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The evolution and classification of marsupials

Michael Archer and John Kirsch

A bit of history

Marsupials have been known to European biologists almost since the discovery of the Americas at the end of the fifteenth century; properly classifying them took some time. While the novelty of the opossum's pouch was instantly appreciated, no special position outside the then-usual classification of mammals seemed needed. Nor could this easily have been done: most arrangements of the time were relatively simple in structure and oriented toward European animals, and these limitations persisted into the eighteenth century. Regardless of his greed for new and exotic specimens, Linnaeus's classifications remained 'folk-like' in this sense; and he named and placed *Didelphis* in a group along with insectivores, armadillos and the pig in his 1758 edition of the *Systema naturae*, the conventional starting-point for modern animal taxonomy. By that year naturalists were aware of several species of opossums – which seemed pretty much to be minor variations on the same theme – but the earliest, seventeenth-century, descriptions of the more distinctive Australasian marsupials (e.g. cuscuses *Phalanger* spp. and tammar wallaby *Macropus eugenii*) did not immediately come to scientific attention. The diversity and range of adaptive differences amongst antipodean marsupials really became obvious only with Captain Cook's voyages, beginning in 1768, and the settlement of New South Wales.

The eastern grey kangaroo *Macropus giganteus* was among the first discovered, and it obviously was not an opossum. Erxleben in 1777 decided it was a very large leaping rodent, and so began the tradition unfortunately still with us of referring to marsupial species in terms of the placentals they somewhat resemble, either anatomically or ecologically: the koala *bear*, the Tasmanian *wolf*, and even the marsupial *bandicoots* (the last name properly applies to large

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southeast-Asian rats). Even within marsupials this (mis)use of common names can be confusing: for example, Australians usually refer to many native arboreal species as ‘possums’, though these animals are very unlike the *o*possums of the New World.

What partially forced recognition that marsupials are a separate, natural group was the even greater challenge to conventional mammalian classifications presented by the monotremes, both the short-beaked echidna and platypus coming to scientific attention at the very end of the eighteenth century. In fact, so apparently chimerical was the second of these – with its duck-like bill, beaver tail, and spurred feet – that it was initially suspected of being a hoax. Nor was the strangeness of monotremes limited to external features, the structure of their reproductive and excretory systems being more reptilian or bird-like. It even seemed possible, although not proved to the satisfaction of biologists until 1884, that monotremes might lay eggs. If so, many felt, they could not also give milk, because egg-laying and lactation were then regarded as mutually exclusive characters pertaining to different classes of vertebrates.

In part under the influence of the French anatomist Cuvier’s not-unreasonable principle that some features, often the literally ‘deeper’ and more ‘vital’ ones of neuroanatomy or reproduction, are more important to classification than others, de Blainville in 1833 formally proposed that monotremes be considered a distinct group, the Ornithodelphia, based on their bird-like reproductive anatomy. This decision also opened the way to recognition of a major and defining difference between marsupials and placentals: whether the female reproductive tracts are dual or (often) single. Indeed, Linnaeus’s generic name, *Didelphis*, refers to the possession of two internal uteri – not, as is frequently assumed, to the presence of that supposedly auxiliary external womb, the pouch. Yet for some considerable time during the nineteenth century, and occasionally in the twentieth, monotremes and marsupials were thought to be specially associated, based partly on their shared possession of some skeletal features but probably also because of geographic propinquity, at least in Australasia.

Usually, however, marsupials and placentals (together, the ‘Theria’) are considered to be more closely related to each other than either is to the monotremes, a conception we owe to T. N. Gill (1872) and Thomas Huxley (1880), with all the implications for comparative biology which that association suggests. However, as we shall see later, it is a grouping again being called into question by some molecular studies. Whatever the interrelations of the three kinds of mammals, mammals as a *group* are very old, part of a lineage that goes back to the very origins of amniotes some 300–400 million years ago, and with apparently no special relationship to any of the living kinds of reptiles (turtles, snakes and lizards, *Sphenodon* and crocodylians) or birds.

This is not to say, however, that marsupials, placentals or monotremes themselves are that ancient; probably the live-bearing mammal groups are no more than half that age. Just how old are marsupials, and where did they originate? These seemingly straightforward questions are difficult to answer. If marsupials are distinguished from placentals mainly on the basis of reproduction, we can't expect much direct evidence of that in the fossil record, but must infer the ages of these kinds of mammals from hard parts that seem to be typical of each kind. For example, a general characteristic of marsupials is that only the third premolars (teeth just in front of the molars) among the postcanine cheek teeth are replaced during maturation. This is a feature that has been observed in fossil mammals about 95–100 million years old, which are then by definition marsupials. They also have other marsupial features, including the metacones being equal to or larger than the paracones on the upper molars and the hypoconulids being closer to the entoconids than the hypoconids on the lower molars.

The oldest fossil with marsupial features, *Sinodelphys szalayi*, was described only in 2003 from remarkably well-preserved deposits from western Liaoning Province in northern China; this find dates to the Early Cretaceous some 125 million years ago (Luo *et al.* 2003). The oldest known placental mammal, *Eomaia scansoria*, hails from the same deposits. Therefore the best guess at the moment is that marsupials and placentals probably separated from their supposed common ancestor at or shortly before this time, most likely in Asia, where the oldest relevant fossils are found. From there marsupials spread to all other continents, and the routes they followed and their subsequent history must have been greatly influenced by the changing positions of the continents. Today, as is well known, marsupials are only found in Australasia and the Americas. Tracing the broad patterns of marsupial evolution and distribution (especially of those subgroups still represented among living marsupials) are the chief purposes of this chapter, requiring first of all an understanding of marsupial classification – and indeed the process of classification itself.

The nature of classification and diversity of marsupials

When the professional administrator and amateur entomologist Alexander Macleay travelled to Sydney in 1826 to take up his post as Colonial Secretary of New South Wales, he brought with him an enormous desk with over a hundred drawers, crafted for him by Chippendale to house Macleay's insect collection. Mr Macleay's desk provides a metaphor for the most important distinction needed to understand classification, that between **categories** and **taxa**. Categories are the drawers, or the subdivisions of drawers, and taxa are the objects put in those categories. Biological classification is hierarchical, meaning that the categories are nested (small sections within larger ones within drawers within the desk), and by implication the taxa in

the smaller categories are thought to be more like each other than taxa in other, more inclusive categories. In the hierarchy we have inherited from Linnaeus and his immediate successors, it is conventional to recognise seven named and nested categories: from least to most inclusive, these are the species, genus, family, order, class, phylum, and kingdom. Sometimes, in a complex classification, it is necessary to insert additional categories (infrafamily, subfamily, superfamily, infraorder etc.). So marsupials are considered a major subdivision of the class Mammalia. It is important to understand what is classified at each level or more inclusive grouping: in a sense, species ‘disappear’ after they are gathered into genera (the plural of genus); similarly, it is a set of genera that are assembled into a family, families are the objects grouped in orders, and so on.

Thus, an organism is said to be classified when – minimally – its position in the seven levels of the Linnaean hierarchy is fully specified. Within any of the three major divisions of Class Mammalia, the largest – that is, most inclusive – subgroupings of mammals are the **orders**, usually defined by a major sort of shared lifestyle, itself reflected in a common general anatomy. Familiar placental orders are the primates (mostly arboreal, herbivorous or omnivorous mammals), carnivores (generally meat-eaters), rodents (usually small species with prominent front teeth), bats (the only flying mammals), and so on. Marsupials encompass seven living and at least four wholly extinct orders among those known at least since the very latest Cretaceous, but none is exactly comparable to any placental order, and some include a much broader range of lifestyles. For example, the marsupial order Diprotodontia consists of various kinds of possums, kangaroos, koalas and wombats, as well as several extinct families like the trunked palorchestids, rodent-like ektopodontids and utterly distinct marsupial lions. Diprotodontians are characterised by enlarged forward-pointing, lower incisors – that is more or less what the name means – and the overwhelming majority of species are herbivorous. However, comparisons with placentals would involve several orders – at least rodents, primates, condylarths, anthracotheres, perissodactyls, artiodactyls and carnivores. On the other hand, placental moles are considered by most (but not by all) taxonomists to be a subset of the order Insectivora, while the marsupial equivalent, the marsupial moles, are placed in an order all by themselves – in part because they are equally distant in terms of morphological divergence from all other marsupial orders. Moreover, it is not universally agreed that the order Insectivora represents one natural group of placental mammals. In terms of numbers of species, living placentals are an order of magnitude more diverse than marsupials, but, with the exception of bats and cetaceans, marsupials represent virtually the entire range of placental lifestyles.

Six of the eleven currently recognised marsupial orders are (or were) found only in the Americas, with a few members once living in Europe, Africa and Asia, and the documented history of at least one of them extends back to at least 63 million years.

Just one of the five Australasian orders (Yalkaparidontia) is completely extinct, reflecting perhaps the poorer fossil record in that part of the world, which is only reasonably continuous for the last 25 million years, although the fossil record of marsupials in Australia goes back to 55 million years. Several additional and much older families of marsupials, or possible marsupials, are known from the northern hemisphere (extending back into the late Cretaceous), but taxonomists are uncertain as to how these are related to the eleven orders.

Here we characterise the orders briefly for the sake of discussion, and will then go on to indicate something of how these groups might be interrelated. Although we first list and discuss the marsupials now (or formerly) found in the Americas, we caution that one of our conclusions will be that the American–Australasian geographic distinction may be little more than a conversational convenience.

Order Didelphimorphia

Opossums, as we have noted, were the first marsupials discovered and classified. They range in size from that of a mouse to a large cat, and are carnivorous, insectivorous, or omnivorous, although members of one of the two living families (Caluromyidae) are arboreal species which take a good deal of fruit and leaves. didelphimorphians are generally considered most like the earliest marsupials, but it is certain that they were preceded by several unrelated forms, and the diversification of the Didelphimorphians largely took place in South America; those now found in North America appear to have invaded that continent at most only a few million years ago.

Order Sparassodonta

This extinct South American group includes species that may be older than, and not very closely related to, didelphimorphians. They were obviously carnivorous, one family (Thylacosmilidae) being remarkably similar to placental sabretooths (Felidae) and others (especially Borhyaenidae) closely resembling the Australasian thylacines (Thylacinidae). Some bear-size forms (among borhyaenids) may in fact have been bear-like and the largest carnivorous marsupials known.

Orders Paucituberculata, Groeberida and Argyrolagida

Only a few, shrew-like species of the first of these three orders persist today (caenolestids), again in South America, and have been of great interest to taxonomists because their forward-pointing lower front teeth are similar in basic form to those of Australasian diprotodontians. Several groups (e.g. groeberiids and some polydolopids) are in some ways analogous in molar form to placental rodents.

Paucituberculatans, known from South America and Antarctica, are very diverse and not clearly a monophyletic group. Groeberidans, which are known only from South America, had almost parrot-like skulls as well as rodent-like dentitions. Argyrolagidans, also known only from South America, appear to have hopped rather like small kangaroos or African jerboas.

Order Microbiotheria

For long considered just a strange opossum, the single living species of this order, *Dromiciops gliroides*, may in fact be an evolutionary ‘link’ between South American and some or all Australasian marsupials. It is a small, semi-arboreal animal found only in the wet forests of southern Chile and adjacent Argentina, subsisting mainly on insects and their larvae. Fossil forms from Murgon in Australia, at 55 million years of age, may represent early microbiotheriid immigrants to this part of Gondwana. Slightly younger fossil forms have also been found on Seymour Island, Antarctica.

Order Dasyuromorphia

The three families of this Australasian order, taken together, are most comparable to the didelphimorphians plus sparassodontans, but lack arboreal herbivores like the caluromyids and yet include a specialised termite-eating species (*Myrmecobius fasciatus*) that has no parallel among the American families. The largest were the once-diverse thylacinids which are so similar to borhyaenids in dental and a few key postcranial features that the two groups were once (but no longer) considered by some phylogeneticists to be each other’s closest relatives. The last known thylacinid was exterminated by Tasmanians in 1936. Dasyurids are the most diverse of the dasyuromorphians, ranging in size from shrew-like planigales to the wolverine-like Tasmanian devil. Myrmecobiids are known only from one living species (*Myrmecobius fasciatus*), their early origins being a complete mystery. There is also a growing range of Oligocene and Miocene dasyuromorphian-like genera (e.g. *Ankotarinja* and *Keeuna*) whose relationships to living dasyuromorphians, or for that matter any other group of marsupials, are controversial despite their having been first described as dasyurids.

Order Notoryctemorphia

This order contains a single genus of living, insectivorous marsupial moles (notoryctids) which are very like the African placental golden moles (chrysochlorids) in terms of dental and some external morphology. There were no similar American marsupials although one group of extinct South American mammals, the

necrolestids, whose relationships within Mammalia are profoundly unclear, may have been mole-like. The relationships of notoryctemorphians to marsupials in other orders have long been a mystery although most (not all) phylogeneticists consider them to be at least distantly related to dasyuromorphians. Recently discovered and far more 'primitive' Miocene notoryctids may help to shed light on the relationships of this group.

Order Peramelemorphia

In contrast to the marsupial mole, there are no close analogues among placental mammals for the marsupial bandicoots. These are all small to rabbit-sized burrowing or terrestrial insectivores, omnivores and herbivores found throughout Australia and New Guinea. There are three living families (peramelids, peroryctids and thylacomyids) and at least two extinct ones (yaralids and an as yet unnamed family). The relationships of bandicoots to other marsupials seem to be getting more rather than less controversial. A bandicoot known from the late Palaeocene deposit at Murgon is the earliest member of a modern Australian marsupial order known from the fossil record, and a demonstration that this group had differentiated before Australia finally separated from Antarctica.

Order Diprotodontia

As already noted, Diprotodontia is the most diverse (largest number of species) and disparate (many kinds which are anatomically and ecologically different) of marsupial orders, including families as distinct as the kangaroos (macropodids, hypsiprymnodontids, potoroids, balbarids), the koala (phascolarectids), wombats (vombatids) and even more extreme fossil families such as the fully lion-size marsupial lions (thylacoleonids), rhino-sized *Diprotodon* (diprotodontids) and tapir-like *Palorchestes* (palorchestids). This group also contains a diverse range of possums, most of which are omnivorous to herbivorous, ranging from cuscuses (phalangerids) to common gliders (petaurids), feather-tailed gliders (acrobatids), ringtail possums (pseudocheirids), honey-possums (tarsipedids) and several extinct groups including the rodent-like possums (Ektopodontidae) and unique miralinids.

Order Yalkaparidontia

Species of the extinct order Yalkaparidontia, known colloquially as 'Thingodonta' because of their bizarre dentitions, must represent a relatively ancient lineage of Australian marsupials. Because they had diprotodontian-like elongate, procumbent

lower incisors but mole-like cheek teeth, as well as a very ‘primitive’ basicranium, the relationship of this order to other marsupial orders remains a mystery.

Our chief purpose in the sections which follow is to attempt to clarify the relationships among these orders and relate this information to the geographic history of marsupials.

The bases of classification

To understand where this ordinal classification comes from – and even more importantly how the orders are related – requires an outline of the objectives of and bases for modern classification. A nested hierarchy such as Linnaeus’s looks a lot like a genealogy or pedigree, but it is important to state again that in a biological classification the nature of the objects changes at each level. In contrast, a pedigree always involves individuals that mate or are born to mated pairs.

Despite the incomplete analogy between pedigrees (or other sorts of hierarchies, like chains of command) and classifications, it was natural enough when evolution became an accepted principle of biology to interpret taxonomic arrangements as the result of relatedness through time. In fact, Darwin included a whole chapter on classification in the *Origin of Species*, arguing that the pedigree or family-tree metaphor only made sense as a result of descent with modification and divergence, driven by natural selection of the more fit. Darwin predicted that acceptance of his theory would provoke a revolution in the aims and methods of taxonomists, as biologists came to realise that a primary aim of classification should be to recover and represent the results of evolution.

That revolution has taken over a century to accomplish, in part because it is not obvious how the features of organisms should be used to discern relatedness in Darwin’s literal sense. To begin with, the theory of natural selection predicts that unrelated organisms are very likely to evolve the same features independently, as a result of their experiencing similar selective demands, particularly if they are found in different geographic regions: diprotodontians, for example, have (as their name suggests) two forward-pointing lower teeth much like those of placental rodents. In both cases this dental feature seems primarily associated with herbivory. Worse, some South American marsupials now thought to be unrelated to diprotodontians have the same dental feature (these are the paucituberculates, groeberidans and argyrolagidans). Thus, some similarities may be ones of **analogy** (fit for a similar function and independently evolved) and not of **homology** (defined as features inherited from a common ancestor which may or may not serve the same function). But how do we know that diprotodonty is homologous even for all the members of Order Diprotodontia? Many other features unique to Diprotodontia, such as their manner of connecting the hemispheres of the brain and possession of a second,

external thymus gland, suggest that the order consists of related families; so far as we know, the South American ‘diprotodonts’ lack – or lacked – these. Thus, detecting analogy is often dependent on considering a number of features when deciding whether two or more groups are related. If many features indicate a certain grouping but only one or two point to an alternative arrangement, it is more economical – or **parsimonious** – to bet on the arrangement that is supported by the most evidence.

But it is not even enough to distinguish homologous from analogous features. Two kinds of homologous features must themselves be recognised: those which are ancestral or primitive (or **symplesiomorphic** in cladistic terminology) and those which are derived or advanced (or **synapomorphic** in cladistic terminology). Only the latter can provide the ‘markers’ of evolutionary change and so provide evidence for related groups. This is not an obvious point, and only in the last 40 years have taxonomists started to make rigorous use of the distinction. For example, one of the most important reasons we think monotremes are distinct from therians (marsupials plus placentals) is that monotremes lay eggs, an obviously primitive feature. Therians, on the other hand, are live-bearers: they are thought to be specially related at least partly because their (more recent) common ancestor changed to this style of reproduction. At the same time, this does not mean that monotremes are more closely related to lizards, snakes, birds or any of the other land vertebrates that lay eggs. Monotremes and these other groups have all simply retained the primitive reproductive feature (laying eggs) from the earlier common ancestor of all land vertebrates (hence egg-laying is a symplesiomorphic feature in these groups). Also, of course, monotremes have a number of mammalian features (e.g. hair and milk production). Thus, shared primitive (symplesiomorphic) features tell us little or nothing about branching sequences; shared derived (synapomorphic) ones tell us everything. Moreover, establishing the sequence of changes in several characters allows us to construct a history of the progressive derivation of groups.

It is for these reasons that overall similarity is generally not a sufficient basis for an **evolutionary** classification (that is, one which has as its chief object the recovery of branching sequences, or phylogeny), because similarity that does not make the distinctions described above confounds not only analogy with homology, but also primitive with derived homologous features. For example, a marsupial classification based on simply counting up similarities and differences (or making some more sophisticated statistical analysis of these) would probably put all the carnivorous forms (from whatever continent) together; in fact, conflation of just this sort were a feature of earlier marsupial arrangements. Thus, some taxonomists argued that the thylacine was a ‘foreign element’ in the Australian fauna because it was so much like the extinct (American) sparassodontans in the shapes of its

teeth, lack of certain skeletal elements (e.g. marsupial or epipubic bones), and even in the arrangement of some of the bones of the skull. It now seems evident that these resemblances were either separately evolved (tooth form, loss of bones) or primitive (symplesiomorphic) features inherited from very early marsupials (some aspects of skull morphology).

Finally, we take it for granted that no evolutionary tree is complete or likely to be true unless fossils are included. Indeed, some years ago, while pursuing the thylacine–sparsassodont question using computer-aided analyses, we found that the tree was very different when relevant fossils were included than when they were not. If just one sparsassodont was included, it definitely paired with the thylacine; if additional members of the American order were included, sparsassodontans formed a quite separate branch nearer to didelphimorphians than to dasyuromorphians. One reason for these results is that the features of living taxa are the end points of a *sequence* of changes, and these end points may be reached by very different routes in different lineages (or from different starting points). Including only the (very similar) end points meant that terminal species representing two distinct branches necessarily went together on the tree. The sequence *is* the synapomorphy.

Classic and some modern anatomical schemes for ordering marsupial diversity

De Blainville having established the taxonomic independence of marsupials, and Gill and Huxley having suggested their position vis-à-vis monotremes and placentals, mammalogists were then free to do what they do best: classify the diversity of marsupials based on teeth and feet. With the accelerating discovery of both American and Australasian species, they had much to do. Two dichotomous systems developed, based on the number of the lower front teeth or incisors (two or more), and whether or not the second and third digits of the foot are united (a condition known as syndactyly). Five of the eleven orders have the inferred primitive states (many incisors and free digits); one, Peramelemorphia, has many incisors but combined digits; three are known or presumed to be diprotodont but not syndactyl; and at least one (Diprotodontia) has both derived states. The structure of the foot of diprotodont yalkaparidontians is unknown so its balance of features in this regard is uncertain.

If shared possession of derived states (i.e. synapomorphies) indicates relationship, these dental and pedal characters provide inconsistent arrangements. The derived pedal distinction (syndactyly) indicates a special affinity of bandicoots and the diprotodontians, suggesting that they shared a common ancestor that was syndactyl but not diprotodont; the latter condition would have evolved when or after the two orders became distinct. However, diprotodontians share diprotodonty but