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Fossil Focus: Marsupial evolution - A limited story?

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Introduction:

There are three groups of mammals alive today: the egg-laying monotremes (echidnas and platypuses); the marsupials (those with pouches); and the placentals (those that develop a placenta in the womb and give birth to comparatively developed young). Marsupials and placentals are sister groups, more closely related to each other than to monotremes. Along with their closest fossil ancestors, marsupials belong to the <u>clade</u> metatheria, whereas placentals belong to the clade eutheria. Together, metatheria and eutheria comprise the therian mammals. Marsupials are much less diverse than placental mammals in terms of numbers of different groups, range of lifestyles, range of body shapes and where they live. Why this is the case is still not well understood, and although research into the mystery of marsupial evolution is beginning to shed some light, there is still much work to be done.

Metatherian development:

One major physiological difference between marsupials and placental mammals is how they reproduce. Placental mammals give birth to well-developed young. By contrast, marsupials give birth only a few days after conception, to small and comparatively underdeveloped young. Some marsupial newborns are so tiny and at such an early stage of development that they breathe through their skin because their lungs have not yet properly formed. The marsupial newborn must find its own way into its mothers pouch and latch on to a nipple to survive. Those from different groups of marsupials manage this in different ways, but perhaps the most impressive is the long uphill climb of a small, sticky kangaroo newborn. About the size of a jelly-baby, the tiny joey has to crawl up the hairy abdomen of its mother using only its forelimbs (the hind limbs are not well developed; see Fig. 1, which shows not a joey, but a similar newborn) to reach the safety of the pouch. Because the pouch is a soft-tissue feature, it is currently impossible to tell from the fossil record whether early metatherians reproduced in the same way.
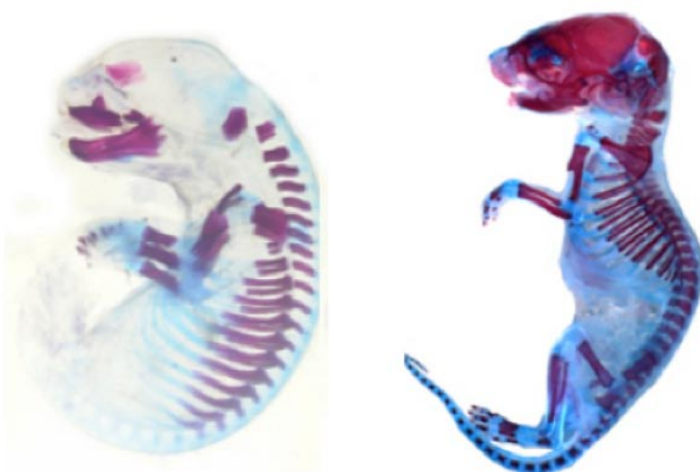
FIGURE 1 — CLEARED-AND-STAINED POST-NATAL MARSUPIAL (GREY SHORT-TAILED OPOSSUM, MONODELPHIS DOMESTICA; LEFT) AND PRE-NATAL PLACENTAL (FOUR-STRIPED GRASS MOUSE, RHABDOMYS PUMILIO; RIGHT), SHOWING DIFFERENCES IN DEVELOPMENT AT TIME OF BIRTH. BONY ELEMENTS ARE HIGHLIGHTED IN PINK. (IMAGE MODIFIED FROM GOSWAMI, A., WEISBECKER, V. AND SÁNCHEZ-VILLAGRA, M. R.. 2009. DEVELOPMENTAL MODULARITY AND THE MARSUPIAL-PLACENTAL DICHOTOMY. JOURNAL OF EXPERIMENTAL ZOOLOGY PART B, MOLECULAR AND DEVELOPMENTAL EVOLUTION 312B, 186– 195. DOI:10.1002/JEZ.B.21283)

The relationship between marsupials and placentals:

Despite having evolved from one common ancestor, groups within the therian mammals are not equally closely related. The closeness of their relationships depends on how much evolutionary history they share (Fig. 2). Evidence from DNA and anatomical features of both living and extinct therians has been used to work out these relationships. Although not everyone agrees about how this evidence should be interpreted, there is a general consensus on the major groups of living theria.
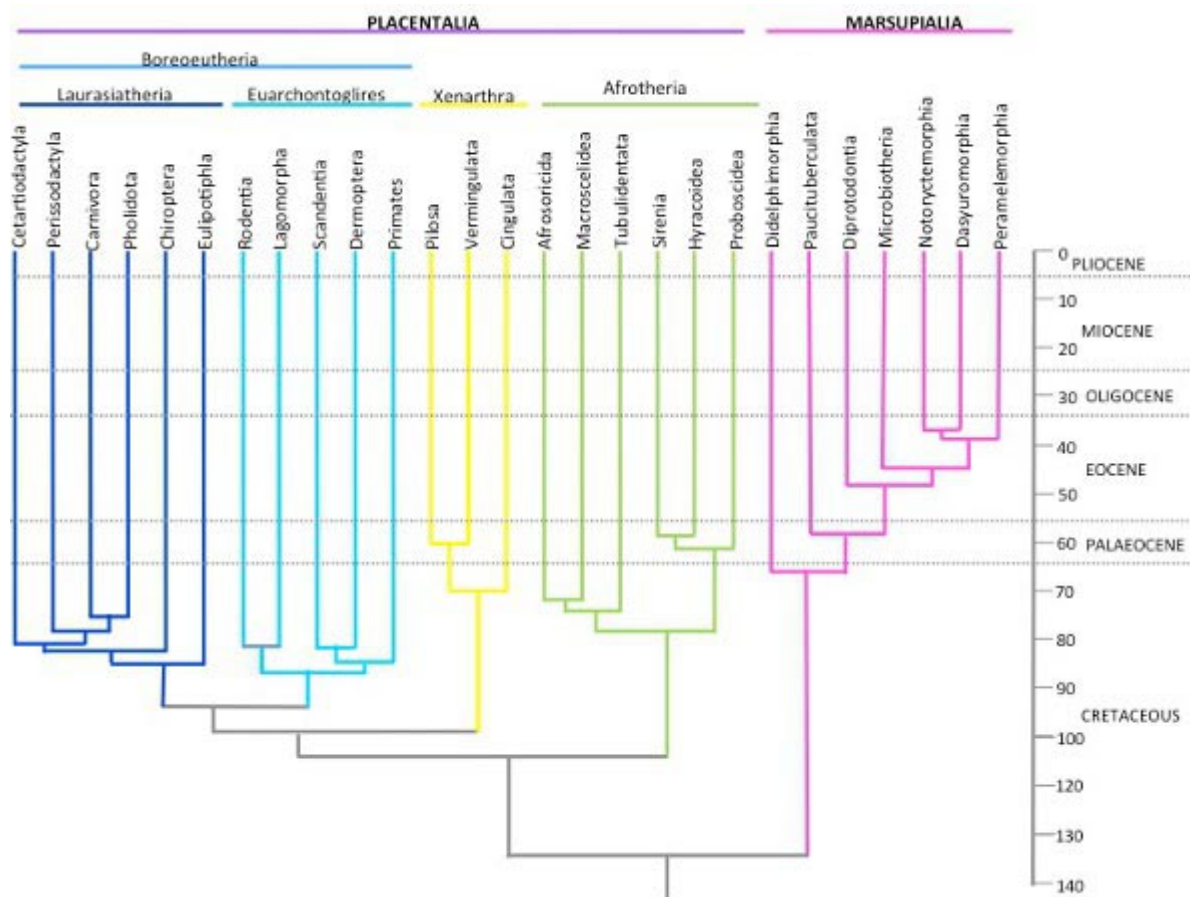

FIGURE 2 — CLADOGRAM REPRESENTING THE RELATIONSHIPS OF THE MAJOR ORDERS OF LIVING EUTHERIAN AND METATHERIAN ORDERS (POSITIONS OF EUTHERIAN ORDERS BASED ON MADSEN ET AL., 2001 AND MURPHY ET AL., 2001; METATHERIAN ORDERS BASED ON NILSSON ET AL., 2010).

There are more than 4,000 species of placental mammals in 20 orders. They live on every continent, and occupy ecological niches covering almost all altitudes, latitudes, habitats and diets, and have specialized limbs for many different ways of moving about.

By contrast, there are only 331 species of marsupials, in seven modern orders (there are also three known extinct orders). They are very common in Australia, but apart from that, marsupials are found only in South America (about 90 species) and North America (one species). Living forms range from the single species of the mouse-like order Microbiotheria in South America to the Australian order Diprotodontia, which includes more than 100 species, from kangaroos to wombats.

There are no marsupials that are highly specialized runners and none that live in water or have powered flight. However, some fill very similar ecological niches to some placental mammals, and look superficially similar. For example, Notoryctes is called the marsupial mole; the sugar glider, Petaurus, glides between trees in the same way as the placental flying squirrel; the numbat, Myrmecobius, is a marsupial anteater; and the Thylacine, which sadly went extinct in the 1980s, is called the marsupial wolf. Despite the limited geographical range of modern metatherians, they are found in the fossil record on every modern continent.

Metatherian fossil record:

The earliest known metatherian, the opossum-like Sinodelphys szalayi (Fig. 3), comes from the early Cretaceous Yixian Formation of China (125 million to 121 million years old). Cretaceous metatherians have been found elsewhere in Asia and in Europe, but they are found much more often in North America. This is probably a reflection on the collection effort in different parts of the world.
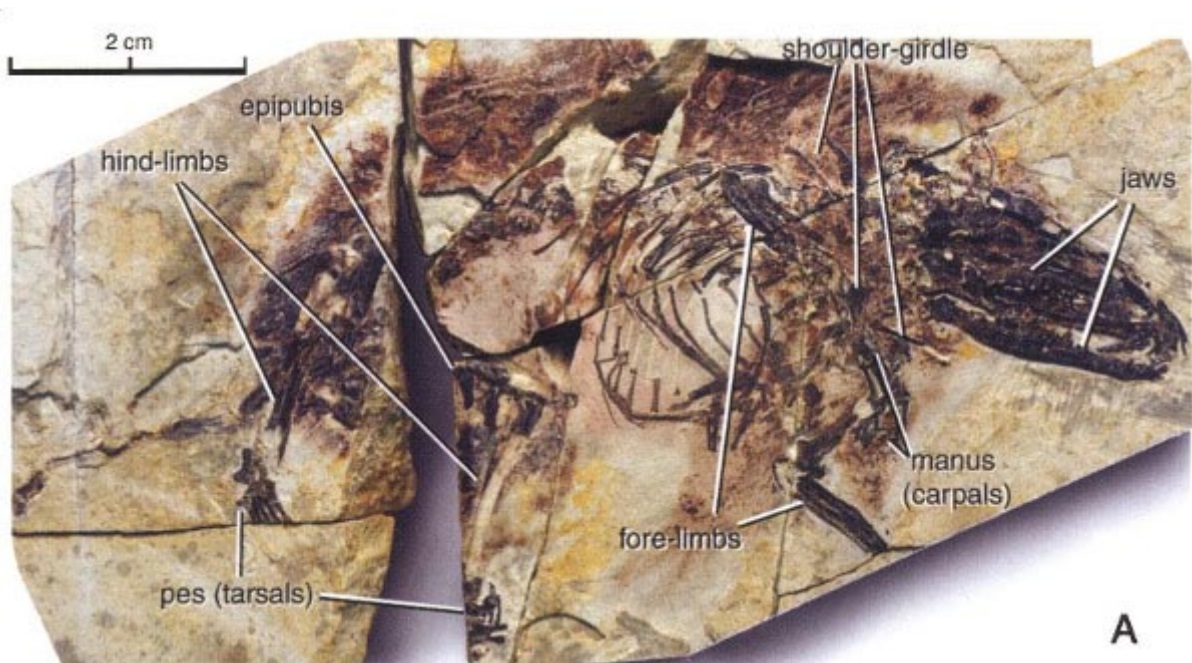
FIGURE 3 — SINODELPHYS SZALAYI FROM LUO, Z.-X., JI, Q., WIBLE, J. R. AND YUAN, C.-X. 2003. AN EARLY CRETACEOUS TRIBOSPHENIC MAMMAL AND METATHERIAN EVOLUTION. SCIENCE 302, 1934–1940. DOI:10.1126/SCIENCE.1090718.

Most palaeontologists agree that Metatheria originated in Asia, diversified throughout the northern continents, dispersed into Gondwana (the modern Southern Hemisphere) around the beginning of the Palaeocene epoch (65 million years ago), then moved through Antarctica to Australia before the Australian continent was isolated by the opening of Drake Passage between South America and Antarctica. But the fine details of these dispersals and radiations are not well understood. Whether metatherians took a western route through Europe to North America or an eastern one through North America to Europe is undecided, mostly because the European fossil record is quite poor.

The early Metatherian fossil record is confined to the northern continents until the end Cretaceous period. Metatheria appear in South America in the Palaeocene then seem to diversify throughout Gondwana, but die out in Laurasia (the modern Northern Hemisphere) after the Eocene epoch (55 million to 34 million years ago).

European metatherians fall into two extinct, opossum-like families: the Herpetotheriidae and Peradectidae, both of which are also known from North America and Asia. The European and North American herpetotheriids are very similar, which is strong evidence that they travelled between the two continents during the late Cretaceous period (100 million to 65 million years ago). However, it is not clear for how long they would have been able to use this route and whether there was a preferential direction of travel; it is also possible that early metatherians travelled to both Europe and North America from Asia.

The only undoubted fossil metatherian from Africa is Peratherium africanum, a herpetotheriid known from the Oligocene of Egypt (34 million years ago to 23 million years ago), is thought to have originated from European stock.

North American metatheria have a good fossil record, possibly because preservation conditions were favourable, because there has been a large effort to collect fossils here or because there were in fact once very large numbers of marsupials on the continent. Most taxa belong to families of Didelphimorphia, or opossums.

The fossil record for metatherians in the Southern Hemisphere is far more substantial than that in the Northern Hemisphere. Palaeontologists know of several sites with fossils of many different kinds of animals.

The first South American Didelphimorph is Szalinia from the early Palaeocene site Tiupampa in Bolivia. More recent Didelphimorphs include the only living North American species, the Virginia opossum Didelphis virginiana, and are for the most part tree-dwelling (arboreal) insectivores, carnivores or omnivores. One genus, Chironectes, spends much time in the water and even has webbed feet, although it is not fully aquatic.

The extinct order Sparassodonta is known from the Palaeocene and Pliocene of South America (65 million to 3 million years ago). Sparassodonts were the largest South American metatherians, ranging from opossum-sized to bear-sized, and had ecologies ranging from carrion eaters to sabre-toothed predators, with molars specialized for cutting (Fig. 4). Their relationship to other marsupials is uncertain.

Only one genus of the South American order Microbiotheria survives: Dromiciops or 'monito del monte', a small, arboreal insectivore. The relationships of Microbiotheria are unclear; learning about them would help us to understand how metatherians evolved in Australia, particularly because there are almost no fossil marsupials in Australia until the Oligocene. Most morphological and DNA studies of metatherians place Microbiotheria with Australian forms. This would imply either that Microbiotheriids returned to South America after reaching Australia, or that Australian forms diversified before reaching Australia. Without fossil evidence, it is hard to tell for sure how species evolved.

FIGURE 4 — ARTIST'S IMPRESSIONS OF THE SPARASSODONT PREDATORS THYLACOSMILUS (LEFT / SOURCE) AND BORHYAENA (RIGHT / SOURCE).

Antarctica, the 'stepping stone' between South America and Australia, potentially holds a wealth of significant fossils, but recovery of such evidence is limited by the difficult working conditions on the continent. However, a small number of metatherian fossils are known from the middle Eocene La Meseta Formation of Seymour Island, Antarctica, and include some from the orders Didelphimorphia and Microbiotheria. Species must have crossed into Australia from South America before the continents separated, between 43 million and 35 million years ago. It is possible that animals were still crossing through Antarctica well into the early Palaeocene; evidence for this is Chulpasia, an Eocene genus found at both Chulpas in Peru and Tingamarra in Queensland, Australia.

The Tingamarra site marks the beginning of the Australian fossil record for metatherians. There is then a significant gap in the Australian fossil record following this until the Riversleigh deposits of the boundary between the Oligocene and Miocene epochs (about 23 million years ago), by which point all extant orders of marsupials have made their appearance.

Most Australian fossil orders have recent representatives; the only extinct order is Yalkaparidontia, which appears in the Miocene deposits of Riversleigh. Specimens have molar teeth similar to those of Notoryctes, and skulls similar to those of bandicoots. It has been suggested that these animals could have been 'marsupial woodpeckers' that fed on wood-dwelling insect larvae, as does the living Indonesian Diprotodont Dactylopsila.

Diprotodontia are by far the most abundant and diverse Australian marsupials. They first appear in the late Oligocene, and were even more diverse in the Oligocene–Miocene period than they are now. Diprotodontidae, an extinct family, includes the largest known marsupials: the very largest, Diprotodon, was a fully quadrupedal form estimated to weigh more than one tonne. Members of the Palorchestidae, including the horse-sized Palorchestes, look similar to diprotodontids, and persisted until the late Pleistocene epoch (about 10,000 years ago). Thylacoleonidae, or the marsupial lions, Priscileo, Wakaleo and Thylacoleo, known from the boundary between the Pliocene and the Pleistocene epochs (about 2.5 million years ago), are carnivores with large cutting premolar teeth and an extremely powerful bite.

Living members of Diprotodontia fall into three major groups: the Phalangeriformes, the Macropodiformes and the Vombatiformes. Phalangeriformes comprises five arboreal families including the Trichosurus or brush-tailed possum; the Spilocuscus or common spotted cuscus; the nectar-feeding Tarsipes or honey possum; and the Petaurus or sugar glider. Macropodiformes comprise three families of bipedal bounders including the kangaroos.

Vombatiformes include the quadrupedal, digging wombat family Vombatidae and the koalas (Phascolarctidae), which are now endangered because they eat only eucalyptus, which is disappearing.

The most abundant marsupial group in the late Oligocene and Miocene was Peramelemorphia, with around a dozen species of omnivorous hopping bipeds. The two extant families of this order are the Peramelidae (bandicoots) and the Thylacomyidae (bilbies). There is also one recently extinct family, the Chaeropodidae or pig-footed bandicoots.

The order Dasyuromorphia includes Myrmecobius, the numbat or marsupial ant-eater. Myrmecobius is interesting because no similar forms are known in the fossil record before the occurrence of still-living species in the Pleistocene.

Our knowledge of metatherian history fluctuates in volume and geographical location of fossils over time. Notable sites such as the Bolivian Tiupampa, the Brazilian Itaborai and Oligocene–Miocene deposits of Riversleigh in Australia provide a wealth of material. Yet time periods such as the Eocene in Australia and the early Palaeocene in South America are notably devoid of information. Significant gaps in the fossil record and large variations in the rigour of collection across the world also make an accurate interpretation of metatherian evolutionary history difficult despite the increasing popularity of techniques that investigate it through DNA and body shape.

Why marsupials are less diverse than placentals — the constraint hypothesis:

Palaeontologists sort fossils into species and families mostly on the basis of anatomical similarities and differences, but this classification system cannot explain much about why animals have different shapes. However, during the 150 years since Charles Darwin proposed his idea of evolution by modification through descent, our understanding of the mechanisms through which animals come to differ from each other has grown considerably. The concept of evolutionary constraints — limits on the nature of forms that can be evolved — has received much attention.

Biological form is produced during development: growth from the fertilized egg into an adult organism, as dictated by inherited genetic information. It has been recognized that early events in an animal's development, such as the sequence or timing of the growth of individual body parts, have significant roles in the range of shapes that can be produced. If the mechanisms guiding the developmental process can change easily, diversity is promoted. By contrast, constraints in the developmental pathways can limit diversity.

The possibility that marsupials might be limited to certain shapes, owing to the need to crawl into the pouch after the short pre-natal development period, was first discussed in the 1970s as a way of explaining the lack of aquatic or flying marsupials. Study of shape changes during growth in the bones of the shoulder and a comparison of adult diversity in the shoulder blade and pelvis have found evidence for constraint in marsupial shoulder morphology.

Biomechanical demands on the skull change throughout growth, as the animal stops feeding by sucking and begins to use processes such as chewing. This is a key transition in skull growth for all therians. The sucking period is longer for marsupials than for placentals, and it is during this phase that the skull bones not present at birth in marsupials ossify (become bone rather than cartilage). It is possible that skull shape is also constrained in

marsupials owing to these early mechanical demands. However, a recent study of morphological variation in the skulls of extant and extinct carnivorous metatherians and eutherians does not seem to support this hypothesis. Further study is under way to see whether skull shape is constrained for other metatherians.

Summary:

The difference in evolutionary history between metatherian and eutherian mammals is key to understanding the current contrasts in diversity between the marsupials and placentals. However, the fossil record is incomplete and biased, which potentially obscures our perception of true patterns. Work is under way to tease out true diversity patterns from the metatherian fossil record using statistical techniques. Patterns in species diversity and geography, however, tell only part of the story. The diversity of shape, appearance and ability, which must enable or limit ecological diversity of mammal groups, surely plays a major part in their evolutionary history. Physiological differences between placentals and marsupials such as those relating to the early mechanical demands on the newborn may well have caused metatherians to be limited where eutherians were not, and thus is a possible explanation for the greater diversity of today's placental mammals. The combination of many lines of evidence and techniques from fields such as palaeontology, maths, molecular biology, developmental biology and even biomechanics is important for the comprehensive understanding of evolution. Such an interdisciplinary approach requires collaboration and communication between specialists in those fields but also a broad understanding of all areas.

Suggestions for further reading:

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