whole, they were small, lightly built, agile forms well suited for moving over uneven terrain, and some were also adapted for gliding flight. Also present were a series of small rhynchocephalians (related to the modern Tuatara of New Zealand). Many of these small reptiles, especially the lizards, were like the earliest mammals and probably insectivorous. Therefore, in late Triassic time, both lizards and mammals seem to have produced a significant radiation of insectivorous forms. If the improvement of auditory and olfactory senses and the enlargement of the brain in the early mammals were associated with a predominately nocturnal way of life, it is possible that the insectivore niche may have been partially divided between mammals and reptiles on a nocturnal–diurnal basis. The well-established fauna of large, medium, and small and presumably diurnal reptilian carnivores and herbivores living alongside the mammals appear to have prevented mammals from evolving into this niche. This situation was to continue for the next hundred million years, and the successful adaptive radiation of mammals during this time appears to have taken place in a nocturnal niche.

The most common of the early mammals (late Triassic), namely the Morganucodontidae, are found in deposits in southern Africa, China, and Europe. Morganucodontids from these countries, despite their extensive dispersal, are almost identical in structure and level of organization. This suggests a rapid dispersal of mammals shortly after their origin. This rapid dispersal and lack of diversity would be expected if the characteristics associated with the earliest mammals had enabled them to exploit a vacant or partially vacant niche for nocturnal insectivores. Diversity within this niche in different countries and regions would be expected in later times, and it is adequately documented by the fossil record.

One encounters a similar phenomenon with the late Triassic dinosaurs, the prosauropod dinosaurs. At the same time that the mammals were expanding in a nocturnal niche, these dinosaurs appear to have invaded and dominated the niche for terrestrial herbivores. Whether they are found in North America, South America, Europe, Africa, or China, these forms are almost identical in structure. The rapid dispersal and lack of an adaptive radiation, in both dinosaurs and mammals, may have been aided by the close connections that existed between the continents at that time and not only by the rapid dispersal in a new adaptive zone.

We (Crompton et al., 1978; see also Taylor, this volume) have argued that the successful exploitation of a nocturnal niche requires the ability to maintain a constant body temperature. Diurnal habitats present a wide mosaic of

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microenvironments suitable for the behavioral control of temperature (i.e., direct solar radiation, shaded areas, burrows). By selecting one of these micro-environments or by moving from one to another, a diurnal poikilothermic reptile can control its temperature within narrow limits. This mosaic does not exist at night, and if nocturnal temperatures fall significantly below a preferred temperature, poikilothermic animals are not able to forage effectively. We have suggested that this could be achieved under certain conditions without a significant increase in the basal metabolic rate. We have argued that the temperature regulation of early mammals was probably similar to modern Tenrecinae and Erinaceinae. These forms have a lower basal metabolic rate than “typical” mammals of similar size. Our hypothesis is that the earliest mammals achieved a constant body temperature by (1) restricting their periods of activity to twilight or night hours to avoid high external heat loads; (2) opting for a low body temperature (probably between 25 and 30 °C); (3) adding insulation (fur or superficial fat); and (4) retaining a basal metabolic rate similar to that of a “typical” reptile of the same size and at the same temperature. The main innovation of the earliest mammals was presumably their ability to increase metabolic rate, probably by shivering when ambient temperatures dropped below body temperature, and to control the loss or retention of heat by adding fur and fat and by improved peripheral vascular control.

The Triassic mammals can safely be referred to as primitive mammals. Unfortunately, there are no living survivors of these early mammals, and it is inadvisable to refer to some of the living mammals as “primitive.” We know nothing about the phylogenetic history of monotremes other than that they appear to be related to a group of Triassic mammals different from the therian mammals. Therefore, at least 180 million years of independent evolution separates them from all of the living therian mammals. Both the marsupials and eutherians appear to have arisen from a common stock (Crompton and Kielan-Jaworowska, 1978) sometime in the early to middle Cretaceous, therefore, living marsupials and eutherians have had at least 70 to 80 million years of independent evolution. Little is known about edentate evolution other than a phylogenetic history dating back some 60 million years to the early Tertiary. Dilambdodont insectivores, such as the hedgehogs, arose before the end of the Cretaceous, and although it is probable that the zalambdodont insectivores, such as the Tenrecidae and Solenodontidae, arose from dilambdodont insectivores (Mills, 1966; Butler, 1972), their origin is unknown and they may be survivors of an early radiation of eutherian mammals (Eisenberg, this volume). Consequently all the so-called primitive mammals have had a long and independent history with more than adequate time to develop numerous specialized features. Some of these living “primitive” mammals retained several primitive or conservative features that characterize the earliest mammals. But without exception, they are found alongside highly specialized features in living forms. The most we