



FAUNA *of* AUSTRALIA

19. BIOGEOGRAPHY AND PHYLOGENY OF THE METATHERIA

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INTRODUCTION

During the latest Cretaceous and Cainozoic, a period of some 80–90 million years (my), marsupials were members of the faunas of all continents. Today the group has a restricted biogeographic range. In the New World, particularly in Central and South America, the opossums (family Didelphidae, *sensu lato*) and rare caenolestids form a minor part of mammalian fauna dominated by eutherian species. Only in Australia do marsupials occupy a wide variety of niches as terrestrial omnivores, herbivores and carnivores.

In recent decades the tempo of research on marsupials has quickened as more biologists and palaeontologists have become interested in the group and new approaches to research have been employed. For example, application of the underwater screening technique of collecting fossils (McKenna 1965) has greatly expanded samples of small marsupials. Immunological and karyological analyses are providing new data on systematic relationships of living species.

We must introduce the following study with a disclaimer. Our intent is not to produce an annotated summary of all lines of research or detailed compendia of data. What follows is an overview of the current status of research on the biogeography, systematic relationships and phylogeny of marsupials that is biased by our own perspectives, but annotated with references that will direct the reader into the various specific areas of research.

Among the recently published compendia containing papers dealing with marsupials, several warrant special citation. Among palaeontological studies, *The Fossil Record of Australasia* (Rich & Thompson 1982) summarised records of marsupials and other vertebrates from this area. Savage & Russell (1983) presented a global survey of the mammalian record. The Pleistocene fossil record of Australasia received special attention in several chapters in *Quaternary Extinctions, a prehistoric revolution* (Martin & Klein 1984). *Carnivorous Marsupials* (Archer 1982c), *Possums and Gliders* (Smith & Hume 1984) and *Possums and Opossums* (Archer 1987) are the subjects of major collections of reports of current research. Other pertinent articles are to be found in *Vertebrate Zoogeography & Evolution in Australasia* (Archer & Clayton 1984). Some recent suggestions concerning classification of the marsupials and references to others can be found in papers by Marshall (1981b) and Woodburne (1984a).

This account is arranged in four sections. First is a review of many of the character sets that are being used in analyses of systematic relationships of marsupials. This is followed by comments on the current state of knowledge of the records and relationships of the families of marsupials. Emphasis is placed on the Australian groups; Eurasian, African and New World marsupials are briefly considered. A section is devoted to a resumé of the changing distribution and topography of continents during the Jurassic, Cretaceous and Cainozoic. Finally, we present and comment on some of the current interpretations of the history of evolution of the group.

CHARACTER SETS EMPLOYED IN ANALYSES OF SYSTEMATIC RELATIONSHIPS

The study of phylogenetic relationships is based on interpretations of variation in a range of different character sets (see Chapters 12A and 12B, for a general introduction). Some of these involve use of terms and concepts peculiar to the subjects. Before proceeding to a consideration of the phylogeny of marsupials these character sets are introduced with references to papers that contain more information on each character set.

When only modern mammals are considered, the membership of the Marsupialia can be precisely diagnosed. Their reproductive system, as blatantly demonstrated by the morphology and function of the females' pouch, clearly differentiates them from both monotremes and eutherian ('placental') mammals (note Lillegraven 1984). Some osteological characters have proven utility in distinguishing modern and other Cainozoic marsupials from eutherians. When considering the earliest and most primitive members of the Marsupialia, however, few stand as diagnostic apomorphies.

Cranial Characters

Diagnoses of the Marsupialia frequently include some characters of cranial morphology (Fig. 19.1). Several of these appear to be primitive characters of therian mammals (see Chapter 14) that are retained in many if not all marsupials but were lost in eutherians. Though having practical utility in differentiating Cainozoic marsupials from eutherians, they must be applied with caution in attempts to determine the affinities of Mesozoic mammals:

medial inflection of the angular process of the dentary occurs in most marsupials and some Cretaceous eutherians. Apparently this inflection was lost early in the evolution of most eutherian lineages only to evolve again in some groups, for example, the caviomorph rodents;

in marsupials the jugal extends posteriorly to reach the glenoid cavity and contributes to the lateral margin of the articulation of the dentary with the skull. Although the jugals of eutherians usually do not extend as far posteriorly, in hyraxes and proboscideans these bones are greatly elongated; and,

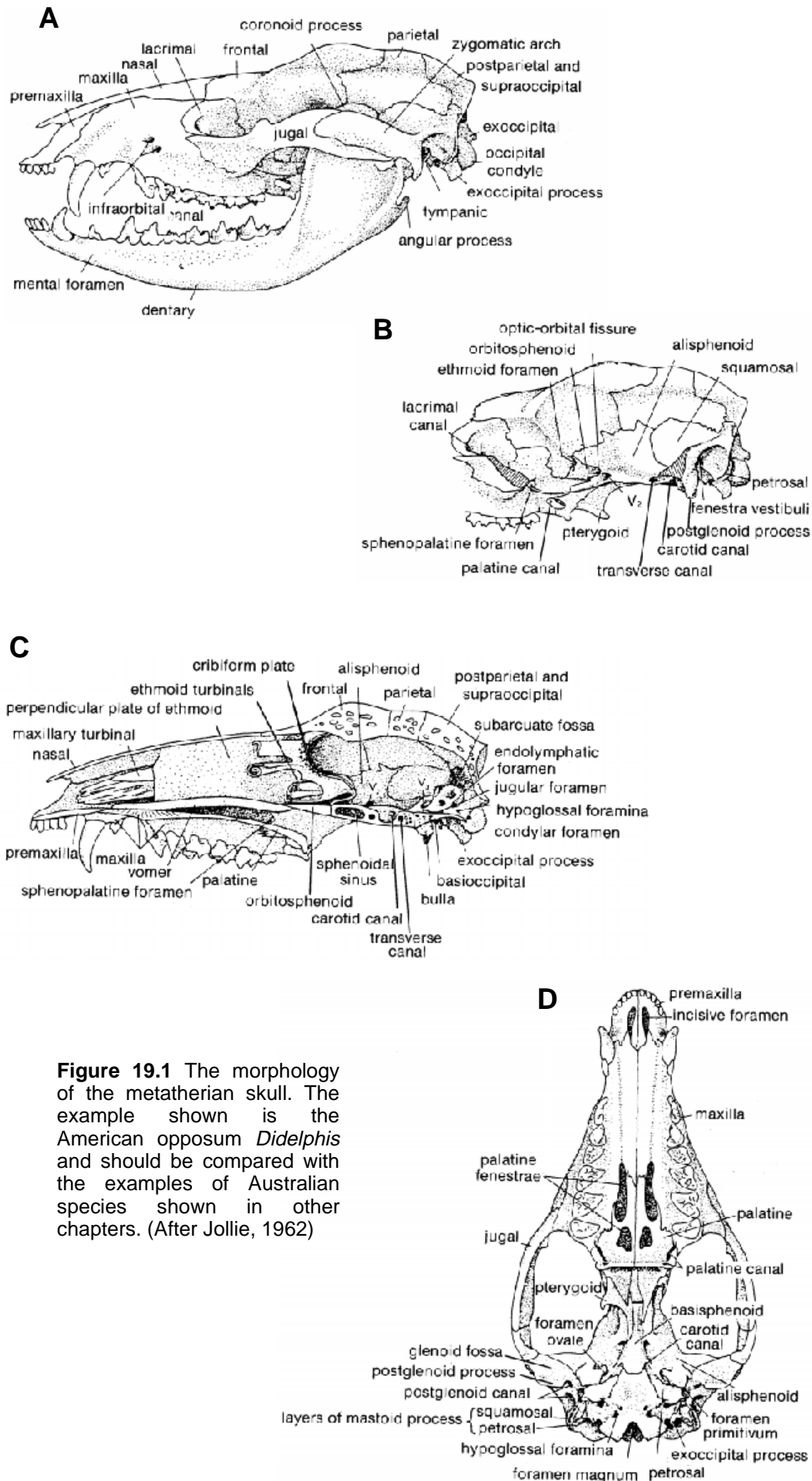
retention of the *vena capitis lateralis* passing through the middle ear and other elements of the venous drainage of the skull is reflected by a series of canals and foramina in and about the petrosal and adjacent bones.

Incomplete ossification of the palatine bones producing prominent vacuities, characteristic of most marsupials, also is found in some eutherians and non-therian mammals, for example, some multituberculates. Fenestration appears likely to be a specialisation evolved independently in several, distantly related lineages.

At what point in mammalian evolution ossification of the walls of the chamber – occupied by the middle ear – to produce a bulla began is not documented clearly in the fossil record. Whether it started in a late common ancestor of eutherians and marsupials or independently after these lineages differentiated remains an open question. Whichever the case, in almost all marsupials the alisphenoid forms a major part of the bulla. In only a few eutherians does the alisphenoid contribute to the bulla.

Within the Marsupialia, cranial morphology has not provided a wealth of characters of use in systematic analyses. Notable exceptions are to be found in some species of diprotodontids, the largest of Australian marsupial herbivores, in which the zygomatic arches are greatly enlarged and adorned with extraordinary processes. In addition, the macropodids are characterised by the enlargement of a slip of the masseteric muscle that penetrates the horizontal ramus of the dentary, a specialisation used widely in systematic analyses.

Studies of cranial morphology by Archer (1976), Marshall (1979) and Novacek (1977, 1986) provided both modern analyses of character polarities and extensive references to earlier works.



Dental Characters

Dental characters frequently employed in analyses of systematic relationships of marsupials are the dental formulae and morphology of the incisors and molar teeth.

Dental formulae of mammals comprise counts of teeth found in four regions of the dentition. In computing the formula, only one side of the dentition is considered. The key to the widely used system for designation of homologous teeth is identification of the upper canine (C^1), the tooth set in a socket (alveolus) situated at or just behind the suture joining the premaxillary and maxillary bones. The lower canine is the tooth that occludes against the front of the upper canine. Incisors (I) are the teeth anterior (mesial) to the canines. The cheek teeth posterior (distal) to the canines are identified as premolars or molars on the basis of their ontogeny. The premolars are those teeth posterior to the canine to and including the most posterior diphyodont tooth – a permanent tooth replaces a tooth with a ‘milk tooth’ predecessor (DP). The cheek teeth posterior to the premolars are the molars, which are monophyodont, lacking a ‘milk tooth’ predecessor.

In most texts marsupials are differentiated from eutherians on the basis of their dental formulae. Primitive marsupials are said to have a dental formula of I 5/4, C 1/1, PM 3/3, M 4/4 while eutherians are said to have a primitive dental formula of I 3/3, C 1/1, PM 4/4, M 3/3. Investigations of dental embryology and increasing knowledge of the ancestry and early members of the Eutheria and Marsupialia challenge this comfortable dichotomy (Clemens & Lillegraven 1986).

Primitive Marsupialia and Eutheria and their immediate common ancestors probably had at least 5/4 incisors. During the Late Cretaceous in many eutherian lineages the number of incisors was reduced to 3/3. In lineages of marsupials reduction went at a slower rate; for example in modern didelphid species 5/4 incisors are retained.

One upper and one lower canine is apparently the primitive mammalian condition. Embryological studies indicate that the development of dental alveoli and teeth might not be correlated closely with formation of the premaxillary-maxillary suture (see Clemens & Lillegraven 1986, and references cited). Thus, the teeth identified by the proximity of their alveoli to this suture might not be strictly homologous. Until this question is answered, we shall continue operating on the assumption that the upper canines of marsupials and eutherians are homologues.

The number of premolars in dentitions of the common ancestors of marsupials, eutherians and ‘tribotheres’ (see below) is unknown. The presence of five premolars in the dentitions of some Cretaceous eutherians and ‘tribotheres’ suggests that at least this number was the primitive condition. Also, most of the premolars, possibly excepting the premolar directly posterior to the canine, apparently were primitively diphyodont teeth.

The number of premolars was reduced to four in most Cretaceous eutherian lineages and most of the premolars were diphyodont teeth. In the dentitions of the oldest Cretaceous marsupials yet discovered the number of premolars has been reduced to three and diphyodonty suppressed. Archer (1974, 1984a) argued that the replacement of cheek teeth that occurs in marsupials involves loss of the ‘first molar’, traditionally designated DP3, which is pushed out of the jaw by the erupting permanent last premolar (PM3). If this interpretation is correct, marsupials have gone much farther in suppression of diphyodont than eutherians. In the following discussions we will adopt Archer’s interpretation that only three monophyodont premolars characterise the primitive marsupial dentition.

Following Archer's interpretation many current students have assumed that the dentitions of primitive marsupials contained five molars. The first is pushed out of the jaw by the erupting PM3; the others are strictly monophyodont teeth. We adopt these designations.

In an analysis of polarities of dental characters, Clemens & Lillegraven(1986) found the weight of the very limited available evidence suggested that the common ancestors of marsupials, eutherians and 'tribotheres' had but four molars in their dentitions. If this is the case, then addition of a fifth molar would be an apomorphy of the Marsupialia. At the moment the honest answer to the question of the primitive numbers of premolars and molars in the dentition of marsupials is admission of ignorance.

The number and general shape of the incisors and canines played an important role in early attempts to develop classifications of marsupials. In the primitive polyprotodont condition, the incisors are small, usually peg-like teeth followed by much larger canines. In two groups of marsupials the median upper and lower incisors became greatly enlarged and in some species these teeth are tilted forward (procumbent). The other incisors and canines are reduced in size or lost. This derived condition, diprotodonty, is shared by many Australian groups, for example, possums, kangaroos and wombats. A similar modification, probably involving different incisors, also characterises members of the South American caenolestoids.

Cheek teeth have been used extensively to assess phylogenetic relationships, since especially the molars are commonly preserved as fossils and exhibit a wide range of morphologies reflecting different dietary adaptations. Like all other character sets, the evolution of molar morphology includes cases of convergence and parallelism (Kirsch & Archer 1982). These often lead to anomalous results in the phylogenetic analyses and make it as difficult to determine relationships exclusively from molar morphology as it is from any other single character set.

The common ancestor of marsupials and eutherians was characterised by a derived molar morphology, the tribosphenic molar (see Chapter 14). Molars of this type are distinguished from those of primitive therians by the addition of a protocone to the upper molar that occludes with another new structure, the talonid of the lower molar (see Fig. 19.2). The available fossil record suggests that the tribosphenic molar pattern evolved some time during the Early Cretaceous or possibly earlier in the Late Jurassic.

During the middle of the Cretaceous, an adaptive radiation of mammals with tribosphenic dentitions appears to have taken place. The first records of marsupials and eutherians, recognised on the basis of both dental and cranial characters, are found in rocks of Late Cretaceous age. Amongst them is an increasing number of mammals with tribosphenic dentitions that cannot be referred to either the Marsupialia or Eutheria. For some of these tribosphenic therians, our inability to refer them to one group or the other probably reflects the limited amount of data provided by isolated teeth or fragments of jaws. However, other tribosphenic therians are known from partial skeletons and are not clearly referable to either group. They appear to represent separate lineages that stemmed from the mid-Cretaceous radiation of mammals with tribosphenic dentitions. These lineages, as well as groups of Cretaceous mammals whose phylogenetic affinities are not known because of a lack of data, are provisionally designated 'tribotheres' (Clemens & Lillegraven 1986).

The type of upper tribosphenic molar thought to be primitive for marsupials consists of several high, conical cusps separated by shelves and basins. The stylocone, paracone, and metacone (Fig. 19.2) are cusps found in pretribosphenic molars. The diagnostic feature of the tribosphenic upper molar is the addition of the protocone and, later, the paraconule and metaconule. In

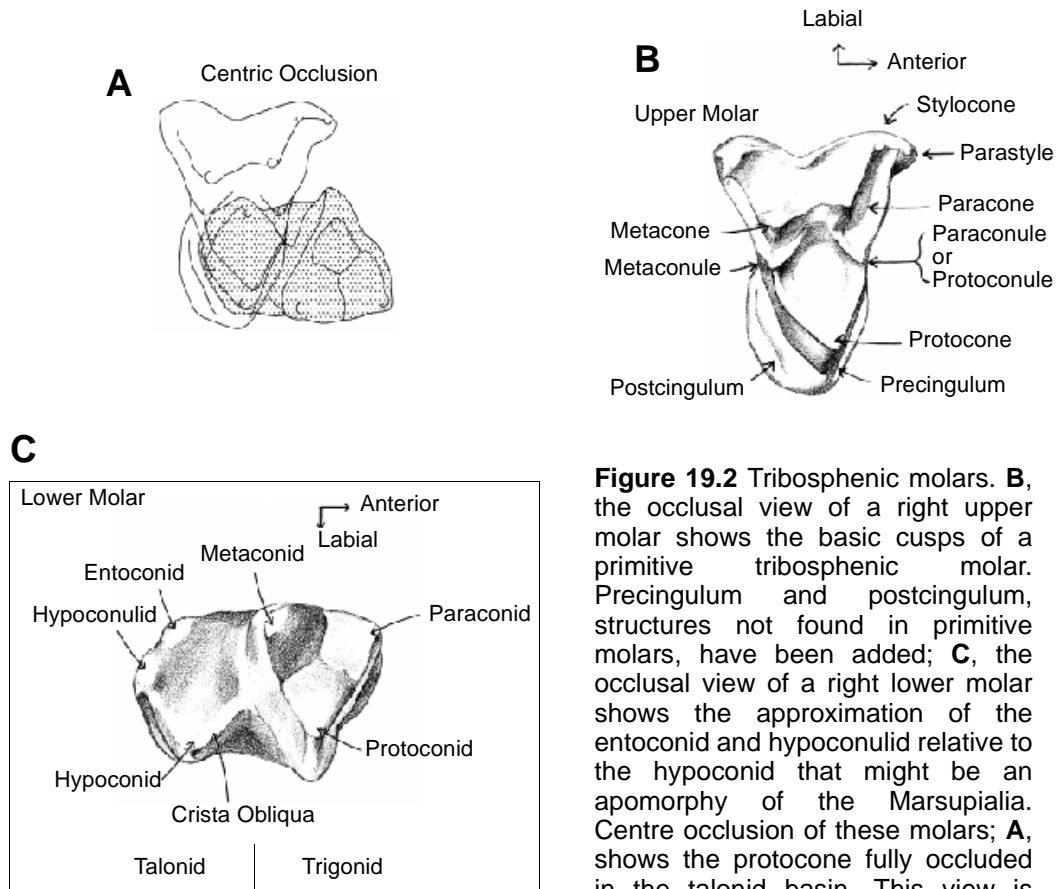


Figure 19.2 Tribosphenic molars. **B**, the occlusal view of a right upper molar shows the basic cusps of a primitive tribosphenic molar. Precingulum and postcingulum, structures not found in primitive molars, have been added; **C**, the occlusal view of a right lower molar shows the approximation of the entoconid and hypoconulid relative to the hypoconid that might be an apomorphy of the Marsupialia. Centre occlusion of these molars; **A**, shows the protocone fully occluded in the talonid basin. This view is drawn from the perspective of looking through the lower right molar. (© ABRs) [J.P. Lufkin]

contrast to eutherians, in the evolution of the dentitions of marsupials, the ‘stylar shelf’, that area of the crown labial (toward the cheek) of the paracone and metacone bearing the stylocone, tends to be maintained and apparently additional cusps were added to its labial margin. Another evolutionary pattern which distinguishes many lineages of marsupials and eutherians is the development of a precingulum and a postcingulum on the flanks of the protocone. These are rarely developed on molars of marsupials, but they appear early in the evolution of several lineages of eutherians.

The primitive tribosphenic lower molar consists of three anterior cusps forming the trigonid and, diagnostically, a lower, basined talonid which receives the protocone of the upper molar when the jaws are brought together. One feature of the lower molar that might be an apomorphy of the Marsupialia is the relative positions of the three cusps of the talonid. Origin of the tribosphenic lower molar involved the evolution of a basined talonid from the blade-like talonid of pretribosphenic molars. In marsupials, the entoconid and hypoconulid tend to remain closely approximated (the marsupial condition is illustrated in Fig. 19.2), but in eutherians the hypoconulid is usually positioned medially, approximately equidistant between the entoconid and hypoconid. Clemens & Lillegraven (1986) and references cited therein provided analyses of character polarities and hypotheses concerning the pattern of evolution of the tribosphenic dentition.

In the course of the evolution of the marsupial dentition the primitive tribosphenic type of molar was modified in a number of ways. From the primitive, high-spined morphology, the individual cusps in some lineages evolved low rounded shapes, a condition termed bunodonty (from *bunus*, ‘hill’). Another frequent modification is the incorporation of the individual cusps into

high crests, a condition termed lophodonty (from *lophos*, 'yoke'). Finally, in several groups the shape of the cusps is modified by the evolution of strong, curved, antero-posteriorly directed crests. In occlusal view, the cusps and crests resemble crescent moons, a morphology termed selenodont (from *selene*, 'moon'). The molars of some species are modified with crenulations of the enamel or evolution of ridges or struts radiating from the cusps.

The outline of the tribosphenic molars has been altered in a number of ways. Primitively, the high trigonid of the lower molar (Fig. 19.2) slipped into an embrasure between the triangular upper molars. Passage of the sharp crests of the talonid past crests on the edges of the upper molars produced a shearing action. Crushing of foodstuffs was limited to the movement of the protocone into the talonid basin. A common evolutionary pattern reflecting selection for greater emphasis on crushing by the dentition involves reduction of the height of the trigonid and development of cusps or a shelf on the upper molar to oppose the cusps of the trigonid. In eutherians, this was usually the result of enlargement of the postcingulum to oppose the trigonid of the following lower molar. In many instances a new cusp, the hypocone, evolved on the postcingulum. In many lineages of marsupials an analogous expansion of the upper molar apparently resulted from enlargement and a shift of the metaconule into the position of a hypocone.

Pedal Morphology

Structure of the ankle and the development of the toes of the hind foot have been used in considerations of marsupial relationships. The structure and function of the tarsal bones has received recent attention (Fig. 19.3; Szalay 1982a, 1982b). Evolution of the ankle can be tracked by changes in the mode of articulation of the astragulus and calcaneum. Two separate articulations link the two bones in protoeutherian and other primitive eutherians, and in most South American and Holarctic marsupials. This pattern is interpreted to be the primitive condition for marsupials. In the derived pattern, found in all Australian species examined, as well as *Dromiciops* from South America, the facets are merged, forming a single articular surface.

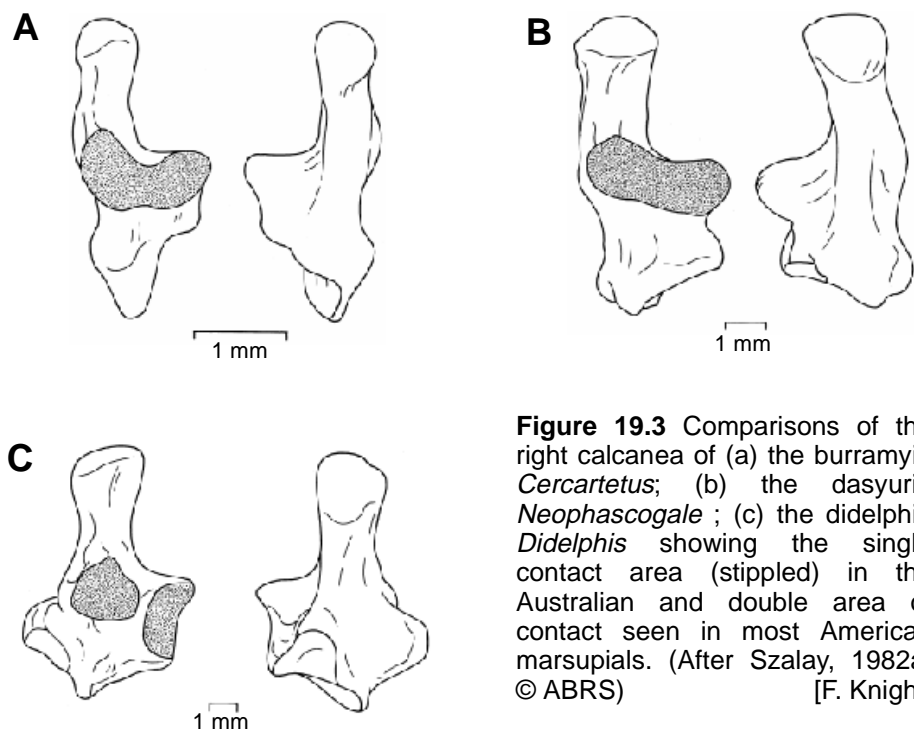


Figure 19.3 Comparisons of the right calcanea of (a) the burramyid *Cercartetus*; (b) the dasyurid *Neophascogale*; (c) the didelphid *Didelphis* showing the single contact area (stippled) in the Australian and double area of contact seen in most American marsupials. (After Szalay, 1982a; © ABRS) [F. Knight]

The five toes of the hind foot of primitive marsupials are well developed and separate, the didactylous condition. A derived morphology, syndactyly, is found in a limited number of Australian lineages. In a syndactylous foot, the phalanges of the second and third digits of the hind feet are reduced and bound with soft tissues into a single 'toe'. Szalay (1982a, 1982b) argued that this modification evolved to facilitate arboreal locomotion and later was adopted for use as a small 'comb' in grooming (Fig. 19.4). This unusual structure is found in the bandicoots and the possums and their relatives. A similar modification of the structure of the toes is found in the eutherian insectivore, *Potamogale*, and testifies to the reality of parallel evolution. If this complex structure evolved but once in the marsupials, the interpretation favoured by Szalay (1982a, 1982b), it indicates that the bandicoots and the possums must be closely related. As always, however, the possibility that syndactyly evolved twice, as a convergent condition and with the groups not being so closely related, must be considered.

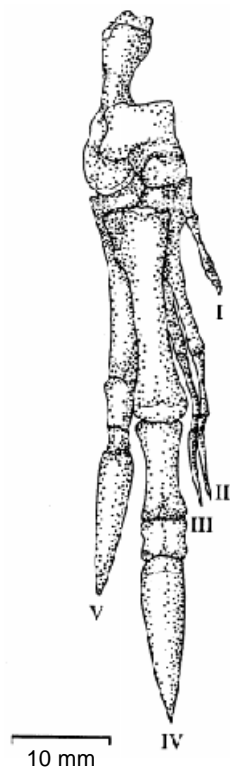


Figure 19.4 The structure of the right hind foot of *Perameles*. I-V = digits one to five, respectively. The syndactylous condition produced by the apposition of digits II and III can be seen. (© ABRS) [T. Cochran]

Amino Acid Sequence Data

The amino acid sequences of many proteins have been determined and, as these data have a genetic basis, they can be used as characters for studying phylogenetic relationships (Air *et al.* 1971; Schulz & Schirmer 1979).

Usually the data are organised as a series of genetic distances between species. This 'distance' may simply be the number of amino acid differences between sequences of the same protein in two species. Alternatively, more sophisticated methods designed to determine the number of 'mutations' that must have occurred to produce the observed amino acid changes may be used (Goodman *et al.* 1978).

Observation has shown that rates of substitution are relatively constant within groups for a particular protein, but differ for different proteins. As a consequence of this 'molecular clock', estimated dates of divergence of lineages can be calculated using such data. As is to be expected, significant levels of convergence and parallelism are present. Changes in the rates of substitution are

such that variation of up to 30% from the estimated 'constant' rate can be expected for an estimate based on the comparison of a single protein between two species.

Nevertheless, such data can be used to estimate approximate dates of divergence of lineages and can be especially useful in cases where fossil data are lacking, for example, the date of divergence of the South American and Australian marsupial lineages.

Sequence data are available for the globin sequences of kangaroos, opossums (*Didelphis* species), the Echidna, Platypus and several eutherians. Average numbers of amino acid substitutions between lineages have been calculated (Table 19.1). To determine dates of divergence, the 'molecular clock' represented by the data must be 'calibrated'. Unfortunately, there are no unequivocal dates available. A date of 135 mybp has been assumed for the separation of marsupials and eutherians and the estimated dates of divergence of the various lineages calculated proportionally.

Table 19.1 Average number of amino acid substitutions between lineages for α -haemoglobin, β -haemoglobin and myoglobin combined with estimates of the time since divergence, assuming eutherians and marsupials separated 135 mybp and a constant rate of amino acid substitution.

LINEAGES COMPARED	NO. OF SUBSTITUTIONS	YEARS SINCE SEPARATION
Marsupials to eutherians	98	135
Opossum to kangaroo	93	128
Echidna to platypus	39	54
Monotremes to eutherians and marsupials	108	149

The following points can be made from those data in Table 19.1:

the estimated date of divergence of the monotreme lineage from the combined metatherian/eutherian lineage is probably not significantly greater than that of the metatherian lineage from the eutherian lineage;

the opossum / kangaroo divergence is older than the oldest presently known fossil record of marsupials, raising doubts as to the significance of the known North American fossils in documenting the time of origin of the group. As serological data show the Australian radiation to be Tertiary in age, it probably occurred after the extinction of the dinosaurs in Australia rather than immediately following the presumed dispersal of marsupials into Australia; and, if *Steropodon* (85 mybp) is the ancestor of the Platypus, *Ornithorhynchus anatinus* (Archer *et al.* 1985), then *Steropodon* must also be the ancestor of the Echidna *Tachyglossus aculeatus*. Serological data suggest these lineages separated in the Tertiary and, presumably, also are part of a Cainozoic radiation of the Australian terrestrial fauna.

Immunological Data

Differences in the amino acid sequence of a protein in two different species can be measured by the intensity of the cross-reaction of antibodies (raised against the protein from one species) to the same protein in a second species. The intensity of the cross reaction is transformed into an immunological distance that is proportional to the number of amino acid differences between the species for the protein under study. The data can be interpreted in the same fashion as protein sequence genetic distance data and suffer from the same limitations.

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Immunological distances have been calculated between the major lineages using microcomplement fixation (MCF) techniques and purified albumin (Fig. 19.5a). In an earlier study using other techniques, Kirsch (1977a) obtained slightly different results (Fig. 19.5b).

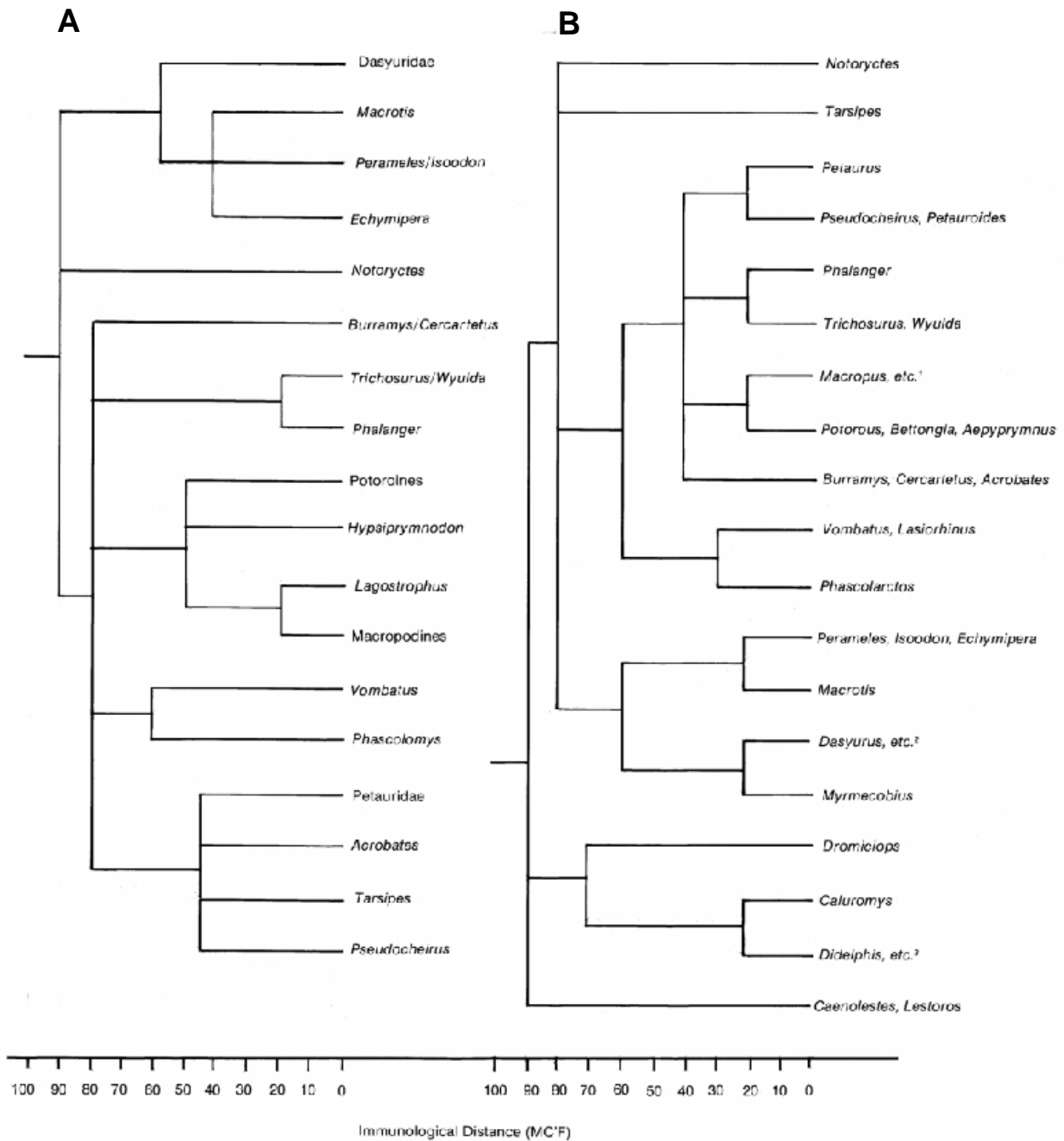


Figure 19.5 Genetic relationships within the extant marsupials as reflected in immunological distances measured using **A**, purified albumin (MCF; Baverstock, unpublished data); **B**, whole serum (Kirsch, 1977). (B, after Kirsch, 1977)

Cytological Data

To be of value as a phylogenetic tool, karyotypic data must be analysed cladistically (see Chapter 12B). The essence of a cladistic analysis is that only derived similarities (synapomorphies) are phylogenetically informative; similarities due to retention of ancestral states (symplesiomorphies) yield no phylogenetic information and unique, derived, character states (autapomorphies) are also phylogenetically uninformative (Hennig 1966).

The ancestral chromosome complement for the Australasian marsupials should be determined before relevant phylogenetic information can be obtained from karyotypic data at the familial level. Having established the ancestral chromosome complement, taxa in each family should be examined for the presence of that chromosome complement. Any family that has even one taxon which possesses the ancestral state will be unplaceable phylogenetically, since (in the absence of convergence) the common ancestor of all members of that family must have possessed the ancestral state. Whether any other taxa in the family have derived complements becomes irrelevant to the phylogenetic affinities of that family to other families, though such information may be useful in determining relationships within families.

For families with no taxon possessing the ancestral state, the actual rearrangements involved need to be assessed to determine whether they are unique to the family (autapomorphies) or occur in other families (synapomorphies). Any that are autapomorphic can also be removed from further consideration.

Step 1: the ancestral complement

Given a fundamental dichotomy between the Australasian and American marsupials, the ancestral complement for the marsupials will be that shared by both groups. As has often been pointed out, the diploid numbers of 14 and 22 occur repeatedly in both groups, an observation that led to considerable controversy over the possible ancestral complement for marsupials (Martin & Hayman 1967; Hayman & Martin 1969, 1974; Hayman 1977; Sharman 1961a, 1973, 1974). Clearly, if 22 were ancestral, then the common occurrence of 14 would be due to convergence (the converse would be true if 14 were ancestral). If due to convergence, the derived 14s would be most unlikely to involve exactly the same fusion elements. Yet, the G-banding studies of Rofe & Hayman (1985) have revealed that the banding patterns of the 14 elements are indistinguishable in both Australian and American forms possessing a $2n = 14$ complement and represent the ancestral state.

Step 2: occurrence of the ancestral complement in families

Given that this complement represents the ancestral state, we are now in a position to assess its presence in each of the Australasian families. Table 19.2 summarises the available data. From this table it can be seen that the families Peramelidae, Vombatidae and Burramyidae all have members possessing the ancestral state and, therefore, none of these families can be placed phylogenetically using karyotypic data alone.

Table 19.2 The families of Australasian marsupials showing the incidence of the ancestral $2n = 14$ complement.

FAMILY	SPECIES POSSESSING $2n = 14$ ANCESTRAL COMPLEMENT
Peramelidae	<i>Isoodon obesulus</i> , <i>Perameles nasuta</i> (<i>Echymipera</i> also possesses the presumed state, but has not been G-banded)
Thylacomyidae	None known (<i>Macrotis lagotis</i> has a highly derived $2n = 19$ ma, $2n = 18$ fe)
Dasyuridae	None known (All the forms of known karyotypes have $2n = 14$, but modified from the ancestral state)
Vombatidae	<i>Vombatus ursinus</i>
Phascolarctidae	None (<i>Phascolarctos cinereus</i> has $2n = 16$ due to a single fission)
Burramyidae (excluding <i>Acrobates</i> and <i>Distoechurus</i>)	<i>Cercartetus concinnus</i>
Phalangeridae	None (<i>Phalanger maculatus</i> and <i>Phalanger gymnotis</i> possess $2n = 14$, but clearly not the ancestral type)
Petauridae	None known
Pseudocheiridae	None known
Macropodidae	None known
<i>Acrobates</i> / <i>Distoechurus</i> (<i>incertae sedis</i>)	None known (<i>Acrobates pygmaeus</i> has $2n = 14$, but with at least two rearrangements; <i>Distoechurus</i> has a modified $2n = 14$ complement)
Tarsipedidae	None
Notoryctidae	None

Step 3: assessment of apomorphies

The next step is to assess the derived karyotypes in the remaining families for possible synapomorphies.

- a) Dasyuridae (for example antechinus, quolls, ningauis, phascogales, planigales and others)

All the dasyurids that have been G-banded except the Kultarr, *Antechinomys laniger*, and some *Ningaui* species, possess a $2n = 14$ karyotype apparently derived from the ancestral state by four rearrangements (Rofe 1979; Young *et al.* 1982). None of the other families with derived karyotypes appear to share any of these inversions (all of the inversions are autapomorphic to the family). The Kultarr and some ningauis possess one additional (but different) rearrangement. The similarity between the complements of some specimens of *Ningaui* and the Chilean *Dromiciops* led Sharman (1982) to suggest a phylogenetic affinity between the Dasyuridae and the Microbiotheriidae, but that the *Ningaui* complement is secondarily derived from the standard dasyurid complement is now apparent (Baverstock *et al.* 1983a). Hence, any proposed similarities of the complements of *Ningaui* and *Dromiciops* are due to convergence.

- b) Thylacomyidae

The Bilby, *Macrotis lagotis*, is the only karyotyped member of this family and it has a highly derived complement of $2n = 19$ (male) and $2n = 18$ (female) (Martin & Hayman 1967). No G-banding has been done. In the absence of G-banding of such a highly derived complement, a search for synapomorphies with other families cannot be carried out validly.

- c) Phascolarctidae

The single extant species of this family, the Koala, *Phascolarctos cinereus*, has a complement of $2n = 16$ (Sharman 1961a). No G-banding has been done, but the gross karyotype suggests a single chromosome fission difference from the ancestral state.

d) Phalangeridae (cuscuses and brushtail possums)

The living genera of this family are possums (*Wyulda* and *Trichosurus*) and cuscuses (*Phalanger*). The Common Brushtail Possum, *Trichosurus vulpecula*, possesses a derived $2n = 20$ karyotype apparently involving a minimum of eight rearrangements of the ancestral $2n = 14$ type. Two of these rearrangements may be common to the Feathertail Glider, *Acrobates pygmaeus* (Burramyidae; Rofe 1979). None of the species of *Phalanger* have been G-banded and only two (*P. gymnotis* and *P. vestitus*) have been karyotyped (Hayman & Martin 1974). Both possess an identical $2n = 14$ complement, but are clearly very different from the ancestral $2n = 14$ type. In the absence of G-banding, to search for synapomorphies with other families would be unwise. The complement of the Scaly-tailed Possum, *Wyulda squamicaudata*, is unknown.

e) Petauridae including Pseudocheiridae (for example gliders and ringtail possums)

Petaurus species ($2n = 22$) and the Striped Possum, *Dactylopsila trivirgata* ($2n = 18$), possess highly derived karyotypes (Sharman 1961a; Hayman & Martin 1974), as does Leadbeater's Possum, *Gymnobelideus leadbeateri*, with $2n = 22$ (Donnellan personal communication). Only *Petaurus* has been G-banded; it is so highly modified from the ancestral state that the precise rearrangements involved cannot be elucidated (Rofe, Baverstock & Gelder unpublished). Thus, a search for synapomorphies with other families at this stage would be futile.

The species in the two genera of Pseudocheiridae possess a diverse array of karyotypes and diploid number from $2n = 10$ to $2n = 22$ (Hayman 1977; Murray *et al.* 1980; McKay 1984). Only two have been G-banded, the Lemuroid Ringtail Possum, *Pseudocheirus (Hemibelideus) lemuroides*, and the Greater Glider, *Petauroides volans* (McQuade 1984). As with *Petaurus*, the rearrangements involved in deriving their complements from the ancestral type appear to be complex, making a search for possible synapomorphies with other families difficult.

f) Macropodidae (kangaroos, wallabies, wallaroos, pademelons and Quokka)

The species of Macropodidae present a diverse array of chromosome morphology and of diploid number from $2n = 10$ to $2n = 32$ (Hayman 1977). The complement of species possessing $2n = 14$ (some members of the genus *Dendrolagus* – tree-kangaroos) is clearly not the ancestral type (Hayman & Martin 1969). G-banding studies of a limited number of species of the family suggest that a diploid number of $2n = 22$ was probably ancestral for the family (Rofe 1979).

g) *Acrobates* / *Distoechurus* group *incertae sedis*

These genera appear to be monophyletic, but are inappropriately placed in the Burramyidae. The Feathertail Glider, *Acrobates pygmaeus*, has $2n = 14$, although G-banding shows that it differs from the ancestral $2n = 14$ by three rearrangements (Rofe 1979). The unbanded chromosomes of *Distoechurus pennatus* have been studied by Westerman, Sinclair & Woolley (1984). This species also has $2n = 14$, but differs from both *Cercartetus* (ancestral) and *Acrobates*.

h) Tarsipedidae

The sole representative of this family, the Honey Possum, *Tarsipes rostratus*, has a $2n = 24$ all acrocentric karyotype (Hayman & Sharp 1982). G-banding has not been done.

i) Notoryctidae (marsupial moles)

The representative of this group, the Marsupial Mole, *Notoryctes typhlops*, possesses a highly derived $2n = 20$, all biarmed, karyotype (Calaby *et al.* 1974). G-banding has not been done.

The foregoing analysis shows that the karyotypic data available so far contribute nothing to our understanding of interfamilial relationships of Australasian marsupials. Some families possess the ancestral state for extant Marsupialia (similarity due to symplesiomorphy), others possess apparently uniquely derived complements (autapomorphies). Most of the remainder either have not been G-banded or possess such complex rearrangements that at present, synapomorphic rearrangements are difficult to discern. Only a few of the living species of Australasian marsupials have been G-banded, but sufficient have been done across most of the families to suggest that even when such data become available, the information will not be useful at the family level.

Phylogeny of Parasites

Parasites frequently (but not always) co-evolve with their hosts, and as a consequence, the distribution between host taxa of related taxa of parasites can be used in studies of phylogenetic relationships. Both internal (nematodes and cestodes) and external (fleas and lice) parasites can be used in this way.

Two fossil fleas have been described from an Early Cretaceous site in Victoria (Riek 1970). One is similar to extant Australian species of the genus *Echidnophaga* occurring on marsupials and monotremes. The leg structure of the second species '... suggests that this insect lived on a sparsely haired (furred) animal' (Riek 1970).

Marsupials lack Anoplura (sucking lice). This group arose in the Jurassic or Cretaceous. Consequently, if marsupials arose in North America they should have acquired anoplurans. Conversely, the Stephanoceridae (helmet fleas) are restricted to Australia and the Neotropical Region where they are also found on rats. Again, if marsupials are of northern origin why are these fleas absent from northern faunas?

Traub (1980) concluded from his study of the systematics and evolution of mammalian fleas that there were metatherians in Australia in the lower Cretaceous. He pointed out that amblyceran lice of mammals are absent from North America, Europe, Asia and the Oriental Region, but are found in South America and Australia, implying separate, southern areas of origin of the marsupials away from the northern eutherians. The diversity of both monophyletic, marsupial-parasitising fleas and lice is greater in South America than in Australia and the Australian fauna, both hosts and parasites, is probably derived.

Trichostrongyloid nematodes of the subfamily Herpetostrongylinae are found in South America and Australia. The most primitive forms are found in the Dasyuridae and Didelphoidea with radiations of derived groups in the perameloids, phalangeroids and macropodoids in Australia and in rodents in South America. No time of origin can be fixed from the data. Durette-Duset & Chabaud (1981) showed it as Cretaceous, but the origin of the date is not given; it may be from the hosts (Beveridge personal communication).

The cestode subgenus *Linstowia* (*Paralinstowia*) is found in a bandicoot and in didelphoids. No date of origin is given. No other data are relevant (Beveridge personal communication).

In a similar fashion to the ectoparasite data, the endoparasite data could be interpreted to imply a southern origin of the marsupials.

REVIEW OF THE FAMILIES OF MARSUPIALS

Increasing diversity of the spectrum of character sets used in systematic analyses and quickening tempo of the rate at which new discoveries of fossils are being made have led to suggestions of a great variety of suprageneric classifications of marsupials. Archer (1984b) provided a thorough historical summary of classifications that had been proposed to that time and presented several of his own devising. Woodburne's (1984a) 'informal classification' took some other data and analyses into account. For the purposes of this review we have chosen to recognise the current state of flux by avoiding adoption of a specific suprafamilial classification. Hypotheses concerning interrelationships of the families are discussed, but not formally expressed.

In the preceding Section, various character sets used in analyses of systematic relationships were introduced. Before launching into this review, comments are appropriate on strengths and limitations of the fossil record documenting the histories of the various families.

Clearly, the protein and parasite data show that the Australian, Antarctic and South American continents formed a significant southern evolutionary theatre for the marsupials. The available fossil record of Australian marsupials extends back into the Oligocene. The presence of a monotreme, *Steropodon*, indicates that at least one group of mammals was present in Australia at a much earlier date (Early Cretaceous, Albian) (Archer *et al.* 1985). The record of South American marsupials apparently goes back into the Late Cretaceous, but documentation of the earliest faunas is limited (note Muizon, Marshall & Sigé 1984). Only recently have marsupials been found in Antarctica in beds of Late Eocene age (Woodburne & Zinsmeister 1982, 1984).

Two critical voids in the fossil record still plague students of marsupial evolution in the Southern Hemisphere. First, the oldest available records of some families are provided by species that are distinctly derived and give little data on the interrelationships of family lineages. The roots of the extensive Australian radiation are to be found in faunas older than Oligocene and, probably, the South American evolutionary radiation began in the Cretaceous.

Secondly, fossils found in Africa and peninsular India (Clemens 1986) demonstrate that primitive therian mammals were members of Jurassic Gondwanan faunas. Analyses of the cladistic interrelationships of therian mammals (for example, McKenna 1975, 1981; Miyamoto & Goodman 1986) suggest the American edentates are distantly related to all other eutherians. This evidence and discoveries of Late Cretaceous, South American mammals representing a group of primitive therians (?Dryolestidae, see Chapter 14) and an early branch of the eutherian radiation (Bonaparte 1986) provide ample warning that Mesozoic mammalian faunas of the Southern Hemisphere were not composed only of monotremes and marsupials with a few other groups added by immigration from the north, but might have had a much more complex composition.

Turning to the Northern Hemisphere, during the Late Cretaceous marsupials were relatively abundant members of the terrestrial fauna and underwent a modest evolutionary radiation in the western part of North America (Lillegraven, Kielan-Jaworowska & Clemens 1979a). At this time the continent was divided by a seaway extending from the Arctic Ocean to the Gulf of Mexico; next to nothing is known of the mammalian fauna of the eastern North American subcontinent. The North American Cainozoic fossil record documents the presence of marsupials from the beginning of the Paleocene until the apparent extinction of these lineages in the Miocene that was followed several million years later by reoccupation of the continent by didelphids dispersing from the south in the Pleistocene.

The earliest terrestrial faunas of Central America currently are known from only a few small collections of Miocene age. Only in the Pliocene and, particularly, the Pleistocene do we have relatively large samples of the faunas of this area. This very limited amount of data about the terrestrial fauna, exacerbated by the complex geological history of the area (see McKenna 1981, for a resumé), has given great degrees of freedom in the development of a wide variety of biogeographic hypotheses calling for dispersals or vicariance events, which might have played major roles in the evolution of the marsupials.

The lack of, or availability of, only limited samples of Late Cretaceous and Paleocene terrestrial faunas of Eurasia and Africa also prevents development of a basic outline of the early phases of marsupial evolution on these continents. The traditional hypothesis calls for dispersal of marsupials from North America to Europe in the latest Cretaceous or Paleocene. Their evolution in Europe is well documented in a series of faunas of middle Paleocene through Miocene age when the group became extinct in this area (Koenigswald 1970; Crochet 1977, 1980). During the early and middle Tertiary, seaways separated Europe from Africa and central Asia. Recent discoveries show that marsupials were able to disperse into both areas, but there is no indication of a significant evolutionary radiation in either continent (Africa: Mahboubi *et al.* 1983; Simons & Bown 1984; Asia: Gabunia, Shevyreva & Gabunia 1984; Russell 1985).

In summary, as will be apparent in the following review, relatively few families of marsupials are known only by their modern representatives. Although certainly not excluding the possibility of the discovery of new lineages, this suggests that the available fossil record probably provides a basic outline of evolutionary history of the families of marsupials from the Miocene to the Recent. In contrast, records from the Cretaceous and early Tertiary are few and do not provide comparable samples from the different continents of the time. This situation has denied us the possibility of adequately testing competing hypotheses of phylogenetic relationships or biogeographic histories of many families. As is becoming apparent, these limitations also have resulted in an underestimation of the complexity of patterns of mammalian evolution in the Southern Hemisphere.

At the moment, the fossil record of North American marsupials documents the oldest and most primitive marsupials, even when *Holoclemensia* from the Early Cretaceous, once thought to be a marsupial, is excluded (Clemens & Lillegraven 1986). In the light of the protein sequence data, this might well be an artifact of the available fossil record which has yet to provide more than a few tantalising clues of the Jurassic and Cretaceous terrestrial faunas of the Southern Hemisphere.

Most analyses of phylogenetic relationships show that the Marsupialia can be reasonably clearly divided into American and Australian groups, with the European and African species most closely linked to the American. Recent classifications reflect this by a high level of taxonomic division of the group; the Ameridelphia and Australidelphia of Szalay (1982a) or Hesperometatheria (American) and Eomarsupialia (Australian) of Archer's (1984b, p. 787) 'classification no. 9'. Going farther, a subgroup of families biogeographically limited to South America and Antarctica can be excised from the American group, leaving what has traditionally been referred to as the didelphoid marsupials. In the following review we begin by trying to summarise current, somewhat conflicting analyses of the didelphoids, provide a brief overview of the South American radiation and then consider the Australian marsupials.

The family Didelphidae originally was established to include the diverse suite of modern American opossums. Until recently, members were diagnosed on the possession of a variety of characters now thought to be primitive for the Marsupialia: polyprotodont incisors (5/4), retention of a little modified

tribosphenic dentition, an alisphenoid lappet making the sole or major contribution to an incompletely ossified bulla and a didactylous pes, for example.

As knowledge of the fossil record of American and European marsupials increased, in addition to inclusion of extinct forms apparently closely related to modern opossums, the Didelphidae became a dumping ground for many primitive American or European marsupials and extinct groups that were judged to be insufficiently diverse or not sufficiently derived to warrant establishment of new families for their reception. The tide is turning; the current trend is to limit the Didelphidae to an apparently monophyletic group including almost all the modern American opossums. *Dromiciops*, a form living at high latitudes in Chile and Argentina, is placed in a separate family, Microbiotheriidae (see below). Reig, Kirsch & Marshall (1985), considering a wide spectrum of characters, classified modern didelphids and closely related extinct species in two subfamilies, the didelphines and caluromyines (note Kirsch 1977a). To these are added the Tertiary South American sparassocyonines, predaceous marsupials with modifications of their cheek teeth resembling those found in the borhyaenids (see below), but features of their cranial morphology (presence of epitympanic sinuses, for example), set them apart. Reig *et al.* (1985) also included some Tertiary Holarctic species, the herpetotheriines.

The phylogenetic interrelationships of the marsupials now excluded from the Didelphidae are being debated and a widely accepted classification has yet to emerge. In his detailed studies of Tertiary European didelphids, Crochet (1977, 1980) suggested that *Peradectes* from the Paleocene and Eocene of North America and Europe be placed in a separate tribe within the Didelphinae. With it, he allied several other early Tertiary species and Cretaceous species of *Alphadon* and *Albertatherium* on the grounds that their dentitions exhibit the complex of characters thought to be primitive for the Marsupialia. Reig *et al.* (1985), for example, continued this pattern using the Peradectidae as a repository for the dentally most primitive marsupials. Szalay (1982a) employed a similar approach, but used a very broadly defined Pediomyidae for reception of these dentally primitive species.

The remaining taxa which have been removed from the Didelphidae are characterised by distinct modifications of their dentitions, which are essentially all that is known of most species. In two groups, low crowned, bunodont dentitions evolved. These modifications suggest a diet, probably including fruits or leaves, that required more crushing than shearing. This similarity has been the basis for suggestions of close phylogenetic relationships between the North American genus *Glasbius* and South American Tertiary and, possibly, Late Cretaceous caroloameghiniines (Pascual 1980a). An analysis of details of cusp morphology (Clemens in prep.) supports the hypothesis that the last common ancestor of the glasbiines and caroloameghiniines was a peradectid with a primitive tribosphenic dentition and bunodonty evolved independently in the two lineages.

Pediomyidae and Stagodontidae originally were based on dentally derived North American Late Cretaceous marsupials. Only a few cranial or postcranial elements of these species are known. Pediomyids are characterised by a borhyaenid-like reduction of the styler cusps and shelves of the upper molars but can be easily distinguished from this South American group by distinct enlargement of the protocones and talonid basins. They underwent an evolutionary radiation in western North America that produced species ranging in size from minute forms, certainly in the range of the smallest modern marsupials, to forms rivalling the size of the mid-sized dasyurids (Fox 1979). The largest species of North American Cretaceous marsupials are found in the Stagodontidae. Their dentition was modified with emphasis on enlargement of shearing surfaces on the posterior faces of the upper and anterior faces of the

lower molars. Premolars of the later stagodontids were greatly enlarged, bulbous teeth and must have produced a crushing-battering action as the jaws were snapped together (Fox & Naylor 1986).

The South American Radiation

One current interpretation (Reig *et al.* 1985) suggested that members of the Peradectidae were ancestral to the radiation of South American marsupials and, possibly, the Australian radiation as well. Didelphids, in the restricted sense discussed above, are represented in most Cainozoic South American local faunas from the Late Paleocene onwards. Only one living South American opossum, *Dromiciops*, is excluded from the Didelphidae. It and *Microbiotherium* (Late Oligocene - Early Miocene) share a plexus of dental modifications including great simplification of the molars with reduction of the stylar shelf and conules of the upper molars (Marshall 1982). The auditory bullae of *Dromiciops* are enlarged and fully ossified, resembling those of dasyurids. Articular facets of the tarsus of *Dromiciops* resemble those otherwise only known in Australian marsupials (Szalay 1982a, 1982b). These derived morphological characters, supported by the modern occurrence of *Dromiciops* in the *Nothofagus* forests of South America, have prompted speculation that the microbiotheres were an early offshoot of the radiation of the Australian marsupials.

Eutherian carnivores do not appear in the fossil record of South America until the late Tertiary; their ecological vicars are to be found, in part, in the Borhyaenoidea. The group, apparently derived from a peradectid ancestry, ranges from the Late Paleocene to the Pliocene. The Borhyaenidae, so-called 'dog-like' marsupials, include a wide variety of species, currently allocated to four subfamilies, that include both large and small carnivores and some species that might have been omnivorous. *Thylacosmilus*, usually placed in a separate family, shows remarkable convergences in many characters with the eutherian sabre-toothed cats (Turnbull 1978). As a group, the borhyaenoids share derived characters such as reduction of the maximum number of polyprotodont incisors to 4/3 and emphasis on dental shear by enlargement of the posteriolabial segment of the upper molars coupled with reduction of the protocone and talonid basin (see Marshall 1981a and references cited). The borhyaenoid pes is didactylous.

The third group of marsupials represented in the modern South American fauna is the Caenolestidae, which has a fossil record extending back into the Oligocene (Marshall 1980). The living genera, restricted to areas in the Andean mountains, are relict of the least-derived of three subfamilies that most likely had differentiated by the end of the Eocene. Dentally, the caenolestoids are distinguishable from other marsupials by modifications of the incisors that were reduced in number, ranging from four to two. A pair of lower incisors is enlarged into elongate dagger-like teeth. Ride (1962) concluded that the enlarged incisors are the I_3 s not the I_1 s or I_2 s that are enlarged in Australian diprotodonts. He dubbed the modification of caenolestoid incisors, pseudodiprotodonty. In some species the last premolar or first molar is a large, blade-like tooth. The molars decrease in size posteriorly. The pes is didactylous.

Serological analyses by Kirsch (1977a) demonstrated that the modern caenolestids were equally distant from the Australian and other American marsupials. In caenolestids, however, the sperm develop in pairs in the epididymus like in modern didelphids, an autapomorphic pattern of ontogeny that has not been found in any Australian marsupials (Biggers & DeLamater

1965). This observation and other data, for example, the different patterns of incisor enlargement, indicate that other similarities of caenolestids and some Australian marsupials are probably the products of parallel evolution.

The phylogenetic interrelationships of caenolestids and three extinct South American families, Polydolopidae, Bonapartheriidae, and Prepidolopidae are being debated (see Reig *et al.* 1985, footnote 1). The latter two families are based on fossils first described at the beginning of this decade and add evidence of the breadth of the evolutionary radiation of South American marsupials in the early Cainozoic. Of the three families, the polydolopids are known from a much larger sample of fossils. These small forms are characterised by enlargement and procumbent orientation of a reduced number of lower incisors and larger canines. The posterior premolars have a sectorial, blade-like morphology. Molar cusps are bunodont and the enamel surfaces of the basins are crenulated in some species. Polydolopids are known from Late Paleocene through Oligocene fossil localities in South America and recently were discovered in Late Eocene strata on Seymour Island, Antarctica (Woodburne & Zinsmeister 1982, 1984).

Though at first regarded as polydolopid on the basis of similarities in dental morphology, discovery of a skull of *Bonapartherium* reveals a number of characters suggesting didelphoid affinities of this early Eocene form (Pascual 1980a, 1981). The posterior premolars of *Bonapartherium* are large with pointed, blade-like crests; on the upper premolars the blade is buttressed lingually by lower cusps. PM₂s are smaller than the last premolars, but mirror their specialised morphology. The upper molars, which decrease in size posteriorly, are quadritubercular. The lowers are similarly modified.

The Prepidolopidae includes two species, also of Early Eocene age. Reduction in size and number of teeth in the anterior lower dentition was regarded by Pascual (1980b) as documenting the transition from polyprotodonty to diprotodonty. The last premolars are enlarged with high, piercing crowns. The upper molars have been modified from the basic tribosphenic pattern by great reduction of the styler shelf, expansion of the paracone and metacone relative to the protocone and conules. Talonids and trigonids of the lower molars are of essentially equal height but otherwise retain a largely tribosphenic morphology.

The final group of South American marsupials consists of two families, Argyrolagidae and Groeberiidae, both characterised by extreme modifications in the dentition and, in the case of the argyrolagids, the skeleton. [A description of a third family based on a form with similar rodent-like specialisations of the jaw and dentition soon will be published by R. Pascual & A.A. Carlini (Pascual personal communication)] In a review of the South American mammalian fauna, McKenna (1981) treated the Argyrolagidae, Groeberiidae and Necrolestidae (see below) as 'possible marsupials' noting that none exhibited a suite of apomorphies clearly definitive of membership in the Marsupialia. This commentary, bolstered by the subsequent discovery of some remarkably different therian mammals in the Late Cretaceous of Argentina (Bonaparte 1986), provokes consideration of the possibility that one or more of these groups is neither eutherian or metatherian, but represents another therian lineage of Gondwanan origin.

The argyrolagids, which range from the Miocene through the Pleistocene, were bipedal, ricochet animals that in many respects resembled the kangaroo-rats of the genus *Dipodomys* (Simpson 1970a, 1970b). Their dentitions are characterised by reduction in number of incisors and presence of evergrowing (hypselodont), high crowned molars. The well-ossified bulla is greatly inflated.

In contrast to the excellent documentation of the skeleton of argyrolagids, the monotypic family Groeberiidae is based on two fragmentary specimens of Late Eocene age. These show that the snout was short, the jaw and zygomatic arches were deep, and the cheek teeth, separated from the large evergrowing incisors by a diastema, were small, rooted and of subequal size (Simpson 1970c).

The presence of five upper and four lower incisors, now interpreted to be a primitive therian character, was one of the characters used to justify the reference of the Miocene fossorial mammal, *Necrolestes*, to the Marsupialia (Patterson 1958). The remainder of the dentition is greatly modified. The first cheek tooth behind the canine is double rooted and shows some minor differences from the five other cheek teeth that are unilaterally hypsodont (one side of the crown is much higher than the other), the crowns of the teeth have small, blunt tips, and each tooth is supported by a single root. In structure of the postcranial skeleton *Necrolestes* shows many modifications associated with burrowing that also are found in the eutherian insectivore *Chrysochloris* and the Australian fossorial marsupial, *Notoryctes*.

The Australian Radiation

Depending upon the classification adopted, the marsupial fauna of Australia consists of approximately 19 families, six of which are known only from the fossil record. Further research on both the modern and prehistoric faunas is likely to increase this number over the next few years. The study of phylogenetic relationships within the Australian marsupial fauna is limited at present by the absence of any information from the fossil record before the Late Oligocene and little information before the Middle Miocene (Archer 1984b). In mid-Miocene assemblages, extant families are clearly recognisable along with others that since have become extinct. Though some modern subfamilies and generic groupings are present in the Middle Miocene, many other branches of earlier radiations also are represented (Archer 1984b). Morphological, physiological, cytological and biochemical information on modern species can be added to data from the fossil record to analyse relationships.

The marsupial fauna of Australia as presently known can be construed as consisting of three major and one minor lineages, the Dasyuroidea, Perameloidea, Diprotodonta and Notoryctidae, respectively. The relationships between these groups are uncertain. Together they are usually assumed to be a monophyletic group and that each group is itself monophyletic. The Dasyuroidea and Perameloidea maintain in common many primitive characteristics, notably polyprotodonty, and as a consequence are often considered more closely related to each other than they are to other marsupial groups. Such a relationship is supported by serological data (Fig. 19.5).

The presence of syndactyly in both groups implies, however, that perameloids are more closely related to the Diprotodonta (Archer 1984b). If this is not true, then syndactyly must have been derived twice and constitutes a convergent condition (Kirsch 1977a; Szalay 1982a, 1982b).

We begin this review with consideration of the most distinctive of these groups, a single family, the Notoryctidae, the marsupial moles (see Chapter 23), which has no fossil record. The morphological specialisations found in these species are so extreme that relationships to other groups cannot be clearly distinguished. Immunological studies show the Notoryctidae to be distinct from all other lineages. The structure of the ear shows some similarities to that characteristic of the Diprotodonta and the morphology of the pes indicates a syndactylous heritage. The weight of available evidence, which is far from compelling, suggests diprotodontan affinities (Calaby *et al.* 1974).

The first of the major groups is the Dasyuroidea which includes the Dasyuridae, Myrmecobiidae and Thylacinidae. These carnivorous or insectivorous marsupials are known from fossil remains from the Middle Miocene to the Recent. The group is characterised by the retention of many primitive characteristics, including polyprotodonty and didactyly. The Dasyuroidea can be characterised by the reduction of the upper and lower incisor numbers to four and three respectively, the presence of a large neocortex, the loss of the calcaneal vibrissae and a number of adaptations of the tarsal morphology for terrestrial existence (Archer 1984b). The Dasyuridae and the Myrmecobiidae have in common the replacement in the basicranium of the foramen ovale by a foramen pseudovale (for passage of the trigeminal nerve).

The single modern species of the Myrmecobiidae (the Numbat, see Chapter 22) has extreme specialisations for its life pattern which includes feeding on termites. The palate is extended posteriorly. The cheek teeth are vestigial and either the deciduous premolar is retained or six molars are present. There is no fossil record of the family earlier than the Pleistocene.

The Dasyuridae (see Chapter 21) is found in Australia and New Guinea in all habitats from rainforest to desert. The animals range in size from weighing 4 g, shrew-like animals to the native cats and the Tasmanian Devil, which may weigh 8 kg. The family is known from the fossil record from the Middle Miocene to the Recent. The modern New Guinea genera *Murexia* and *Neophascogale* resemble Middle Miocene forms from central Australia, which was cooler and wetter at that time.

The last family in this group, the Thylacinidae, includes only one modern species, the Thylacine (see Chapter 20). This species was widespread on the mainland 4000 years ago, though restricted to Tasmania at the time of European settlement. In the Thylacinidae, the styler cusps and metaconids are reduced, the paracone and metacone are approximated while the postmetacrista and paracristid are enlarged. Epipubic calcification is lost. The family is known from fossils found in deposits from the Late Miocene to the Recent in Australia and New Guinea. Similarities in dental morphology with South American borhyaenids are presumably due to convergence in the life patterns of the two groups. Immunological data, basicranial anatomy and tarsal morphology support the view that the thylacines are part of the Australian radiation rather than independently derived from South American stock. Their cranial morphology is primitive for the Australian radiation having, as a consequence, much in common with the South American didelphids and borhyaenids.

The second major lineage of Australian marsupials comprises the Perameloidea. The bandicoots and bilbies are placed, respectively, in two families, the Peramelidae and the Thylacomyidae. The perameloids, with a fossil record beginning in the Middle Miocene, are insectivorous, ground-dwelling animals; all are syndactylous and polyprotodont. Metatarsal IV is enlarged and supported by the ectocuneiform (Fig. 19.4). The tarsals are modified to fit the terrestrial life pattern of the group, there is a rectus femoris scar on the posterior face of the femur, the calcaneal and medial antebrachial vibrissae are lost and the patella is ossified (Archer 1984b). The perameloids form a single distinguishable immunological group (Fig. 19.5).

The separation of perameloids into two families is based on several distinctive characteristics found in the Thylacomyidae, notably the unusual XY_1Y_2 sex chromosome system, the enlarged middle ear with tympanic sinuses and the linguallally displaced metacone, which functionally serves as an analog of the eutherian hypocone (Archer & Kirsch 1977). The peramelids carry the primitive forms of these characters and are, as a consequence, a 'default' group. Immunological data (Fig. 19.5a) show three

equally divergent lineages occur in the Perameloidea, one being the Thylacomyidae, and that the overall level of divergence is less than that between most other families studied.

The Peramelidae (see Chapter 24) is found in habitats ranging from desert to rain forest in Australia, New Guinea and other islands including Ceram. The Thylacomyidae (see Chapter 25) is found only in the drier regions of mainland Australia.

The third major group of Australian marsupials is the Diprotodonta. It contains all the remaining Australian marsupials and can be characterised by the presence of diprotodonty, syndactyly, a superficial thymus gland and a *fasciculus aberrans* (Archer 1984b). The latter is a bundle of nerve fibres connecting the two hemispheres of the brain and is found only in diprotodonts. The group ranges throughout Australia, New Guinea and surrounding islands and, as recognised here, is made up of thirteen families in five superfamilies.

The first diprotodontan superfamily, the Vombatoidea, includes two extant families, the Phascolarctidae and Vombatidae. Four extinct families, the Wynyardidae, Palorchestidae, Diprotodontidae and Thylacoleonidae, were added to this grouping by Woodburne (1984a). He supported this allocation by noting that, where known in these families, the squamosal contributes to formation of the ossified auditory bulla; the postcranial skeleton shows 'vombatoid' characteristics; and the crowns of cheek teeth primitively have complex, biselenodont cusps with or without a cusp in the position of a hypocone.

Close relationship of the Vombatidae and Phascolarctidae also is demonstrated by the following characters of living members of these families. The paraflocculus in the temporal region of the brain is reduced in prominence, the brain is ovoid in shape and gyrencephalic (Fig. 19.6). In extant species, the head of the spermatozoan has a prominent hook, a cardiogastric patch is found on the stomach wall and the pancreas is compact rather than diffuse (Archer 1984b).

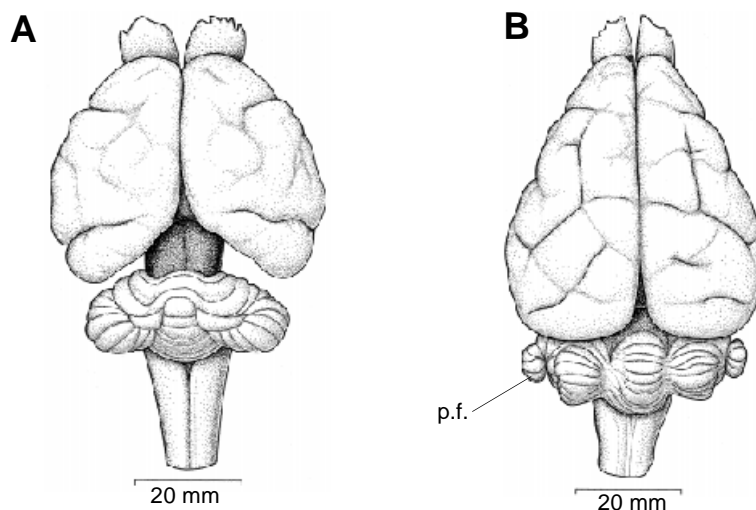


Figure 19.6 Dorsal view of the brains of: **A**, *Vombatus* and **B**, *Macropus* showing the markedly larger paraflocculus present in all diprotodonts except vombatoid species; p.f. = paraflocculus. (© ABRS) [G. Milledge]

The Phascolarctidae (see Chapter 31) is known from fossils from the Middle Miocene to the Recent and includes one extant species, the Koala. In phascolarctids the number of incisors tends to be reduced. The molars are low crowned with selenodont cusps and their enamel often is crenulated. The alisphenoid hypotympanic sinus is markedly enlarged relative to the condition in other diprotodonts. The Middle Miocene *Litokoala* has molars only slightly modified from the presumably primitive condition found, for example, in some peramelids. The Koala is a highly specialised browser, but the family maintains the primitive form of many of the characters found in diprotodonts.

The Vombatidae, or wombats (see Chapter 32), has a fossil record extending back to the Miocene. In the dentition of the modern wombat the incisors have been reduced to one pair in the upper and lower dentitions. The cheek teeth are high crowned, bilobed in occlusal outline, and evergrowing (hypsodont), apparently an adaptation to their coarse diet. Evolution of hypsodont teeth might have taken place during the late Tertiary as the climate of Australia was modified. The cheek teeth of *Rhizophascolonus* from the Middle Miocene are high crowned but were not evergrowing. Pleistocene species of wombats reached sizes twice that of the modern forms.

Tedford *et al.* (1977) described teeth of Miocene age from South Australia that have very complex crowns. The upper molars, for example, have well-developed styler cusps that, in peramelid fashion, are linked to the paracone and metacone by distinct crests. The two lingual cusps of these molars are weakly selenodont. These teeth are found in association with postcranial skeletal elements that share many, apparently derived, characters with those of wombats. These fossils both testify to the diversity of the Miocene marsupial fauna and indicate that through such a common ancestry vombatids might be closely related to groups lacking the extreme modification of the vombatid dentition.

The phylogenetic position of the Wynyardidae is uncertain (Archer 1984b). The family is based on Early Miocene fossils found in Tasmania. Studies of endocasts of the brain of the type specimen of *Wynyardia* show characters suggesting phalangeroid affinities; features of the auditory region are quite primitive, didelphid-like; but the dentition, known only from the alveoli of the teeth, is diprotodont. Some of the material from South Australia described by Tedford *et al.* (1977) was tentatively referred to this family. The upper molars of these referred specimens resemble those of the primitive 'vombatoid' type; the lower molars are distinctly lophodont.

The Palorchestidae, which in some classifications is linked with the Diprotodontidae in a separate superfamily, is based on several genera of medium to large, extinct herbivores. These are known from fossils in Miocene to Pleistocene local faunas. Palorchestids were originally thought to be related to the kangaroos, because of similarity in morphology of their molars, and in older texts are shown in reconstructions as such. The discovery of postcranial material of the genus *Palorchestes* demonstrated, however, that they were quadrupedal with powerful forelimbs and large laterally compressed claws on the fore and hind limbs. The skull of *Palorchestes* is characterised by retracted nasal bones, a narrow elongated rostrum and enlarged infraorbital foramina capable of carrying large bundles of nerves and blood vessels probably supplying a trunk. The animals were the size of a bull (Fig. 19.7c). An older genus, *Ngapakaldia*, does not have these cranial specialisations (Archer 1984b).

The Diprotodontidae is known from fossils of Miocene through Quaternary age and contains two subfamilies, the Diprotodontinae and the Zygomaturinae. The sheep- to cow-sized adult animals in this family may have been browsers with the males larger than the females. The brain case of most diprotodontids is filled

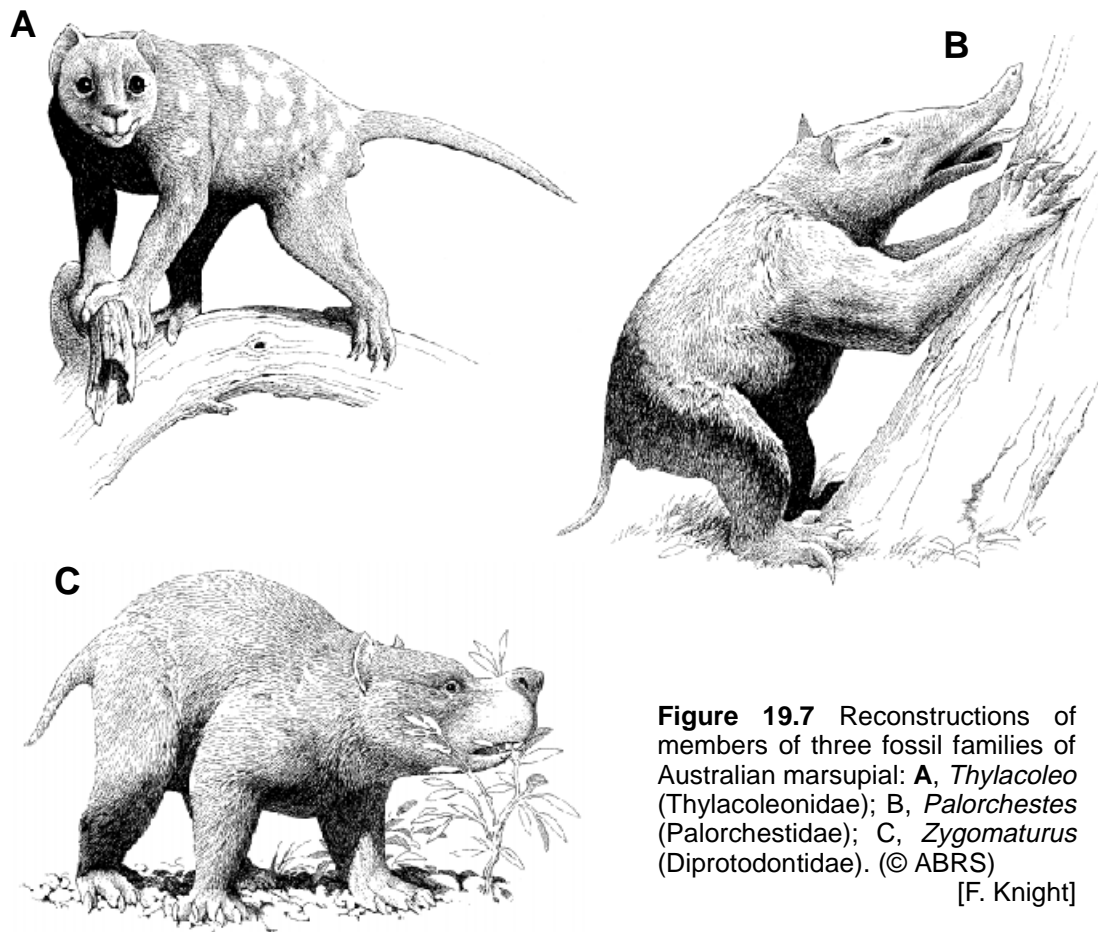


Figure 19.7 Reconstructions of members of three fossil families of Australian marsupial: **A**, *Thylacoleo* (Thylacoleonidae); **B**, *Palorchestes* (Palorchestidae); **C**, *Zygomaturus* (Diprotodontidae). (© ABRS) [F. Knight]

with sinuses, leaving only a small (hand-sized) brain to manage a very large animal. In Middle Miocene deposits, when present, the cow-sized *Neohelos* is usually the commonest large mammal present (Archer 1984b).

Diprotodontids had an extensive biogeographic range. Fossils of zygomaturines, for example, have been found in New Guinea, New Caledonia (Guerin *et al.* 1981), as well as throughout Australia. Probably the last surviving species, *Zygomaturus trilobus* (Fig. 19.7b), was found in forested areas of south-western and south-eastern mainland Australia and Tasmania. It probably overlapped with the Aboriginal settlement of Australia. Amongst the diprotodontines, the most famous is *Diprotodon optatum*. This 3 m long and 2 m high browser was found in central Australia during the Pleistocene.

One group of large carnivores of Australia is placed in the Thylacoleonidae. It is known from fossils from the Middle Miocene to the Late Pleistocene. Dental evolution in this family has been towards increasing specialisation with convergence on some patterns found in felids. PM_3 was modified into a long cutting blade with a concomitant reduction in the role and size of the molars (Fig. 19.8).

The absence of large, lion-like canines (though the incisors are carniform) provoked doubts that these animals could have been carnivorous. Recently, the demonstrated use of diprotodont-like lower incisors as stabbing weapons by the South American caenolestids, plus the discovery of fossil kangaroo bones apparently bearing thylacoleonid tooth marks support the suggested carnivorous lifestyle of these animals (Wells, Horton & Rogers 1982). There are two genera including eight species presently known. These varied in size between bobcats and lions. There is some evidence of sexual dimorphism in size within some

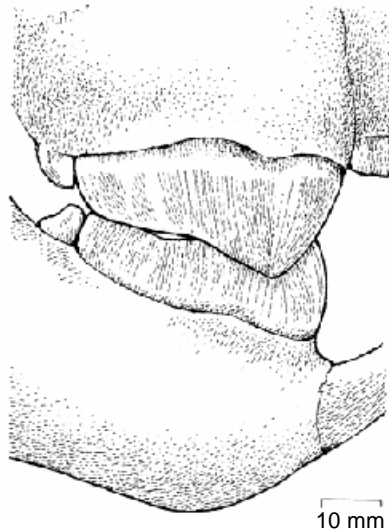


Figure 19.8 Carnassial development of the molar in *Thylacoleo*. (© ABRS) [F. Knight]

species. The teeth of thylacoleonids, as well as their heavily clawed forepaws and powerful forearms, would have made them dangerous opponents (Fig. 19.7a).

Study of the hind feet of fossil thylacoleonids shows that they were similar in form to those of *Trichosurus vulpecula* and thylacoleonids probably were at least partly arboreal. Perhaps, like leopards, they hunted both on the ground and in trees. The largest and last surviving genus, *Thylacoleo*, may well have overlapped with Aboriginal settlement.

The phylogenetic relationships of this family were long believed to lie with some group of possums. Some recent work, however, suggests that the Vombatoidae might be more likely relatives. The data on which these suggestions are based are far from compelling; probably the best summary is to admit that the relationships of the thylacoleonids to other diprotodontans are unknown.

The second superfamily of the Diprotodonta is the Macropodoidea which is often considered to contain two families: the Macropodidae and the Potoroidae. Both are represented in the modern fauna and known from fossils as old as Middle Miocene. The superfamily can be defined by the presence of a masseteric canal, an enlarged masseteric foramen, the loss of PM_1 , enlarged and finely ridged PM_2 , sectorial PM_3 , the presence of a rectus femoris scar on the posterior face of the femur, loss of the medial antebrachial, calcaneal vibrissae and the close genetic relationships of the two families detected using serology and protein electrophoresis (Archer 1984b).

The Potoroidae (see Chapter 30) contains four subfamilies, two known only from the fossil record, which extends back into the Middle Miocene. The family can be defined by extension of the masseteric canal anteriorly to a position beneath PM_3 in some species, elongated and finely serrated PM_3 , minimal contact between the squamosal and frontal bones and presence of a proximo-ventral process on the fifth metatarsal (Archer 1984b). Amongst the rat-kangaroos, the single extant species of *Hypsiprymnodon* is, in many ways, the most primitive. It does not hop and is found only in rainforest, the original habitat of the family. A second subfamily, the Potoroinae, includes all the remaining extant species.

The Macropodidae (see Chapter 29), which includes, for example, the kangaroos, wallabies, tree kangaroos and others, is subdivided into three subfamilies, one known only from the fossil record. The family is found in all environments from desert to rainforest in Australia and New Guinea and is found in fossil assemblages from Middle Miocene through the Quaternary.

Characters defining the family include the loss of the first toe on the hind foot, reduction in length of the masseteric canal, presence of lophodont molars that increase in size from M_1 to M_5 (Archer 1984b) and genetic relationships of the species detected using protein electrophoresis (Richardson & McDermid 1978) and serology (Fig. 19.5).

The third superfamily of the Diprotodonta is the Phalangerioidea. It contains all of the extant possums as well as many fossil groups. These can be grouped into five families, one of which is extinct. Interpretations of relationships within and between the families in this group are in a state of flux at present, and there must be some doubt as to the validity of this superfamily as a phylogenetic entity (for example, Smith & Hume 1984).

Three families, the Phalangeridae and Burramyidae, which have living members, and the extinct Ektopodontidae can be linked by such shared characters as presence of bunoselenodont molars in primitive forms, the buccal position of the paracone and metacone plus serological affinities (Archer 1984b).

The Phalangeridae (see Chapter 26), which includes the common Brush-tail Possum and cuscuses, is known from fossils of Miocene through Pleistocene age; it constitutes one of the most widespread families in the Australian marsupial radiation. They occur throughout Australia, New Guinea and the surrounding islands, ranging as far east as the Solomon Islands. Though they are most common in rainforest, two genera, *Trichosurus* and *Wyulda* have invaded the drier regions of Australia.

The molars of phalangerids have low crowns, are rather lophodont and the enamel is slightly crenulated. In contrast to other groups with bunolophodont molars, the primitive tribosphenic morphology of the lower molars is reflected in an angulated cristid obliqua.

The Burramyidae (see Chapter 27) contains a number of very small possum species, including the pygmy possums, *Cercartetus*, found in Australia and New Guinea, and the Mountain Pygmy-possum *Burramys parvus*, which lives in the Australian Alps. The family can be diagnosed by the presence of a well-developed, posterio mesial expansion of the tympanic wing of the alisphenoid, reduction of PM_1 and PM_2 and the bicuspid crown of PM_3 . The group is known from fossils as old as Middle Miocene.

Two other genera, *Acrobates* and *Distoechurus*, are still formally treated as part of this family, though they clearly form a distinct group. They are found in Australia and New Guinea and are known from fossil material from Late Miocene and younger faunas. These genera can be distinguished by the development of a periotic hypotympanic sinus, presence of a feather-like tail, loss of M_5 , and serological characteristics (Archer 1984b). Both genera show serological affinities with the Petauridae and Tarsipedidae (Fig. 19.5).

The Ektopodontidae is presently known from Miocene and Pliocene deposits. The genera are represented by only isolated teeth and fragmentary mandibles and maxillae. Cheek teeth of ektopodontids are bunolophodont, but the lophs are remarkably modified by subdivision into a series of almost plate-like cusps linked by reticulate patterns of crests in some species.

The available fossils indicate the animals were the size of large possums with large forward pointing eyes, perhaps implying a nocturnal, arboreal existence. The procumbent incisors and grinding molars could fit an animal eating nuts, leaves, fruits or seeds. Alternatively, the similarity of the teeth and skull shape to that of otters might imply an aquatic lifestyle (Pledge 1982). The ektopodontids disappeared from the fossil record at about the time the rodents first appear. Though smaller, the rodents have similar teeth to the ektopodontids and might have displaced them (Archer 1984b).

The ektopodontids have been allied with the Phalangeridae as the result of the discovery of a Miocene form, *Chunia*, which has complex molar crown patterns, but retains the angulated cristid obliqua (Woodburne & Clemens 1986).

The Petauridae (possums and gliders; see Chapter 28) is known from a large number of fossils ranging in age from the Middle Miocene to the Recent. It includes many species of possums living in a wide range of environments in Australia, New Guinea and surrounding islands. They reach their greatest diversity in rainforests. Two lineages are apparent in the serological data for this group (but see Kirsch 1977a) and these may be given familial rank as the Petauridae (*Dactylopsila*, *Gymnobelideus* and *Petaurus*) and Pseudocheiridae (*Pseudokoala*, *Pseudocheirus*, *Hemibelideus*, *Petauroides*, *Pseudocheirops* and *Petropseudes*). The petaurines have simplified, bunodont cheek teeth unlike those of the pseudocheirines; the much more complex teeth of the latter resemble those of *Phascolarctos*.

The Tarsipedidae (see Chapter 33) contains only a single species, the Honey Possum, *Tarsipes rostratus*. Extreme morphological specialisation and the lack of fossil data make it difficult to determine the relationships of this species. Serological studies place it in the same group as the Petauridae (Fig. 19.5). Characters of its chromosomes and reproductive biology show similarities to the phalangeroids in general and the macropodids in particular (Hayman & Sharp 1982). It occurs only in south-western Australia, where it feeds on a diet of nectar and honey.

BIOGEOGRAPHY

An account of the Mesozoic evolution of the 'mammal-like reptiles' and mammals has been presented elsewhere (Chapter 14), but a few points warrant repetition. The oldest records of primitive therian mammals have been found in rocks of Late Triassic age, a time when the supercontinents of Gondwana and Laurasia were only beginning to separate (Lillegraven, Kraus & Brown 1979b). The level of terrestrial faunal similarity of these northern and southern supercontinents was high. Primitive therian mammals have been found in Late Triassic or Early Jurassic deposits in what are now Europe and peninsular India, fragments of Laurasia and Gondwana respectively. Clearly, primitive therians and representatives of the various non-therian lineages might have been members of the Jurassic Australian, South American, Antarctic and African faunas. A therian has been found in the Late Jurassic deposits of Africa (Clemens *et al.* 1979).

The evolution of the tribosphenic dentition, a major turning point in therian evolution, appears to have occurred in the Early Cretaceous, if not earlier (Air *et al.* 1971; Clemens & Lillegraven 1986). This derived type of dentition is shared by marsupials and eutherians and several lineages of Cretaceous therians that cannot be certainly referred to the Marsupialia or Eutheria, the so-called 'tribotheres'. The origin of tribosphenic therian lineages appears to be broadly contemporaneous with the major fragmentation of Gondwana into the modern continental units. There is a reasonable possibility that any mammalian lineage that differentiated in the Late Jurassic or Early Cretaceous might have had a broad distribution across many of the southern continents.

No longer can hypotheses concerning the origin of the Australian marsupial fauna begin with the assumption that the continent was 'mammal-free' in the Jurassic and that its mammalian fauna evolved from immigrants from other areas. The possibility that Jurassic and Cretaceous mammalian faunas of Australia were just as diverse as those of Eurasia and North America, for example, must be considered (Clemens 1986).

Finally, the Late Cretaceous fossil record is beginning to provide a dim perception of the diversification of mammalian faunas that had occurred prior to the extinction of the dinosaurs. The faunas of western North America and Mongolia were clearly differentiated; for example, marsupials were part of the former, but absent from the latter (Clemens *et al.* 1979). Little or nothing is known of the Late Cretaceous mammalian faunas of Europe, Africa or Antarctica.

In contrast, recent discoveries in South America document what appears to be major regional differentiation. Mammalian faunas thought to be of Late Cretaceous age have been found in Peru (Sigé 1971, 1972) and Bolivia (Marshall *et al.* 1985). The members of these faunas are all tribosphenic therians. Most, possibly all, are probably marsupials. In contrast, the composition of a Patagonian mammalian fauna of approximately contemporaneous age is distinctly different (Bonaparte 1986). This fauna includes a possible triconodont, a non-therian order, and what appears to be a dryolestid, a primitive, pretribosphenic therian group. Also present is *Gonwanatherium*, a mammal with highly specialised and hypselodont cheek teeth, which might be related to the edentates (a group which formed a significant part of South American Cainozoic faunas). So far, there is no evidence of the presence of marsupials, eutherians or other groups of therians with primitive tribosphenic dentitions.

The samples of these South American Late Cretaceous faunas are small and the negative evidence of absence of groups from available collections must be treated with caution. What data are available suggest a major regional differentiation of the South American Late Cretaceous fauna into distinct northern and southern components. If the newly discovered fauna from Patagonia proves to lack tribosphenic therians, in particular marsupials, it has major significance in evaluating the various hypotheses concerning early phases of marsupial evolution. Is this evidence demonstrating that dispersal of marsupials between northern South America and Australia did not take place until after the end of the Cretaceous? The possibilities of dispersal of terrestrial vertebrates between Australia, Antarctica and South America at this time are good (see below). Is the Patagonian Late Cretaceous providing a sample of the diversity of Australian Cretaceous terrestrial faunas?

In summary, both the available palaeontological and geological evidence strongly suggest that any group of mammals that differentiated in the Triassic or Jurassic might have achieved a broad geographic distribution and have been a member of the Australian fauna. The assumption that Australia was 'mammal-free' until the monotremes and marsupials immigrated should be abandoned. Documentation of additional regional differentiation of mammalian faunas in the Late Cretaceous is adding greater complexity to the biogeographic analyses.

Against this background of ignorance and uncertainty, no definitive evaluation of the competing hypotheses concerning the time and place of origin of the marsupials can be presented. Almost every continent on which marsupials have existed has been nominated as an area of origin of the group. At the moment Asia stands as the only clear exception, but then the occurrence of marsupials there in the Oligocene was only discovered a few years ago. Europe, though not considered an area of origin, has figured in speculations about early dispersal of marsupials. The following comments are ordered geographically with no implication of particular support for one or the other.

Because the Cretaceous fossil record of North America documented the oldest known marsupials, the oldest known evolutionary radiation of the group, representatives of the dentally most primitive species and a suitable ancestral stock, it has been cited as a possible area of origin of the Marsupialia (Clemens 1979). All these points still remain true. In the absence of older records of more

primitive forms in other areas, this hypothesis remains unfalsified. Particularly in light of data from the gradually growing record of Cretaceous marsupials in South America and recent studies both of the geological evolution of the continents and biogeographic patterns of distribution of other groups of organisms, however, other hypotheses now appear to have equal, if not greater, attraction (Woodburne 1984a).

Currently, hypotheses suggesting origin and early radiation of marsupials in the southern continents, particularly Australia, Antarctica and South America are favoured by many workers. This possibility is supported by analyses of patterns of distribution of other vertebrates and plants (Patterson 1981).

Studies of the geological history of the three continents indicate that they were closely approximated in the Cretaceous and routes for the dispersal of terrestrial organisms probably were available during the Late Cretaceous, if not earlier. The rifting of Australia from Antarctica probably began in the Jurassic and appears to have been completed with a deep oceanic gulf separating the two by the end of the Eocene. Separation of South America from Antarctica might have occurred later in the Oligocene (Woodburne & Zinsmeister 1982, 1984; Woodburne 1984a).

Geological data on the timing and extent of fragmentation of continents, or waxing and waning of epicontinental seas, certainly provide a broad framework for biogeographic analyses, but lack the degree of resolution necessary to address many specific problems (Patterson 1981; Coney 1982). In this case these data, coupled with evidence of the beginning of a marked trend in cooling of the global climate in the Oligocene, suggest that by the Oligocene dispersal of mammals between Australia and South America via Antarctica had ceased.

When the oldest known fossils indicated that the South American fauna consisted of three major groups, the marsupials, eutherian condylarths and edentates and that the Australian consisted of two, the marsupials and monotremes, biogeographic hypotheses focused on dispersal of marsupials between these areas. Monotremes could be treated as a group of great antiquity (Late Triassic or Jurassic origin) in Australia; the edentates and condylarths were assumed to be derived from immigrants from the Northern Hemisphere. The absence of evidence indicating interchange of these three groups could be attributed to ecological filters or chance.

Although certainly not falsifying any of these hypotheses, the evidence provided by the newly discovered Late Cretaceous Patagonian fauna adds to the complexity of the problem. To add an admittedly extreme working hypothesis to the many others available, these new data might indicate that the Cretaceous faunas of Australia, Antarctica and southern South America included representatives of at least three ancient mammalian lineages: the triconodonts and dryolestids; the monotremes; and eutherian edentates. The area of origin of marsupials was in either northern South America or North America and dispersal of marsupials to Australia occurred after the end of the Cretaceous.

Before moving on to the Cainozoic, one other recently mooted hypothesis should be mentioned. Discovery of Eocene records of what appear to be primitive marsupials in Africa has been cited in support of the view that the area of origin of marsupials included both South America and Africa. Going farther, this information is taken as indicating that marsupials had differentiated prior to the separation of these continents during the middle of the Cretaceous (see Mahboubi *et al.* 1986, and references cited). The separation of the marsupial and eutherian lineages and the separation of the Australian and American marsupial lineages before the middle of the Cretaceous is also supported by the protein sequence data.

By the end of the Late Cretaceous, marsupials are known to have been members of the North and South American faunas. The oldest Paleocene faunas of Europe also include marsupials, but the effective lack of earliest Paleocene or Late Cretaceous faunas prevents determination of their time of origin on this continent. The Australian fossil record begins in the Miocene (or Late Oligocene, depending on the correlations accepted).

The Australian marsupial fauna, probably derived from a small insectivorous, arboreal ancestor, has evolved to fill many of the major ecological niches available to mammals. Rodents, bats and aquatic mammals are present in Australia; no marsupial equivalents to these are known, though ektopodontids might have been the ecological equivalents of some of the rodents. The Australian marsupial radiation includes marsupial moles, marsupial lions, marsupial gliding squirrels, marsupial wolves and marsupial herbivores of many kinds and sizes. The earliest presently known extensive marsupial fossil assemblages are from the Miocene and by that time the basic part of the latest radiation had occurred, with marsupial families specialised for each major niche present.

The Miocene climate in southern and central Australia was cool, wet and temperate. The vegetation cover consisted of closed forest (rainforest) and open forest (sclerophyll forest) (see Chapter 1). The fossil assemblages from this period reflect the faunas expected in such a situation, consisting of arboreal and terrestrial browsers and their predators.

This stable environment, which had persisted from the early Tertiary to this time, now changed due to several factors. As Australia moved away from Antarctica into lower latitudes, the northern edge of the continent came in contact with the Asian block and the New Guinea highlands started to rise. The Great Dividing Range in eastern Australia was also uplifted probably at this time. These events created a rain shadow for rains from the north-east which was accentuated by the northerly movement of Australia into drier latitudes, reducing rain from the west. Towards the end of the Miocene, sea temperatures dropped sharply, also leading to reduced precipitation (see Chapter 1).

This gradual reduction in precipitation led to changes in the vegetation. The rainforests were replaced by open forest and in the inland by woodland and, ultimately, grassland. In central Australia these changes are reflected in changes in fossil assemblages with arboreal and terrestrial browsers giving way to the newly evolved terrestrial grazers. While environmental conditions fluctuated during the Pleistocene, the theme of gradually increasing aridity continued until it reached its peak about 17 000 years ago. At about this time the Australian megafauna disappeared (Archer 1984c).

While these events were occurring, the New Guinea highlands and the Great Divide continued to rise. As well, the northward movement of Australia brought its northern parts into wetter regions. These processes provided areas where the cooler wet conditions, present more widely during the Miocene, continued to prevail and groups previously found in central Australia, including phalangerid possums and browsing macropodids, have continued to live in their original habitats up to the present day.

Alpine conditions first developed in the south-eastern highlands about 2 mybp. This opened up another new series of habitats that have been successfully conquered by two mammal species, a murid, the Broad-toothed Rat, *Mastacomys fuscus*, and a marsupial, the Mountain Pygmy-possum, that occur only in this environment.

As a consequence of these various climatic developments, a wide range of habitats, both new and old, was available to the Australian fauna during the late Tertiary.

The distribution of speciose families of the present-day marsupial fauna between vegetation types is shown in Table 19.3. Only the Phalangeridae have retained their preference for closed forest, but this family also contains the most successful and widespread of all Australian possums, the Common Brushtail Possum, *Trichosurus vulpecula*. Amongst the other families, most have the greatest number of species in open forest. The exception is the Dasyuridae where the largest number of species is found in hummock grassland. This is due to the radiation of the subgroup which includes species of *Sminthopsis*, *Ningaui* and *Parantechinus* in the drier habitats while other genera, for example, *Antechinus*, have largely remained in the 'traditional' wetter environments.

Table 19.3 Distribution of Australian marsupial families between major habitats.

FAMILY	NUMBER OF SPECIES						
	Closed Forest	Open Forest	Woodland	Open Scrub	Low Shrubland	Hummock Grassland	Tussock Grassland
Dasyuridae	10	14	14	10	10	18	14
Peramelidae	4	7	4	1	0	2	4
Vombatidae	0	1	1	0	0	0	0
Petauridae	6	7	5	0	0	0	0
Phalangeridae	4	1	1	0	0	0	0
Potoroidae	1	6	0	1	1	1	2
Macropodidae	9	13	10	5	0	3	7
Total	32	49	35	17	11	24	27
Ground dwelling	24	41	29	17	11	24	27
Species per 1000 km ² of habitat	0.49	0.18	0.03	0.03	0.04	0.08	0.04

If the number of species in a family found in a particular vegetation type is corrected for the area of that habitat available in Australia (Table 19.3), then the greater diversity of species in the wetter habitats, even amongst ground-dwelling groups, is quite marked, with approximately ten times more species per unit area occurring in closed forest and open forest than in the drier habitats. Whether this is due to the failure of the marsupials to take advantage of the newer drier habitats by radiation into them is uncertain. Such niches, traditionally filled on other continents by mammals, may have been filled in Australia by other groups, for example, granivorous birds or ants. Other, less likely possibilities include the loss of species during drier periods in the past or a lower level of niche opportunities available in the Australian arid environments.

The relationship between the number of species in a genus and the number of vegetation types utilised by the genus is plotted in Fig. 19.9a. Predictably, as the number of species in a genus increases so does the range of vegetation types utilised. Thus, more speciose genera are expected to be found over a wider area and this is the case (Fig. 19.9b). It also might be expected that, as the numbers of species in a genus increases, so these species should increasingly 'specialise' on certain vegetation types, but apparently this is not the case (Fig. 19.9c). One should remember, however, that the structural classification of vegetation types used (Specht, Roe & Boughton 1974) is based on the height and density of cover and may not be the best description for studies of habitat selection in mammals.

The number of species known from different regions of Australia is shown in Fig. 19.10. The highest diversity is found in the north-eastern coastal region where closed and open forest are common. Tasmania and the south-western coastal region contain far fewer species than the south-eastern coastal region,

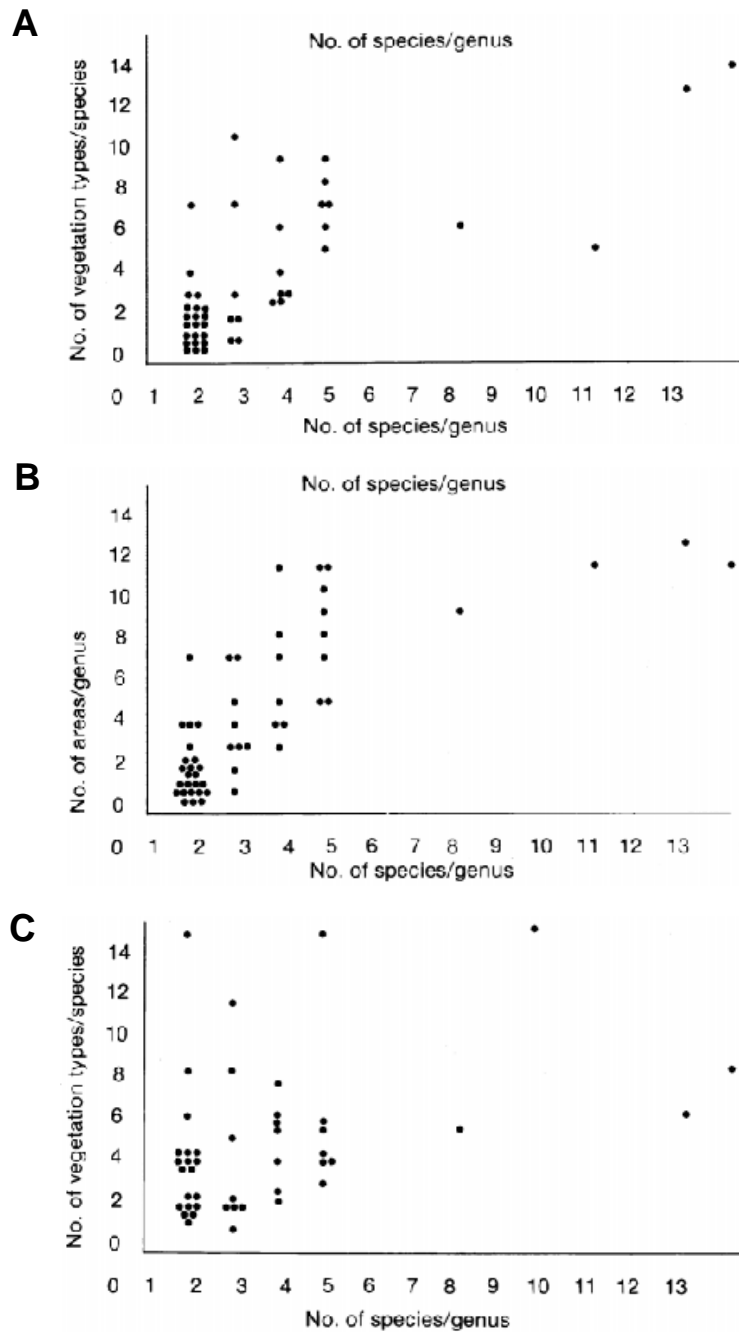


Figure 19.9 The relationships between the number of species in a genus and; **A**, the number of vegetation types used by the genus; **B**, the number of areas (see Fig. 19.10) used by each genus; **C**, the number of vegetation types used by each species. Each point represents the value for a genus.

though forests occur in all three regions. Surprisingly, the harsh, arid Western Plateau region contains many more species than any of the surrounding coastal or inland regions, presumably because of the large size of this area and the latitudinal range it includes.

The major refugia for mammals in Australia maintain remnants of the old 'Miocene' fauna. These refugia consist of the rainforests of the ranges of eastern Australia and the highlands of New Guinea. Though the size of the Australian arid zone has varied from time to time, since the Miocene there has always been a series of 'concentric' ecological zones surrounding that arid zone. These zones, however, may not make complete circles as the arid zone can extend to

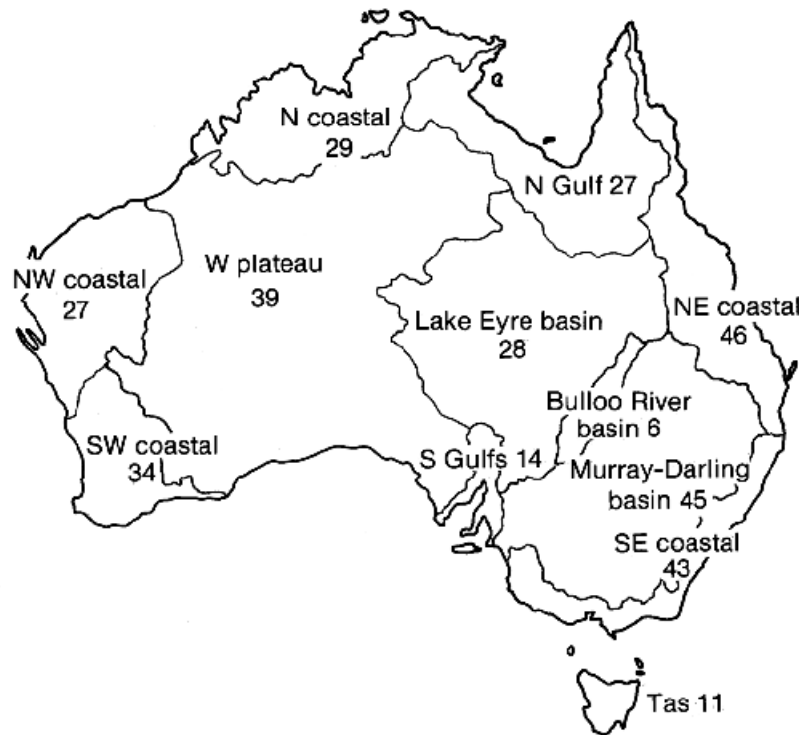


Figure 19.10 The number of marsupial species in each catchment area of Australia.

the sea at several points, notably in north-western Australia and at the Great Australian Bight. The latter barrier separates the forest faunas of south-western Australia from those in eastern Australia. Though many eastern marsupial species are not presently found in south-western Australia, for example, the Koala, only three marsupial species are found in south-western Australia that are not found elsewhere in Australia, the Quokka, *Setonix brachyurus*, the Honey Possum *Tarsipes rostratus* and the Dibbler, *Parantechinus apicalis*.

Many species are found in both the south-east and the south-west. Surprisingly, in several cases these widespread species have proved to be derived from south-western populations.

The flora of south-western Australia contains several genera, namely *Oxylobium* and *Gastrolobium*, that are restricted to the south-west and contain the extremely poisonous substance sodium fluoroacetate (or 1080). Several of the browsing mammal species in the area have developed strong tolerance to fluoroacetate, for example, the Western Grey Kangaroo, *Macropus fuliginosus*. Tests on specimens of *M. fuliginosus* from South Australia have shown that these, too, are resistant to fluoroacetate though populations in this area have never been confronted with the chemical in nature. Consequently these populations must have been derived originally from south-western populations. Other species, for example, the Tamar Wallaby, *Macropus eugenii*, are resistant in the south-west, but not in South Australia (King, Oliver & Mead 1978).

Other barriers that may break up distributions come and go, depending on sea level. These include Bass Strait, Torres Strait and the Gulf of Carpentaria. Bass Strait and Torres Strait separate populations or subspecies of many marsupials, for example, *Cercartetus nanus* and *Macropus rufogriseus* (by Bass Strait) or *Phalanger maculatus* and *Echymipera rufescens* (by Torres Strait). The Gulf of Carpentaria separates populations, but it also separates closely related species, for example, *Trichosurus vulpecula* and the Northern Brushtail Possum, *T. arnhemensis*, or various sections of the *Macropus robustus* / *M. bernardus* / *M. antilopinus* group.

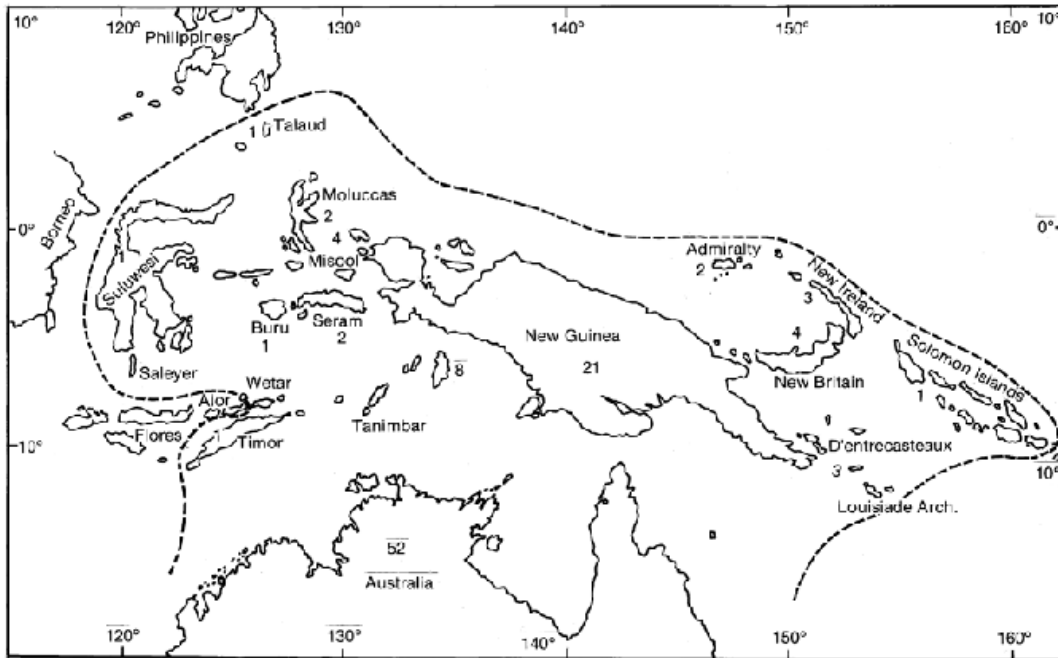


Figure 19.11 The number of genera of marsupials on the Australian mainland and on each of the islands to the north of Australia. The limit of the spread of marsupials away from the Australia/New Guinean homeland is shown by a dotted line.

Since the Miocene, the potential for faunal interchange by island hopping has existed between the Australian and Oriental Regions (Whitmore 1981). To date no marsupial has established itself on the Asian mainland, though marsupials are found as far westwards as Sulawesi and Timor (Fig. 19.11) in Indonesia. The most successful genus has been *Phalanger* (Sulawesi to the Solomon Islands), and *Echymipera* and *Petaurus* are also widespread (Simpson 1977).

Since the European settlement of Australia almost a quarter of the species in the marsupial fauna have become extinct or endangered. During the same period, some species, notably several species of kangaroos, have increased in numbers. These changes have been the result of environmental alterations following the introduction of competitors and predators and by changes to the vegetation of the country resulting from clearing and grazing (see Chapter 10).

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