

Placentals are better adapted to terrestrial life than marsupials and monotremes because they show a greater diversity of locomotory types. Discuss.

Introduction: The evolution of mammals.

Mammals probably first evolved in the Triassic period 245 Million Years (m.y.) ago. Of these first mammals no living examples have survived into the modern era. All three mammal groups existing today are derived from a group that evolved some 230 m.y. ago called the holotheres, because of the arrangement of their teeth. Of these the oldest are the Prototheria, or monotremes which survive as six species in Australia and New Guinea in two groups, the duck-billed platypus and the echidnas. Prototheria lay eggs that are incubated and hatched outside the reproductive tract of the females. Nevertheless they are endothermic, hairy, milk-producing vertebrates with reduced teeth, thus qualifying as vertebrates.

The remaining two groups belong to the subclass Theria. They are viviparous (give birth to live young) which distinguishes them from the monotremes. These two groups are very closely related but have had separate evolutionary histories since the early Cretaceous (144 m.y. ago). The 250 or so species of the metatheria, or marsupials, are distinguished by their short gestation periods, tiny, feebly developed offspring, and (in most species) a protective pouch or marsupium. This pouch lies over the mammary glands of the female and the young crawl into it immediately after birth to feed and complete development.

Eutheria, or placental mammals, comprises some 3800 or so species. They are all born at a more advanced state of development than marsupials: some are even able to run or swim within minutes of birth and most are weaned sooner than marsupials.

The differences between the reproductive patterns of Eutheria and Metatheria reflect different evolutionary responses to the stresses of the environment (Lillegraven 1974). Eutherian young are produced with a higher potential for survival, but at greater cost to the mother. The cost of producing young for metatherian mothers is much less and she can quickly recycle her broods (i.e. abandon pregnancy) if environmental conditions demand it. Metatherian mothers are also capable of a much higher reproductive rate: a female kangaroo can have one mature offspring suckling in her pouch beside a younger individual who has just been born, while a third develops in her womb.

It is undoubtedly true that placentals have proved more successful than marsupials (monotremes are restricted to six species only). Placentals have colonised all major continents (except Antarctica) and are present in all habitats with a wide degree of diversity. By contrast marsupials are restricted to a few species (250 compared with 3800 placentals) confined to Australasia, South America and a single opossum in North America. However, it is equally true that why this is the case is not obvious. To us the placental method of development may appear to be much better, but the flexibility of the marsupial method allows high reproductive rates when conditions are good and low rates when conditions are poor. It is not necessarily true that the more invested in a project the better it is, i.e. placentals are making a bigger gamble than metatherians (Cowen 1995).

Marsupials originated in North America and from there spread around the globe. Placentals first appeared in Eurasia and radiated from there into other continents. In North America they gradually replaced the marsupials, however they were unable to travel to South America or Australasia at that time so the marsupials

there were able to develop there undisturbed. This is why the fauna of these continents is different from that of the other continents. Eventually in the Pliocene, about 2.5 m.y. ago (after 100 m.y.), the American land bridge was restored and the fauna were able to mix freely. Gradually the northern invaders proved to be more successful than the southern invaders which moved north (e.g. the opossum), however the numbers of marsupials was not affected significantly. In the late Pliocene marsupials comprised 19 percent of the genera of mammals; this figure is 17 percent today.

Australasia occupies a unique position because it has never been invaded by placentals until the modern introductions caused by man. The only major group of placentals that diversified in Australia before the arrival of man was the bats. However following the arrival of man the introduction of cats and dogs has caused the extinction of many marsupial forms, notably the Tasmanian Wolf, and hence restricted the diversity of this group of mammals.

The picture that emerges is of three distinct groups: the primitive monotremes and the two groups of theria. Of the theria the placentals have proved the most successful, over time, although why has not been discovered. The result is that placentals have adapted to many different types of terrestrial life compared with the other two, because they have populated many diverse habitats, and therefore show a greater range of locomotory types. However, as will be shown, despite the marsupials restricted geographical location they too have developed many forms of locomotion.

At the basic level the anatomy of the different groups restricts the types of locomotion that can exist.

Fundamental Anatomical differences:

Differences in the Pectoral Girdle: Parasagittal versus Sagittal movement and epipubic bones:

The anatomy of the monotremes sets them apart from other mammals. “If known only by the pectoral girdle, they surely would be classified as reptiles” (Hildebrand 1988). The limbs of most mammals share one highly characteristic feature. All the joints of the limbs lie in the same vertical longitudinal (or sagittal) plane as the shoulder (pectoral girdle) and hip (pelvic girdle) joints, and in this plane the limbs swing backwards and forwards like a pendulum. This means that when standing at rest the limbs are directly beneath the joints supporting the body weight in the most ideal fashion.

The anatomy of the shoulder girdle of the reptiles is, however, different. In reptiles the humerus (upper limb) rotates within the girdle backwards and forwards in the horizontal transverse (or parasagittal) plane, facing horizontally outwards. At rest, therefore, the reptiles’ feet are positioned to one side of the joint, which results in more stress being taken up by the muscles at rest.

“The monotreme girdle is typically reptilian; ... the relatively short but powerful humerus extends horizontally outwards from the body and like that of a reptile it moves backwards and forwards in the horizontal plane when the animal is in motion” (Gray 1968). This demonstrates the evolutionary history of mammals: monotremes, while being endothermic, lay eggs and move in a similar fashion to reptiles.

What does this mean about the locomotion of monotremes compared with other mammals? Effectively in a mammal the joint is part of the limb, giving another

point of flexibility (e.g. chameleons have evolved to move like mammals when climbing) and another point where movement can increase speed, as will be discussed below. It also has implications for the breathing of moving animals (see fig. 1). Reptiles inhale and exhale by contracting the same muscles that produce lateral bending during locomotion (because of the positioning of their limbs). The effect of locomotion is to change the pressure in the lung on different sides of the body, moving the air from one side of the lung to the other. However the total lung volume does not change – i.e. they cannot breathe and move. By contrast mammals flex the vertebral column vertically during locomotion, which actually enhances the filling and emptying of the lungs. No information is available about the breathing of monotremes but it is assumed that they have a diaphragm and are therefore able to breathe whilst moving. Even so their breathing will not be enhanced (like the theria) whilst in motion because of the positioning of their limbs. Obviously this effects the rate of respiration of a monotreme during periods of activity: it is unlikely that they are able to run fast for significant periods of time and maintain the high metabolic rate necessary to produce a constant body temperature above ambient temperature.

A study by Jenkins (1971) which compared the Virginia Opossum with Echidna and rats showed that the movement of the Opossum and the rat was very similar and significantly different from that of Echidna, specifically the movement of the forelimbs.

Effectively therefore the sagittal movement of limbs, practised by marsupials and placentals, is superior to the parasagittal movement of monotremes.

The pectoral girdle of mammals differs, also, in another significant way. Monotremes and marsupials have epipubic bones of uncertain origin that articulate with the pubic bones and extend forward into the ventral wall. In the opossum they provide support for the pouch. It is probable that these vestigial structures have no useful purpose so that it can be said that anatomically the placentals are the most highly developed of the mammals for efficient locomotion.

Anatomical differences in feet:

Mammalian feet have evolved to adapt best to their environment. Three types are recognised. In plantigrade (= sole + walking) feet the heel is on the ground when one stands and strikes the ground first in each stride. All creatures that walk well but seldom run (and may need flexible feet for climbing and burrowing) have plantigrade feet, such as humans, opossums, bears and rodents. Many carnivores have developed a longer leg by standing on the ball of the foot. These are digitigrade feet (= finger + walking). The ultimate adaptation for increasing length of leg is the unguligrade (= hoof + walking) foot posture, where the mammal stands on the tips of its toes (see fig. 2). Examples of unguligrade mammals are most herbivores (horses, antelope, deer etc.).

Unguligrade feet, and to a lesser extent digitigrade feet, result in a gradual increase in leg length causing an increase in stride and hence speed (and endurance because energy is saved by taking less steps) at the cost of a relative reduction in the flexibility of the foot. In addition there are other adaptations which cause increased speed. In plantigrade locomotion the movement of the upper limb caused by muscular contraction produces motion. In digitigrade and increasingly so in unguligrade feet the movement of locomotion becomes increasingly the movement of the whole limb, used as a lever and operated by muscles closer to it (causing an

increase in the motion produced). Digitigrade and unguligrade feet also benefit by containing a greater number of joints in the limb compared with plantigrade feet, a factor that will be returned to later.

Unguligrades have additional adaptations for speed and endurance. Their legs are able to recycle energy by using long springing ligaments that pass down the leg to the phalanges. When the foot strikes the ground the impact bends the joint between the phalanges and the fetlock joint. This stretches the ligaments, which, because they are elastic, recoil giving an upward impetus to the entire body. Not only does this increase speed but it also serves to cushion the joints from some of the forces produced by locomotion. Kangaroos (which have digitigrade feet) have similar ligaments that also cushion the impact of each hop and store energy for release during propulsion.

It is pertinent to note that while there are examples of placental mammals with each type of foot (humans, lions and horses for example) there are no unguligrade marsupials and monotremes only have plantigrade feet. Placental mammals, therefore, show a greater variety in their anatomical structure, which is related to the greater diversity of habitats that they successfully colonised. One of the reasons why there are no large marsupial or monotremal herbivores is because they have never evolved unguligrade feet. Without these adaptations marsupial herbivores (like kangaroos) are unable to match the larger placentals in terms of range, speed and stability (the unguligrade foot is more stable than the other two). For example the maximum speed of a kangaroo is 65 km/hr whilst the speed of a similar sized antelope is 85 km/hr. Larger marsupial herbivores than the kangaroo would be even slower; it maybe that mammals larger than the kangaroo are unable to move fast enough for long enough using saltatorial (hopping) motion. Hence the kangaroo may represent the maximum limit to which a saltatorial mammal can grow. It is possible, also, that the ecological niche of the large herbivore in Australasia was fulfilled by giant birds (the moa in New Zealand and psilopterids and phorusrachids in South America) before invasions of aggressive predators (man for example) forced these birds into extinction. In this scenario the proto-herbivore marsupial was unable to compete favourably with the existing fauna and hence never evolved. It is interesting to consider the largest terrestrial mammals of each type. The largest monotreme is a spiny anteater that weighs 10kg, compared with 90kg (kangaroo) for the marsupials and 7000kg (elephant) for the placentals. This clearly shows the limitations to the size of the marsupials and monotremes, which is probably related in part to the restrictions to their locomotion imposed by anatomical constraints and their inability to evolve further.

This evidence points towards an ability of placentals to specialise more widely than marsupials and hence fill ecologically niches that marsupials never did. Possibly the reason for the limited evolution of large marsupials was the adoption by many of the saltatorial method of motion.

Cursorial, Saltatorial and Graviportal

Animals that travel fast or far on the ground are said to be cursorial. Cursors can either be bipedal or quadrupedal. Quadrupedal walkers evolved into predators and medium-to-large herbivores. Saltators are animals that jump or hop. They are often bipedal, and if the hind legs are used in unison for a succession of jumps, like a kangaroo, the gait is called a ricochet. Graviportals are large and heavy. Cursors in particular have a number of select advantages: they are able to forage over large areas,

move large distances to find new resources and migrate. Speed is important both for predator and prey. Saltators are able to leap over obstacles and arboreal saltators are able to leap from tree to tree.

Species of both placentals and marsupials have evolved to fill these roles (except there are no marsupial graviportals). By contrast monotremes are slow (partly because of their limb structure) and rely on armour or water for defence, not speed. This means that they are unable to move far and hence move into alternative habitats. Of the placentals the majority of large species tend to be cursorial or graviportal, while the existing marsupial large species are saltatorial (medium sized cursorial marsupials did exist but they are now extinct). This is interesting because large saltators tend to be more specialised than cursors.

Cursors:

Most cursors are placental but a few are marsupial. Cursors have developed particular adaptations designed to increase their speed. Speed is dependent on two things – length of stride and rate of stride.

There are many ways a cursor can increase the length of its stride. One is to increase the length and proportions of the legs. It is important to increase the length of the leg relative to size if the object is to contribute to speed. The distal segments of the legs (radius and tibia) usually lengthen so that they are as long as the proximal (humerus and femur). This can be seen in many placental ungulates (e.g. horses), but not in marsupials because there are none in this class. Another way to increase leg length is through the changes in foot posture mentioned above.

Another way a cursor can increase stride is by pivoting the girdle or spine. This is seen in the way humans walk. The rotation of the pelvic girdle is timed to help advance the weight of the unweighted leg and to help swing the weighted leg to the rear. This twisting of the girdles is seen in monotremes, but the analogy is inaccurate because the twisting of the girdles in monotremes is a result of their parasagittal stance, whereas in humans it is an adaptation to bipedal motion. By undulating their spines in the vertical plane smaller quadrupedal cursors are able to increase their speed: the body is longer when the back is extended than when it is flexed. Therefore by extending the back when its hind feet are on the ground the animal is able to move its forequarters forward. The cheetah is so adept at this manoeuvre that it could theoretically move at 10 km/hr without any legs at all. It is probable that marsupial dog-like carnivores, such as the possibly extinct Tasmanian Wolf, practised this manoeuvre, although without the skill of the cheetah.

One other important way to increase stride is by including periods of where the body is unsupported. Most ungulates do this, as to many predators and bipedal runners. Again, apart from the Tasmanian Wolf it is unlikely that any marsupials practise this form of cursorial motion because there are no large fast marsupials that are not saltatorial.

Muscles, too, can be used to increase the length of stride by positioning them closer to the joint so as to create a greater movement around the joint when they contract. Many animals, including kangaroos practise this, however it is most specialised, again, in the ungulates.

Increasing the rate of stride can be another important way of increasing velocity. Obviously the simplest way is to increase the amount of muscle but when this is no longer possible other methods must be used. However raising the

temperature of the muscle can increase the rate of muscle contraction; this is one of the advantages of endothermy over ectothermy. Evidence shows that monotremes, and to a lesser degree marsupials, maintain lower body temperatures than placentals, therefore placentals would be expected to move faster. Another way of increasing the rate of stride is to increase the 'gear' by moving the muscle closer to the joint (see above). Comparisons of saltators shows that kangaroos have evolved in this manner, but wallabies have not.

Another method ungulates in particular have evolved to increase velocity by increasing the number of different limb muscles that move different joints in the same direction to achieve greater motion. The independent velocities they produce are summed to produce the total velocity. This is the principle by which the unguligrade, and to a lesser degree digitigrade, foot posture functions. As there are no marsupial unguligrades and only a few possible digitigrades (the Tasmanian Wolf, for example) this again is a principally placental evolutionary step.

Many placentals have adapted in particular ways because they are large (graviportal). Being large has many advantages (e.g. the giraffe can reach higher food sources, the elephant is hard to kill) but in order to increase body size without loss of speed and endurance the limbs need to be increased in greater proportions and special adaptations need to be made. This, for example is why foxes can move as fast as horses when they are less specifically adapted for speed. One of these adaptations is to reduce oscillating motions (e.g. the feet are not lifted high, the spine is stiff). Another is to reduce unnecessary muscles that often cause oscillating motions (such as muscles that twist the feet). Many bones can be fused, for example especially in the feet to reduce weight and increase support. This, for example, is why the elephant foot is shaped like it is, and why the kangaroo has lost its lateral toes. This process has also produced the canon bone in ungulates. The reduction in the number of digits can range from one (marsupials, carnivores and rabbits), through two digits (rodents and some ungulates), to loss of three or four (most ungulates). This appears as a scale with the more specialised animals (which are placentals) appearing at the end. To guard against dislocations joints have become modified to compensate for the loss of muscles that might otherwise have prevented this.

Many predators and prey are extremely agile. This is seen in kangaroos, marsupial cats, antelopes and many placental carnivores. Their bodies are adapted to be light and supple. Many kangaroos, and the placental equivalent the kangaroo rat, use their tails to steer.

Gait is a regular repeating sequence and manner of moving the legs in walking or running. All cursorial animals have particular gaits, but many placentals have evolved very specialised manners of moving which is more advanced than their marsupial cursorial counterparts. The horse is a familiar example with its four gaits: walk, trot, canter and gallop. Gait selection relates to energetics, rate of travel, manoeuvrability, stability and to the size and structure of the body. A gait is increasingly stable the more the legs move separately and remain on the ground for longer. Conversely a gait is faster if the legs move together and are off the ground for longer. It is more energy efficient to choose the correct gait for your speed. Experiments have shown that horses change gait and select speed within a gait in a manner that minimises energy consumption. The same is true of man, as human beings are known to change from walking to running at a particular speed. Migrating animals are thought also to change gait to suit speed. Gait is one way in which

placentals have adapted to conserve energy and hence increase their chances of survival.

Saltators:

“Ricochet animals can accelerate faster from rest and can alter speed and direction of their motion faster than their quadrupedal relatives” (Hildebrand 1995). These are important escape mechanisms, but they are purchased at the price of efficiency. Repeatedly raising a body against gravity can be very expensive energetically and therefore saltators can rarely maintain high speeds for long, unlike cursors. Some saving is made through recycling spring energy through the use of elastic ligaments, as was discussed above. It is unlikely, however, that kangaroos are able to move long distances (for example they do not migrate).

For saltators the relative lengthening of the hind distal limbs compared with the proximal limbs is more severe than for cursors. Sometimes the tibia is twice as long as the femur (e.g. kangaroos). Often the forelimbs become reduced in size because they are not often used. A long robust tail is essential to act as a third support when standing. It also functions as a counterbalance to bring the centre of mass over the hind legs (just as in some cursors the body mass is positioned so as to bring the centre of mass over the forelimbs). A saltator can also use its tail to change the direction of a jump in mid air. The kangaroo rat can even reverse its position by doing this! These adaptations show the degree of specialisation that exists in saltatorial mammals to increase the effectiveness of their action. Both kangaroos and the placental kangaroo rat are prime examples (both can jump over 2 m high). Whilst the largest saltator, the kangaroo, is marsupial the kangaroo rat (which is smaller) demonstrates that it is possible for placentals also to perfect this style of motion. It is possible that larger kangaroo rats are selected against by nature, because of the presence of certain predators that are absent in Australia. These two animals are an example of convergent evolution.

Adaptations to specialised environments:

Climbing:

Climbing has evolved many times independently because it has many advantages such as protection, food and nest sites. Many marsupials climb (examples include opossums, phalangers, mice, the koala and even a kangaroo) as do many placentals (such as rodents, bats and primates). Monotremes do not climb. While many animals can climb to be successful requires various modifications. Some marsupial and placental climbers move by leaping from tree to tree (e.g. squirrels), for which they have a strong, supple back and a tail for counterbalance. Many placental primates and marsupial opossums are highly adapted for climbing and are able to move by reaching from limb to limb (like orang-utans). Some are able to spring up as much as 2 m vertically to catch a branch (e.g. lemurs). Arm swinging is practised only by the most specialised of primates. This motion uses only the forelimbs for support.

Hands have become very specialised in many climbers, with the first digit often being opposed to the others in opossums and many primates. The koala grasps between the second and third digits. The palms and soles are sensitive and designed to produce grip. Often the tail is very important as a third means of grasping (such a

tail is said to be prehensile) for example in opossums and monkeys. Claws are very important also to grip and interlock with the substrate. Often the hind foot can be reversed (such as in various marsupials and squirrels) to grip the tree trunk more securely. The forward facing and backward facing claws then oppose each other creating grip. Sometimes hooks are used to grip branches, such as the claws of sloths or the hands of primates.

This demonstrates, remarkably, the convergent evolution that has occurred. Many marsupials share similar characteristics with placentals and yet they evolved from different stock. The difference is that a marsupial never evolved features like that of primates and monkeys, in particular the adeptness of hands. This may be because the marsupial brain is slightly smaller than equivalent placental brain. The evolution of primates, with hands capable of manipulating tools, was one step towards the evolution of man.

Gliding and Flying:

Many mammals have evolved beyond being climbers and have developed the ability to glide and fly, thus increasing their mobility and the food sources that they can use. There are four groups: marsupial phalangiers, flying lemurs, rodents and bats. Again, this is an example of convergent evolution. With the exception of bats their performance is limited to gliding, the lifting surface being provided by a membrane covered with fur that reaches from the side of the body to the wrists and ankles. Of the three gliding types the lemur is the most advanced, whose patagium not only extends to the tips of the webbed toes but also extends along the tail.

Bats have adapted extensively for true flight so that their powers of terrestrial movement are very limited. Unlike the gliders they are able to produce forward propulsion through the movement of their wings, in a manner similar to that of birds, although the skeleton is fundamentally different.

While many mammals have evolved modifications allowing limited flight only the placental bat has evolved true flight. Of the gliders a placental lemur is the most proficient. By evolving to make use of the skies, placentals were able to extend their range and reach habitats they would otherwise have been unable to reach. For example, bats were the first placentals to come to the isolated continent of Australia.

Digging:

Mammals that dig are called Fossorial mammals. They have various advantages over other animals. For example, digging can be used to create nests and protective burrows with controlled environments, and to find food. It is not surprising therefore to find that many mammals have taken to digging. Of the monotremes, both the echidnas and the platypus dig. The marsupial mole is among the most highly adapted of all diggers, and one wombat has been known to excavate a burrow 30 m long. Of the placentals both true moles and golden moles are highly adapted, as are badgers, rabbits and many rodents such as mole rats.

There are many different ways of digging, all of which are practised by one placental or another. In scratch-digging the forefeet are extended to the earth and then the claws are used to draw towards and under the body. Examples include many rodents, badgers and wombats. Scratch-diggers have to be modified to provide increased strength to the fore (or hind if they are used) limbs. Most rodents (e.g. mole rats) dig by chisel-tooth digging, where the animal digs primarily with its incisors.

These have highly specialised jaws and very large skulls. Head-lifting is the manner of digging practised by the marsupial mole and the golden mole, and others. In this method the head is used to dig shallow tunnels, the displaced earth then breaking the surface. Head-lifters have highly developed head and neck muscles. Hook-and-pull digging is practised by anteaters, which dig by engaging the large second and third claws of the forefoot in a hole or crevice and then forcefully pulling the foot towards the body.

Of all methods of digging, however, humeral-rotation digging is the most advanced (see fig. 3). Unlike the methods already mentioned this does not require great strength in the shoulder or head. True moles are the only animals that have been shown to dig in this manner. They dig by rotating the humerus around its own long axis, like a drill. To permit this the forearm extends beyond the nose. The effectiveness of this method is attested by the facts that true moles can dig a tunnel at the rate of 4 m/h and can lift 3 kg in such a run. It is effective partly because it uses the most powerful muscles in the body, the *teres major*.

The monotreme, echidna, moves its forearm by humeral-rotation as has already been discussed (this is a product of its reptilian heritage) but it is not known if it digs in the same fashion as moles. Even if it does the adaptations of moles are still truly remarkable because while the echidna moves by humeral-rotation because it's reptilian ancestors did, the mole, which was presumably once had its limbs in the sagittal plane, has, as it were, evolved backwards towards the reptilian design.

Fossorial mammals have many adaptations that improve their effectiveness. True moles, golden moles and marsupial moles all have vestigial eyes beneath the skin that can sense light and dark only, so as to prevent damage to these organs when digging. All diggers have an inherent sense of direction and depth beneath the soil, to enable them to find their way in the darkness. The claws and teeth are well adapted for digging. The teeth of rodents and wombats have enamel only on their forward surfaces, the soft constantly renewing dentine behind wears away providing a self-sharpening mechanism.

This examination of fossorial locomotion has shown that of all the mammals the placentals are the most diverse group. Different placentals practise five different ways of digging, compared with two for the marsupials and one for the monotremes. The most advanced digger, the mole, is also a placental.

Conclusion:

Placental mammals have spread all over the earth. They can be found in deserts (e.g. camels), the arctic (e.g. polar bears), the sea (e.g. whales) and sky (e.g. bats). The largest terrestrial animals are placental mammals (elephants), as are the fastest (cheetahs). Some have evolved into the most sophisticated predators ever known, others have evolved into the most intelligent organisms on the planet. Compared to marsupials there is a much greater diversity of placentals in many different and diverse habitats. All of these species have become highly adapted to the environment in which they live. This includes their method of locomotion, whether it is that their anatomical structure is built for speed, endurance, or to provide support and movement for a large body; or whether it is their unique gait; or their specialised structures to enable locomotion in the sky or beneath the ground. The limited geographical range of marsupials means that there will be a reduced number of ecological niches that they can evolve to fill. But even in Australia, away from competition by placentals, they have not evolved to such a high level of

specialisation. There are no camel-like marsupials which with their distinctive gait (the two feet on the same side of the body move in unison) that enables them to travel 180 km in 12 hours. Nor are there other large ungulates, even though the appropriate habitats exist. For every method of locomotion a marsupial has developed there is an equivalent placental, whether it is the kangaroo and the kangaroo rat, the Tasmanian wolf and the true wolf, the marsupial mole and the true mole, and so on. This is an example of convergent evolution. Even in feeding types the two groups show this convergence; for example the extinct South American borhyaenids were very similar to the sabre-tooth tiger.

The question that remains is why the marsupials and the monotremes failed to develop the diversity shown by the placentals. For the monotremes this is easy to hypothesise: their primitive features, lower metabolic rate, parasagittal limbs and method of reproduction meant that other mammals out-competed them and reduced them to a few species occupying very distinct ecological niches. But for marsupials this question is much harder to answer. For some unknown reason placentals appear to be better adapted to their environment. This is puzzling when the differences between the two groups are so slight and, as has been explained above, the marsupial method of reproduction may not be inferior. What remains is the fact that placentals did reduce the geographical range of marsupials to a few species in South America and the isolated continent of Australia.

The explosion of placental types can then be explained because of the many more varied terrain types that they encountered. But this, as has been said above, does not mean that marsupials could not have evolved into more diverse groups in isolation in Australia, which is a huge continent. Why did they not? There are a few possibilities here. It may be that the presence of the marsupials themselves, and other primitive mammals, was the catalyst that sparked the revolution in mammalian types – i.e. the struggle between the placental and non-placental types in each habitat, which the placentals ultimately won, was the driving force behind their ultimate high level of adaptation and specialisation. It may be that the converse is also true – isolated in Australia without significant interspecific competitive forces at work the marsupials stagnated and did not evolve into such highly specific animals as the placentals. The absence of large predators may have contributed to this effect (this caused the development of flightless birds on New Zealand, for example). The evolution of placental mammals is full of invasions from other continents of other animals that either replaced existing fauna or sparked a change in it. There are lots of examples about the migration of early mammals, e.g. the evolution of camels and lamas occurred in North America and from there these mammals spread to Africa and South America. It may be that marsupials lack a feature present in placentals that makes them 'inferior'.

We are left therefore with two distinct questions – why did the marsupials compete unfavourably with placentals when they came first into contact, and why, when isolated, did marsupials fail to evolve into many diverse organisms like the placentals. The answers are unknown.