

Diversity and Evolution of the Marsupial Mandibular Angular Process

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A medial inflection of the mandibular angular process is present in most marsupials. The few living marsupials that lack this trait either are very specialized forms (e.g., *Tarsipes*) or show a medial inflection at some point in development that is lost in later ontogenetic stages (cf. *Dactylopsila* and *Phascogale*). A medially inflected angular process is not present in any known extant or extinct placental (including all Cretaceous taxa that preserve the back of the dentary bone). Some extant placentals with enlarged auditory bullae evolved a medial flange of the angular process as a strategy to increase gape, but this is not homologous to the marsupial condition. We conclude that the medially inflected angular process is a shared derived trait of extant and extinct marsupials. The significant diversity in the form of the medially inflected mandibular angular process in marsupials, documented here for 53 taxa, shows a general relation to dietary adaptations. Herbivores (with well-developed masseter and medial pterygoid muscles) tend to have a shelf-like angular process, while small, insectivorous marsupials generally have a rod-like angular process. A close connection between the angular process and the ectotympanic is maintained during early postnatal development in all marsupials examined, a relation not seen in the placentals examined. A previous hypothesis suggested that the angular process plays a role in hearing in pouch-young *Monodelphis*. Data on the maturation of the auditory system does not support this hypothesis. Currently there are no data on differences in muscular anatomy or mastication between marsupials and placentals that could serve as a causal explanation for the difference in adult form of the angular process between the two groups.

KEY WORDS: marsupials; jaw; hearing; mastication.

INTRODUCTION

The mammalian mandible or dentary is a complex skeletal structure that is developmentally and functionally divisible into a number of major skeletal regions, including the horizontal ramus, the alveolar components, and the coronoid, condyloid, and angular processes (Atchley and Hall, 1991; Atchley, 1993). The angular process of the jaw is an important feature of the mammalian masticatory apparatus. The evolution of the angular process (as well as the coronoid and condyloid processes) can be understood as part of a complex rearrangement of the masticatory apparatus for reducing the forces acting through the jaw joint and redirecting muscle force for complex jaw movements (Crom-

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ton and Parker, 1978; Crompton and Hylander, 1986). The angular process of the mandible functions in adult mammals as an area for attachment of two jaw elevators, the masseter and the medial pterygoid muscles. These two muscles are largely responsible for the mediolateral movements that characterize the mammalian masticatory system. In addition, the masseter tends to evert the lower border and invert the dorsal border of the mandible, while the medial pterygoid produces the opposite movement (Oron and Crompton, 1985). Several workers have demonstrated that epigenetic factors, in particular, forces arising from the insertion of muscles, are involved in the formation of an angular process (Avis, 1961; Herring, 1985).

Most extant marsupials are characterized by a mandibular angular process that is inflected medially, as opposed to one that projects laterally or ventrally as in most placentals (Darwin, 1859; Wood Jones, 1923; Winge, 1941; Maier, 1987). A medially inflected angular process may be defined as one that projects inward (lingually) at about 90° with respect to the dorsoventral plane of the mandibular ramus. The ventrally situated angular process of placentals lies in the same plane as the ramus with no inward or outward projection, while a perfectly lateral one is angled laterally in a plane 90° from the dentary (Wood Jones, 1923) (Fig. 1).

Although a medially inflected angular process was traditionally used as a defining character of marsupials (Wood Jones, 1923), recent authors have claimed that the medial inflection is not a synapomorphy of marsupials (Marshall, 1979; Archer, 1984; Novacek, 1986; Miao, 1988). It is well-known that most marsupials, in contrast to all extant placentals, possess the angular process inflected medially, yet few authors have explored the basis for this difference (Mellett, 1980; Maier, 1987). Further, virtually no work has addressed the striking morphological diversity in this structure among marsupials. Such diversity is rarely acknowledged and has never been documented comprehensively, beyond anecdotal observations (Winge, 1941) or characterization of a few taxa [see Murray *et al.* (1987) on phalangerids].

In this paper we describe aspects of the morphological diversity found in the mandibular angular process in marsupials, discuss this diversity in the context of both marsupial phylogeny and biology, and provide a hypothesis for the functional basis of this diversity. We also review the ontogenetic and paleontological evidence bearing on previous explanations for the evolution of the inflected angular process and discuss whether the inflection is a marsupial synapomorphy.

MATERIALS AND METHODS

Materials

The form of the mandibular angular process was assessed in a broad spectrum of marsupials and placentals either directly from specimens or indirectly from reports in the literature. Representatives of at least one species of each of 54 extant marsupial genera (of the 83 genera recognized by Wilson and Reeder, 1993) (Table I) were examined in the collections of the American Museum of Natural History, New York (AMNH), the United States National Museum, Smithsonian Institution, Washington, DC (USNM), and the Museo de Historia Natural de La Salle, Caracas (MHNLS). Other abbreviations

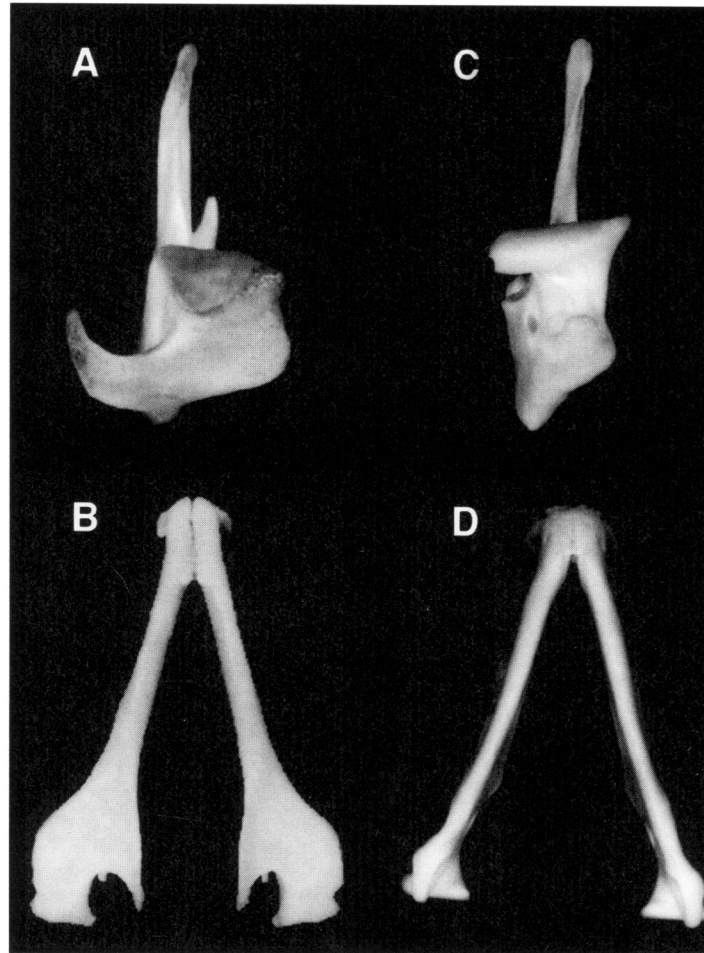


Fig. 1. Posterior and ventral views of (A, B) the dentary of the marsupial *Dasypus* sp. (USNM-238353) and (C, D) the placental *Procyon lotor* (BAA-0016). In A and C medial is to the left. Note how, in the marsupial, the mandibular angular process is bent medially at its posterior end. Not to scale.

used in the text are: Duke University Comparative Embryology Collection, Durham (DUCEC); Duke University Department of Biological Anthropology and Anatomy Comparative Anatomy Collection (BAACAC); Department of Anatomical Sciences and Neurobiology, University of Louisville (ULASN); Instituto Nacional de Investigaciones Geológico-Mineras de Colombia (INGEOMINAS); Hubrecht Laboratory of the National Institute of Developmental Biology, Utrecht, The Netherlands (HL); Kathleen Smith embryological collection (KS). Crown-rump length (CRL) and head length (HL) are defined by MacPhee (1981). PND is the abbreviation for postnatal day; the day of birth is PNDO.

Table I. Information on the Taxa Examined in this Study^a

Species	N	ASL/AL, mean \pm SD (group)	Body mass (g)	Ref.	Diet	Ref.
<i>Didelphidae</i>						
<i>Chironectes minimus</i>	20	0.785 \pm 0.034 (2)	650	7, 8	A	7, 8
<i>Didelphis marsupialis</i>	5	0.764 \pm 0.036 (2)	1,100	8	O	12, 8
<i>Lutreolina crassicaudata</i>	5	0.732 \pm 0.041 (2)	170	7	A	7
<i>Philander opossum</i>	8	0.750 \pm 0.056 (2)	430	3, 7, 8	A	7, 8
<i>Metachirus</i> sp.	8	0.762 \pm 0.059 (2)	304	7	A	7
<i>Gracilinanus dryas</i>	5	0.588 \pm 0.070 (1)	26	7	A	6
<i>Marmosa robinsoni</i>	8	0.719 \pm 0.092 (1)	75	3, 7	A	12, 8
<i>Marmosops fuscatus</i>	8	0.683 \pm 0.019 (1)	70	7	A	9
<i>Micoureus demerarae</i>	2	0.640 \pm 0.023 (1)	116	8	A	8
<i>Monodelphis brevicaudata</i>	8	0.603 \pm 0.065 (1)	90	7, 8	A	12, 8
<i>Caluromys philander</i>	5	— (4)	138	7	O	9
<i>Caenolestidae</i>						
<i>Caenolestes</i> sp.	5	0.776 \pm 0.121 (2)	26	3, 7	A	7
<i>Peramelidae</i>						
<i>Echymipera kalubu</i>	3	0.667 \pm 0.046 (1)	952	2	O	2
<i>Isodon macrourus</i>	5	0.571 \pm 0.053 (1)	1,130	3	A	12
<i>Macrotis lagotis</i>	3	0.658 \pm 0.074 (1)	1,000	3	A	9
<i>Peromyscus nasuta</i>	5	0.636 \pm 0.070 (1)	975	3, 9	A	9
<i>Peroryctes raffrayana</i>	3	0.807 \pm 0.020 (2)	894	2, 9	O	2
<i>Dasyuridae</i>						
<i>Antechinus leo</i>	3	0.656 \pm 0.019 (1)	53	1	A	12
<i>Dasyurus hallucatus</i>	5	0.572 \pm 0.071 (1)	400	3	A	12
<i>Murexia longicaudata</i>	3	0.751 \pm 0.027 (2)	140	2	A	9
<i>Phascogale calura</i>	3	0.621 \pm 0.087 (1)	53	1, 9	A	9
<i>Sarcophilus laniarius</i>	5	0.638 \pm 0.064 (1)	7,000	1	A	12
<i>Sminthopsis virginiae</i>	5	0.632 \pm 0.088 (1)	20	1	A	12
<i>Myrmecobiidae</i>						
<i>Myrmecobius fasciatus</i>	5	— (4)	338	9	A	9
<i>Notoryctidae</i>						
<i>Notoryctes typhlops</i>	2	0.804 \pm 0.101 (2)	53	9	O	9
<i>Microbiotheriidae</i>						
<i>Dromiciops gliroides</i>	2	0.712 \pm 0.136 (1)	24	10	A	9
<i>Phalangeridae</i>						
<i>Ailurops ursinus</i>	5	0.902 \pm 0.016 (3)	7,000	9	H	11

<i>Phalanger orientalis</i>	5	0.950 ± 0.034 (3)	2,500	2	H	13
<i>Spilocuscus maculatus</i>	5	0.929 ± 0.025 (3)	3,500	9	H	9
<i>Trichosurus vulpecula</i>	5	0.915 ± 0.026 (3)	2,500	3	H	12
Petauridae						
<i>Dactylopsila trivirgata</i>	2	—(4)	318	9	O	9
<i>Petaurus breviceps</i>	5	0.743 ± 0.024 (2)	126	2, 13	O	12, 13
Pseudocheiridae						
<i>Hemibelideus lemuroides</i>	5	0.784 ± 0.034 (2)	1,050	13	H	15
<i>Pseudocheirus cupreus</i>	3	0.869 ± 0.015 (3)	1,724	2	H	9
<i>Pseudocheirus peregrinus</i>	5	0.689 ± 0.013 (1)	830	3, 13	H	12, 13
<i>Petauroides volans</i>	5	0.781 ± 0.034 (2)	1,350	13	H	13
Acrobatidae						
<i>Acrobates pygmaeus</i>	2	0.529 ± 0.195 (1)	13.5	1, 13	O	13
<i>Distoechurus pennatus</i>	3	0.716 ± 0.076 (1)	50	9	A	13
Burramyidae						
<i>Cercartetus caudatus</i>	3	0.695 ± 0.099 (1)	30	1, 2, 13	O	13
Tarsipedidae						
<i>Tarsipes rostratus</i>	3	—(4)	10	9	O	9
Potoroidae						
<i>Aepyprymnus rufescens</i>	5	0.820 ± 0.042 (3)	3,300	3, 5, 6	O	12, 6
<i>Bettongia penicillata</i>	5	0.740 ± 0.083 (2)	1,300	3, 5, 6	O	12, 6
<i>Hypsiprymnodon moschatus</i>	5	0.889 ± 0.039 (3)	525	3, 5, 6	O	6
<i>Potorous tridactylus</i>	5	0.910 ± 0.050 (3)	1,150	5, 6	O	12, 6
Macropodidae						
<i>Setonix brachyurus</i>	5	0.925 ± 0.023 (3)	3,000	1, 5	H	12
<i>Dendrolagus matschiei</i>	3	0.929 ± 0.019 (3)	7,200	9	H	9
<i>Dorcopsis muelleri</i>	2	0.910 ± 0.006 (3)	5,000	2	H	9
<i>Lagorchestes conspicillatus</i>	4	0.916 ± 0.051 (3)	3,000	5, 9	H	9
<i>Macropus eugenii</i>	5	0.904 ± 0.028 (3)	6,500	1, 5	H	12
<i>Petrogale penicillata</i>	5	0.892 ± 0.056 (3)	5,300	3, 5	H	12
<i>Thylogale brunii</i>	5	0.885 ± 0.036 (3)	6,000	11	H	12, 9
<i>Wallabia bicolor</i>	5	0.931 ± 0.028 (3)	15,000	5	H	12
Vombatidae						
<i>Vombatus ursinus</i>	5	0.763 ± 0.055 (2)	25,000	9	H	9
Phascolarctidae						
<i>Phascolarctos cinereus</i>	2	—(4)	9,300	9	H	9

References: (1) Lee and Cockburn, 1985; (2) Flannery, 1990; (3) Tyndale Biscoe and Renfree, 1987; (4) O'Connell, 1983; (5) Norbury *et al.*, 1989; (6) Seebeck *et al.*, 1989; (7) Pérez-Hernández *et al.*, 1994; (8) Emmons and Feer, 1990; (9) Nowak, 1991; (10) Marshall, 1978; (11) Flannery, 1995; (12) Thompson, 1987; (13) Smith and Hume, 1984; (14) MacDonald, 1984; (15) Strahan, 1995. Diet categories: A, animalivory (including carnivory and insectivory); H, herbivory; O, omnivory.

Diversity of Mandibular Angular Process Form

We classified the form of the mandibular angular process in the marsupial taxa we examined into four categories: (1) rod-like, (2) intermediate, (3) shelf-like, and (4) non-inflected (Fig. 2). These categories can be represented quantitatively by two measurements: angular process length (AL), from the anterior departure of the process from the horizontal ramus to its most posterior tip, and angular process shelf length (ASL), from the anterior departure of the process from the horizontal ramus to the mid-point of the

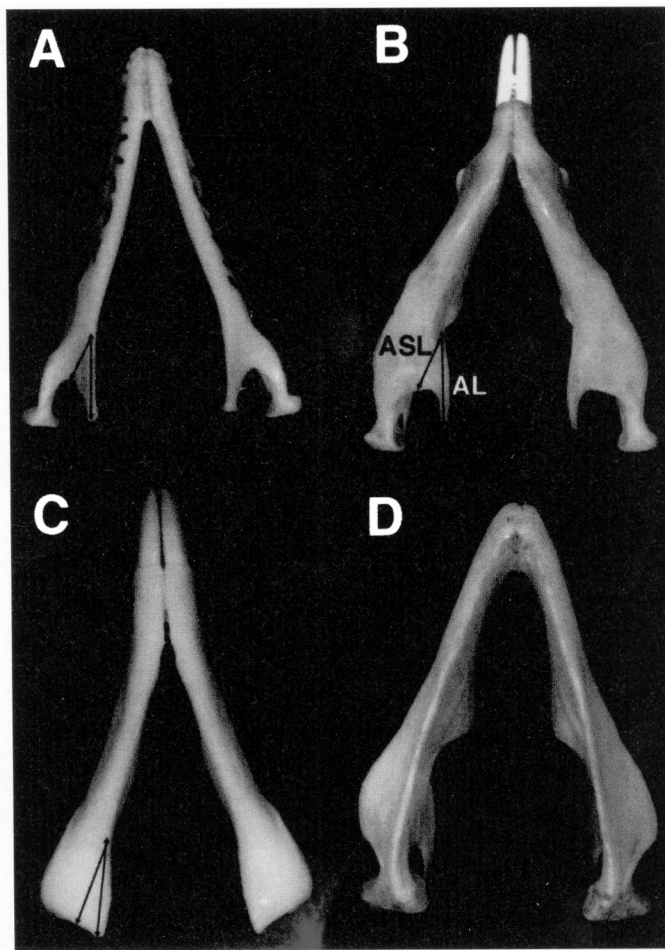


Fig. 2. Ventral view of the dentary of (A) *Sminthopsis* sp. (USNM-283971), which has a rod-like angular process; (B) *Bettongia* sp. (USNM-237726), which has an intermediate angular process; (C) *Macropus* sp. (M. Sánchez-Villagra, personal collection), which has a shelf-like angular process; and (D) *Phascolarctos cinereus* (USNM-521411), which has an angular process that is noninflected. The two measurements that describe mandibular angular process form in marsupials are shown in A–C. AL, angular process length; ASL, angular process shelf length. Not to scale.

pterygoid shelf (Fig. 2). The ratio ASL/AL defines the shape of the angular process. Rod-like angular processes correspond to specimens with an average ASL/AL ratio <0.72 , intermediate angular processes correspond to ratios between 0.72 and 0.81, and shelf-like angular processes correspond to ratios >0.81 . Measurements were taken with dial calipers on dry museum specimens. For each species, at least three individuals were measured except for seven species in which no more than two were available (Table I). In most species five or more individuals were measured. Almost all measurements were on dental adults in which all teeth of the adult dental formula had erupted, although in a few individuals the last molar had not erupted.

In order to explore the relationship of diet with mandibular angular process form, we used the following dietary categories: (1) animalivory (including both carnivory and insectivory), (2) omnivory, and (3) herbivory. Among the omnivores we included exudate feeders (*Petaurus*) and nectarivores (*Acrobates*, *Cercartetus*, and *Tarsipes*), although we note differences between these taxa and other omnivores in the results and discussion sections. Both mandibular angular process form and diet were examined relative to body mass data, which were obtained from diverse sources, including reviews and primary references (Table I).

Marsupial Phylogenies

The distribution of angular process form was mapped onto a phylogeny of marsupials in order to assess the overall pattern of evolution of the angular process. In particular, we were interested in documenting patterns of homoplasy that might be correlated with dietary and body size features. In recent years there has been a proliferation of molecular, anatomical, paleontological, and reproductive data relevant to the study of the evolutionary relationships among marsupials (see reviews by Luckett, 1994; Springer *et al.*, 1994; Szalay, 1994). We used the phylogenetic scheme of Luckett (1994), based on a total evidence approach combining molecular and morphological data, to plot angular process form. Luckett's (1994) marsupial phylogeny is to the family level. For phylogenetic relationships within families we followed Baverstock *et al.* (1989) for the macropodids, Kirsch and Palma (1995) for the didelphids, Kirsch *et al.* (1990a) and Krajewski *et al.* (1994) for dasyurids, Kirsch *et al.* (1990b) for peramelids, Springer *et al.* (1992) for pseudocheirids, and Springer *et al.* (1990) for phalangers.

Our aim in mapping angular process form onto phylogeny (as an unordered character) was not to reconstruct the ancestral state for all marsupials or for monophyletic groups within marsupials; rather, we were looking for specific patterns of homoplasy that would give clues to the functional correlations of angular process form.

Ontogeny

The development of the angular process and its spatial relation to basicranial structures was studied in serially sectioned and histologically stained pouch young specimens of *Monodelphis domestica*, *Macropus eugenii*, *Phascolarctos cinereus*, *Dactylopsila* sp., *Petauroides* sp., *Petrogale* sp., and *Vombatus ursinus* (marsupials) and embryonic *Mus musculus*, *Procyon* sp., and *Rousettus leschenaulti* (placentals).

RESULTS

Phylogenetic Distribution of the Mandibular Angular Process Form

The plot of the form of the angular process on phylogeny (Fig. 3) reveals that although all categories for the form of the process exhibit homoplastic distribution, several monophyletic groups appear to be characterized by regular patterns. The macropodids and phalangers largely possess shelf-like angular processes, while the peramelids and dasyurids examined are mostly characterized by rod-like processes. The phylogenetic distribution of rod-like angular processes and shelf-like processes appears mutually exclusive. A group characterized primarily by one of these two conditions may have members with intermediate conditions; however, a group with primarily rod-like angular processes has no members with shelf-like processes, and vice versa. The medially inflected angular process has been lost multiple times independently. The “intermediate” condition is found in virtually all groups of marsupials.

Alternative views on the suprafamilial relationships among marsupial superfamilies exist (Luckett, 1994; Springer *et al.*, 1994; Szalay, 1994; Kirsch *et al.*, 1997). However, no matter which of these phylogenies is used, similar patterns of homoplasy are present. Specifically, in all phylogenies loss of the inflection of the mandibular angular process has occurred multiple times, and rod-like, intermediate, and shelf-like processes appear convergently across the phylogeny.

Dietary and Body Size Correlates of the Mandibular Angular Process Form

The distribution of angular process form exhibits a general relation to diet (Fig. 4). Herbivores (macropodids and phalangers) for the most part have shelf-like angular processes, and animalivores generally have rod-like (peramelids, dasyurids, *Dromiciops*) or intermediate angular processes (didelphids, *Caenolestes*). As diet is correlated with body size (see Kay, 1984), angular process form and body size show a general relation as well; that is, larger marsupials tend to have shelf-like angular processes, and most marsupials of small size have rod-like processes (Fig. 6). There are exceptions to both of these patterns. Several of the smaller herbivores have intermediate angular processes, and some of the larger animalivores also have intermediate processes. Animals with omnivorous diets show all types of angular processes, with a general relation with size: the smaller omnivores, in particular, the nectarivores *Acrobates* and *Cercartetus* and the exudate feeder *Petaurus*, have rod-like and intermediate angular processes; the larger omnivores have intermediate to shelf-like angular processes. Some individuals of all dietary categories have lost a medially inflected angular process.

Sarcophilus, the Tasmanian devil, has a rod-like angular process, just as all other dasyurids and most animalivorous marsupials do. The relatively large size of *Sarcophilus* seems to have no effect on the form of the angular process. All Peramelidae have rod-like angular process except for *Peroryctes* which has an intermediate angular process. *Peroryctes* has a more generalized diet than other, more animalivorous, peramelids and is considered an omnivore. Among didelphids, all didelphines (*sensu* Kirsch and Palma, 1995) have an intermediate angular process and all are ecological generalists. Marmosans [Thylamyinae and Marmosinae (*sensu* Kirsch and Palma, 1995)] all show a rod-like angular process, possibly correlated with their more animalivorous diet than that of

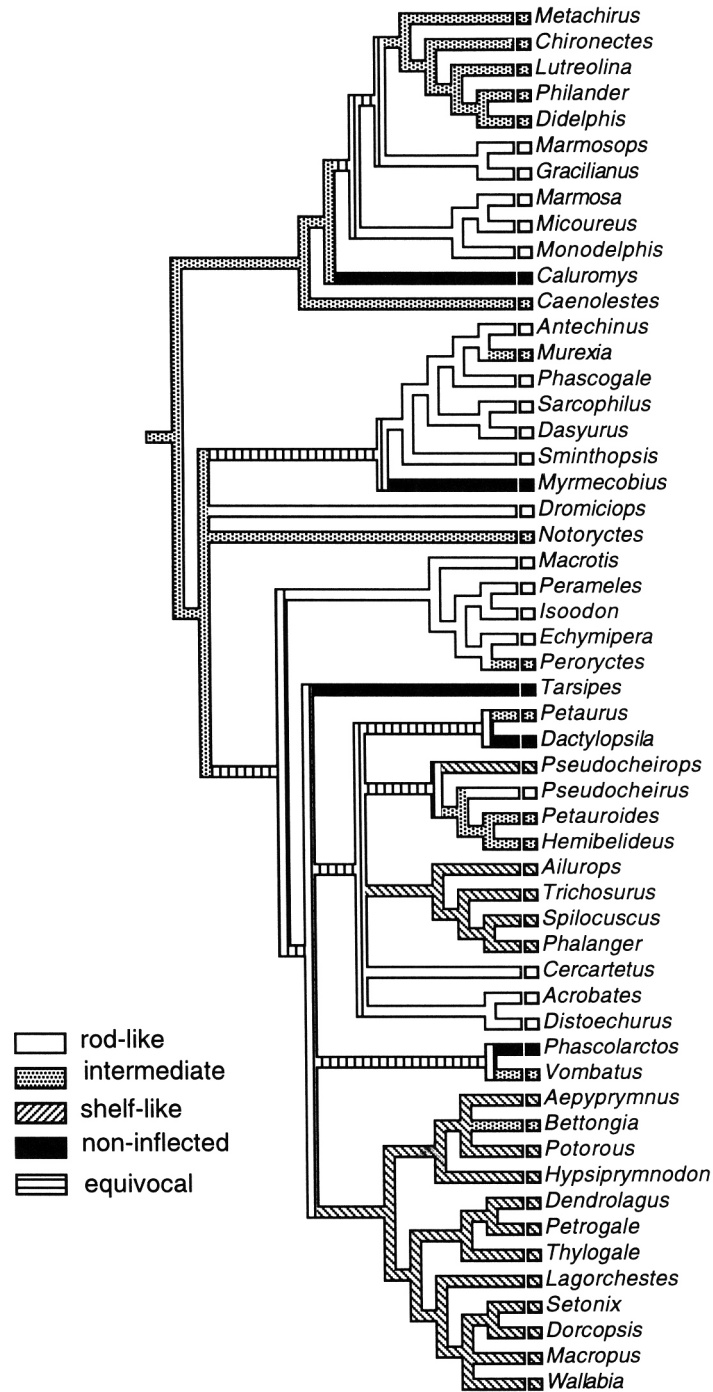


Fig. 3. Angular process form plotted onto a marsupial phylogeny based on Luckett (1994) for interordinal relationships and several other references for relationships within families (see text). Data on angular process form from Table I.

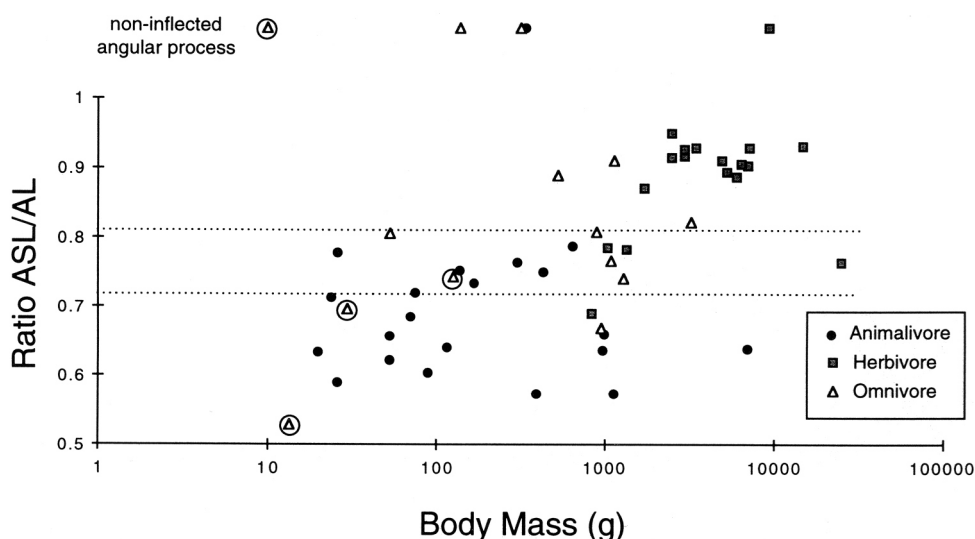


Fig. 4. Plot of the ratio angular process shelf length/angular process length (ASL/AL) vs. body mass. The dotted lines represent the boundaries between the angular process categories used in this paper. Angular processes above 0.81 are shelf-like; those below 0.72 are rod-like. Marsupials that lack an inflected angular process (for which the ratio ASL/AL does not apply) are depicted at the top of the graph. Nectarivores and the exudate feeder are presented as a triangle within a circle. Data from Table 1.

other didelphids. Individuals in the latter group are also smaller than the didelphines that have an intermediate angular process. *Pseudocheirops* is the only pseudocheirid with a shelf-like angular process; all others have an intermediate angular process. *Pseudocheirops* is also the taxon examined in this family with the largest body size. *Pseudocheirus*, the smallest pseudocheirid examined, was the only herbivore with a rod-like process. However, the ratio of ASL/AL was very close to the boundary of 0.72. Further, its gross morphology appeared more intermediate than rod-like.

Thus these data indicate a complex relation among diet, size, phylogeny, and angular process form. Clear trends exist: large, herbivorous animals (primarily macropodids and phalangers) have shelf-like angular processes, and smaller or more animalivorous animals have rod-like angular processes.

Loss of an Inflected Mandibular Angular Process

The loss of an inflection in the mandibular angular process has occurred independently at least five times in marsupial evolution, a pattern seen in several alternative phylogenies we could use to plot angular process form (Springer *et al.*, 1994; Szalay, 1994; Kirsch *et al.*, 1997).

The most extreme example of loss of the medial inflection of the angular process is seen in the "honey possum" *Tarsipes*, in which the mandible is reduced to a slender bony rod (Flower, 1885; Thomas, 1888; Abbie, 1939; Winge, 1941; Rosenberg and Richardson, 1995). The medial inflection of the hook-shaped angular process in the numbat (*Myrmecobius fasciatus*) is poorly developed (Marshall, 1979). The angular process in *Caluromys* and *Caluromysiops* is atypical in that the medial inflection does not

reach 90 degrees with respect to the dentary. This finding had been reported by Winge [(1941) his genus *Philander*]. All other didelphids show a medial inflection of the angular process. *Dactylopsila* has an angular process which is medially inflected but very poorly developed, forming only a small shelf (Fig. 5) (Tate, 1948). Finally, the koala (*Phascolarctos cinereus*) has an angular process that is extended ventrally until it is almost in line with the ramus (Fig. 2) (Abbie, 1939; Winge, 1941; Tate, 1948).

Juveniles of both *Dactylopsila* (DUCEC-8323; Fig. 5B) and *Phascolarctos* (HL-ms356) show a well-developed medial inflection, which is subsequently reduced in the adult (Fig. 5A). Other taxa lacking a medially inflected angular process as adults were not examined.

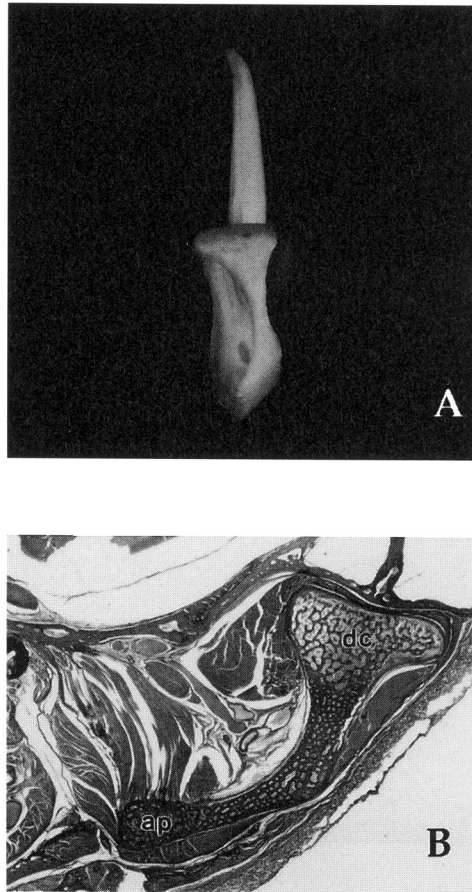


Fig. 5. (A) Posterior view of the right dentary of *Dactylopsila trivirgata* (USNM-120912), medial is to the left. (B) Coronal section of a right side portion of the head of a pouch young *Dactylopsila* sp. (DUCEC-8323; CRL = 132 mm) showing a medially inflected angular process. dc, dentary condyle; ap, angular process of the dentary. Not to scale.

The Mandibular Angular Process in Fossil Marsupials and Deltatheroideans

All the fossil marsupials examined, or for which information on this trait is available in the literature, have a medially inflected angular process. These include *Asiatherium reshetovi*, from the late Cretaceous of Mongolia (Szalay and Trofimov, 1996), the borhyaenid *Anachlysictis gracilis* (Goin, 1997) (Fig. 6), the didelphoids *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Sparassocynus derivatus* (Reig and Simpson, 1972), marsupials from the Eocene of Messel, Germany (von Koenigswald and Storch, 1992), from the late Oligocene–early and middle Miocene of Riversleigh, Australia (Archer *et al.*, 1991), fossil vombatimorphs (Tedford and Woodburne, 1987), the South American argyrolagids (Simpson, 1970; Sánchez-Villagra and Kay, 1995, 1997), *Groeberia* (Pascual *et al.*, 1994), and polydolopids (Paula Couto, 1952), and the Australian zalamdodont *Yalkaparidon coheni* (Archer *et al.*, 1988).

As we did not measure the angular process of any fossil specimens, they are not included in the phylogenies. However, it is clear, following the phylogenetic interpretations of Pascual *et al.* (1994) and Szalay (1994), that two South American fossil taxa evolved shelf-like angular processes independently: *Groeberia* (Pascual *et al.*, 1994) and *Polydolops* (Paula Couto, 1952). Among extinct marsupials the Paleocene didelphoid *Pucadelphys andinus* has an intermediate angular process similar to that of *Didelphis* (Marshall and Muizon, 1995), as does the borhyaenid *Anachlysictis gracilis* [INGEOMINAS-184247 (Fig. 6)].

The recently described metatherian *Kokopellia juddi* from the early Cretaceous of western United States preserves part of the inferior border of the dentary bone and is supposed to show a medially inflected angular process (Cifelli, 1993a).

Deltatheroideans (a predominantly Old World group of primitive tribosphenid mammals) are regarded by some authors as a sister group of all other marsupials (Marshall and Kielan-Jaworowska, 1992; Kielan-Jaworowska and Nessov, 1990; but see Cifelli, 1993b). The mandibular angular process of deltatheroideans is yet unknown, but recent discoveries in the Cretaceous of Mongolia might reveal information about the back of the dentary in this group (Novacek *et al.*, 1996).

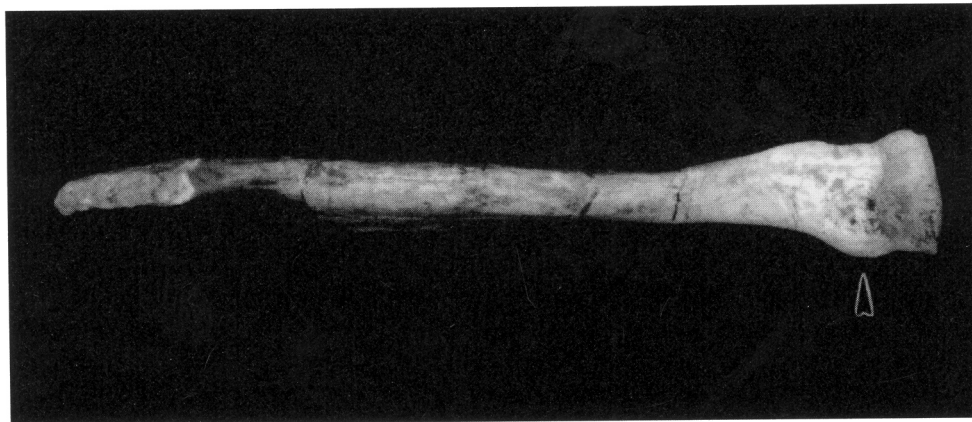


Fig. 6. Ventral view of the right dentary of the borhyaenid *Anachlysictis gracilis* (INGEOMINAS-184247). The medial inflection of the angular process is indicated by the white arrow. Medial is to the top; anterior, to the left.

The Mandibular Angular Process in Placentals

Placentals show a great diversity of angular process form although none exhibits the medial inflection characteristic of marsupials (Fig. 7). Some rodents show medial and lateral flanges in the angular process [e.g., *Dipodomys*, *Jaculus* (see Osborn and Helmy, 1980, p. 343 and Fig. 106; Howell, 1932), *Aplodontia* (Fig. 7)], but these are clearly late and independent acquisitions because early rodents did not have a medially inflected angular process (Carroll, 1988). For the most part the inflection of the angular process of rodents serves to increase gape in animals that possess greatly enlarged auditory bullae, which crowd the basicranial region (see Nikolai and Bramble, 1983).

It is often claimed that Late Cretaceous placentals possess a mandibular angular process that is medially inflected [*Gypsonictops hypoconus* (Novacek, 1986); *Cimolestes cerberoides*, *C. magnus* (Lillegraven, 1969); *Asioryctes nemegetensis* (Kielan-Jaworowska, 1975; Lillegraven *et al.*, 1979); *Barunlestes* sp. (Kielan-Jaworowska, 1975); *Kennalestes* sp. (Lillegraven *et al.*, 1979)]. From these reports it has been concluded that the medially inflected angular process is not a good diagnostic character for marsupials (e.g., Marshall, 1979; Archer, 1984; Novacek, 1986; Maier, 1987; Miao, 1988). However, we believe that an inflected angular process has not been rigorously defined previously and that, under the definition of "inflected angular process" provided here, the placentals that have been claimed to have such a trait do not have it. For example, the angular process of *Asioryctes nemegetensis* (Kielan-Jaworowska, 1975, p. 17, Plate 1) is almost identical to that of *Tupaia* (Fig. 7), which has an angular process that projects ventrally. A better assessment of the diversity of angular process form in the earliest placentals will be gained once the material from the Cretaceous of Mongolia under study by Novacek and colleagues (1996; Novacek, 1995) is described.

Marshall (1979) reported that a strongly inflected angular process occurs in the Didymoconidae, a group that was present in Asia in the Late Eocene to Mid-Oligocene and possibly the Cretaceous. This report was based on the observations of Mellett and Szalay (1968) on the type of *Kennatherium shirensis* (AMNH-26295) from the Eocene of Asia. One of us (M.R.S.V.) examined this specimen; although the angular process

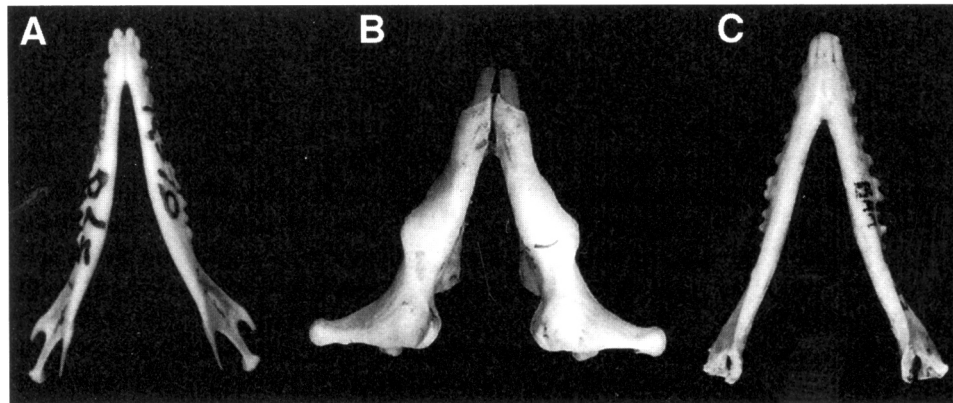


Fig. 7. A sample of variation in mandibular angular process form in placentals. Ventral view of the jaw of (A) *Elephantulus* sp. (USNM-382601), (B) *Aplodontia rufa* (USNM-42789), and (C) *Tupaia glis* (BAA-83). Not to scale.

is now partially broken, preserved parts demonstrate that it is not medially inflected but instead projects ventrally as in *Tupaia* (Fig. 7).

The Mandibular Angular Process in Nontherian Mammals

The aegialodonts (sensu Marshall and Kielan-Jaworowska, 1992) are the oldest known mammals with tribosphenic molars and are considered by Marshall and Kielan-Jaworowska (1992) as putative ancestors of marsupials and not of placentals. Cifelli (1993b), presenting a more conventional view, places aegialodonts in a basal position within Tribosphenida. The back of the dentary of aegialodonts is unknown; only partial jaws have been described (Dashzeveg and Kielan-Jaworowska, 1984).

Vincelestes, a prototribosphenid (Rougier *et al.*, 1996) from the Early Cretaceous of Argentina, does not have an inflected angular process according to Rougier (1993, personal communication).

Extant monotremes do not have an inflected angular process (Kuhn, 1971; Zeller, 1989). The jaw in these taxa is reduced and highly specialized, related to their dietary habits (reviewed by Nowak, 1991).

Previously it was thought that multituberculates had a mandibular angular process that was medially inflected and homologous to the marsupial condition [(Miao, 1988); Miao followed the notion that the earliest placentals had a medially inflected angular process]. However, Gambaryan and Kielan-Jaworowska (1995, p. 87), clearly demonstrated that “the different portions of the dentaries that are inflected in multituberculates and in therians, strongly suggest that the inflection occurred separately.” A pterygoid shelf is present in the oldest known late Jurassic multituberculate dentaries and in a variety of later multituberculates (Gambaryan and Kielan-Jaworowska, 1995, and references therein; Rougier *et al.*, 1996). The pterygoid shelf [= “pterygoid crest” of Simpson (1926)] of the posterior portion of the dentary of multituberculates has been considered as the point of insertion of the medial pterygoid muscle (e.g. Parker, 1977; Clemens and Kielan-Jaworowska, 1979; Krause, 1982; Miao, 1988; Wall and Krause, 1992; Gambaryan and Kielan-Jaworowska, 1995) and, therefore, functionally convergent with the medially inflected angular process of marsupials.

Relationships of the Mandibular Angular Process to Basicranial Structures During Ontogeny

In all the marsupials examined of early pouch-young age (*Dactylopsila*, *Dasyurus*, *Macropus*, *Monodelphis*, *Petauroides*, *Petrogale*, and *Phascolarctos*), there is a close relation of the angular process to the ectotympanic (Fig. 8), due to the inflection of the former, as has been previously documented for *Monodelphis* by Maier (1987; see below). Such a relation is not present in embryos of the placentals *Mus*, *Procyon*, or *Rousettus* at any of the stages examined.

In *Monodelphis domestica*, by PND-35 a tympanic process of the alisphenoid has developed and is found between the inflected angular process and the ectotympanic, therefore precluding the direct contact between these two structures (see Maier, 1989, p. 152, Fig. 1). A similar phenomenon occurs in other marsupials at some point in development (Maier, 1989).

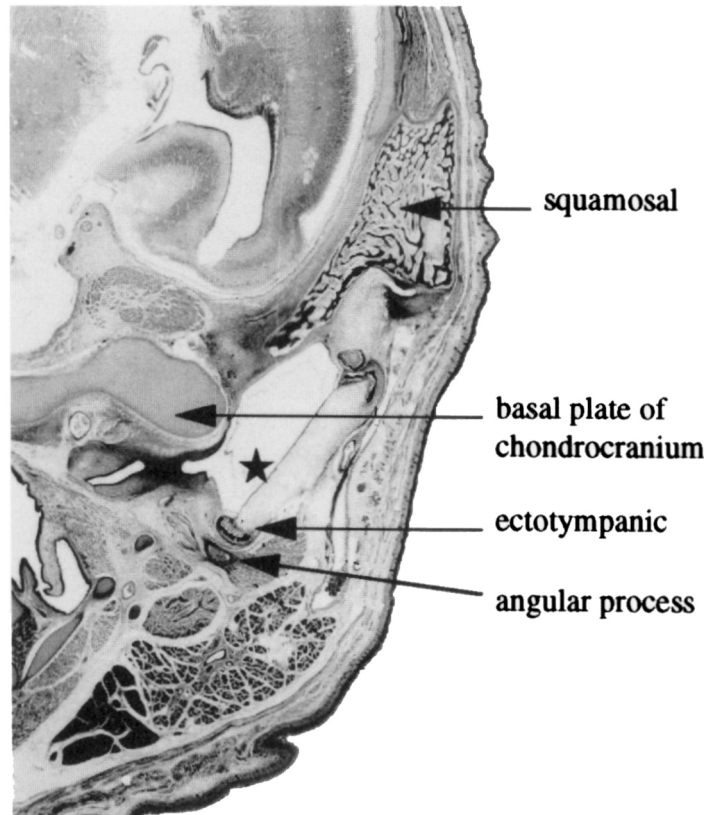


Fig. 8. Coronal section of a PND-55 pouch-young *Macropus eugenii* (KS-255B) showing the relation of the inflected mandibular angular process with basicranial structures. Note the close relation of the angular process with the ectotympanic. The star is medial to the tympanic membrane, in the cavum tympani.

DISCUSSION

The Medial Inflection of the Mandibular Angular Process: A Marsupial Synapomorphy?

Review of the relevant paleontological and neontological information suggests that the medial inflection of the mandibular angular process is a derived condition of a clade that includes all known extant and fossil marsupials (see also Kuhn, 1971). This conclusion is reinforced by the fact that *Vincelestes* does not have an inflected angular process (Rougier, 1993, p. 174, Fig. 45). The few marsupials that do not show an inflection as adults, do so as juveniles (cf. *Dactylopsila* and *Phascolarctos*), which supports the notion that an inflection is the primitive condition of marsupials.

It is difficult to characterize the form of the marsupial angular process by studying the standard lateral and/or medial views of mandibles usually presented in the literature,

since the angular process is medially inflected. When such views are presented of placentals with a vertical angular process, what appears as a medial inflection is an artifact of the camera angle. This fact might have led some researchers in the past to state erroneously that the earliest known placentals have a medially inflected angular process.

Diversity in the Mandibular Angular Process of Extant Marsupials and Its Functional Significance

The diversity in angular process form of adult marsupials exhibits a complex relation with size, diet, and phylogeny. The shelf-like angular process and, to a lesser extent, the intermediate angular process provide expanded areas of attachment of the masseter and medial pterygoid muscles. These muscles are well developed in animals with lateral jaw movements and are usually large in herbivorous mammals (Turnbull, 1970). These muscles are not as well developed in animalivorous marsupials, which have smaller areas of muscle attachment on their rod-like angular processes.

Significant variation in details of angular process form, other than that revealed by the ratio ASL/AL , arises out of various strategies for the expansion of these muscle attachments. For example, under the category "shelf-like angular process," we included marsupials with very different configurations in their masticatory apparatus. All macropodoids have a masseteric canal through which the masseter muscles invade the body of the dentary (Flannery, 1987). The masseteric canal has been interpreted to be an adaptation to control the plane of premolar occlusion and thereby increase the efficiency of premolar shear (Ride, 1959; Flannery, 1987). Both phalangerids and *Pseudocheirops*, which have evolved a shelf-like angular process independently, lack a masseteric canal (Flannery, 1989). The only macropodoid that does not have a shelf-like angular process by our measurements is *Bettongia*. This is not a reflection of any peculiarity of *Bettongia* among macropodoids in terms of diet or size but rather is an artifact of the way in which we measured the angular process. *Bettongia* has as extensive an area of muscle attachment in the angular process as other macropodoids. However, the lateral tip of the angular process extends posteriorly and thus decreases the ratio ASL/AL .

Marsupials that lack an inflected angular process can be adduced to illuminate further the significance of the diversity in angular process form. *Tarsipes* shows extreme cephalic adaptations to nectarivory that involve a reduction of most of the cranial musculature (reviewed by Rosenberg and Richardson, 1995). The reduction in musculature is accompanied by the complete loss of the angular process. The reduction of the process in *Myrmecobius* might be correlated with its adaptations to ant-eating, which include reductions of teeth size and jaw size, as is seen in placental myrmecophagids. The peculiarities of the angular process of *Dactylopsila* and caluromyines are more difficult to explain.

The lack of an inflection in the angular process of *Phascolarctos* (Fig. 2) is particularly interesting. Koalas are arboreal folivores that subsist on a high-fiber diet of leaves from a limited number of *Eucalyptus* species (e.g., Ellis *et al.*, 1995). Placental herbivores, as well as other marsupial herbivores with diets that demand a grinding apparatus, have well-developed pterygoid muscles (Turnbull, 1970), which are in turn correlated with the development of an angular process (Turnbull, 1970; Radinsky, 1985). In this regard, it is striking that the koala has poorly developed medial pterygoid mus-

cles. Davison and Young (1990) presented a detailed study of the masticatory muscles of the koala and found that the pterygoid muscles account for only 12.5% of the total masticatory muscle mass (they studied two females and one male; the number above is an average). In a "typical" herbivore, this figure would be about 25% (Turnbull, 1970). The masseter muscle in the koala is well developed (representing 48% of the masticatory muscle mass), and related to this, it has a prominent crest on the lateral side of the jaw ("oblique masseteric crest") for the attachment of the deep masseter (Davison and Young, 1990). It is singular that the koala develops a very large masseter, for medio-lateral masticatory movements, but does not possess a large medial pterygoid muscle. In addition, the koala possesses dorsoventrally tall auditory bullae, and it is possible that these bullae could restrict gape in animals with medially inflected angular processes.

The sister group of the koala is the wombats (Fig. 3). Both *Vombatus* and *Lasiorhinus* have what we classify as an "intermediate" angular process. This categorization results from the elongate shape of the angular process in wombats (Fig. 9). However, the area for muscle attachment is proportionately as large as that characterizing shelf-like angular processes in other large herbivorous taxa, and wombats have large inflections on the lateral surface of the angular process as well. The form of the angular process in fossil vombatimorphs (including several extinct families) is similar to that of extant wombats and is considered a synapomorphy of Vombatimorphia (Tedford and Woodburne, 1987).

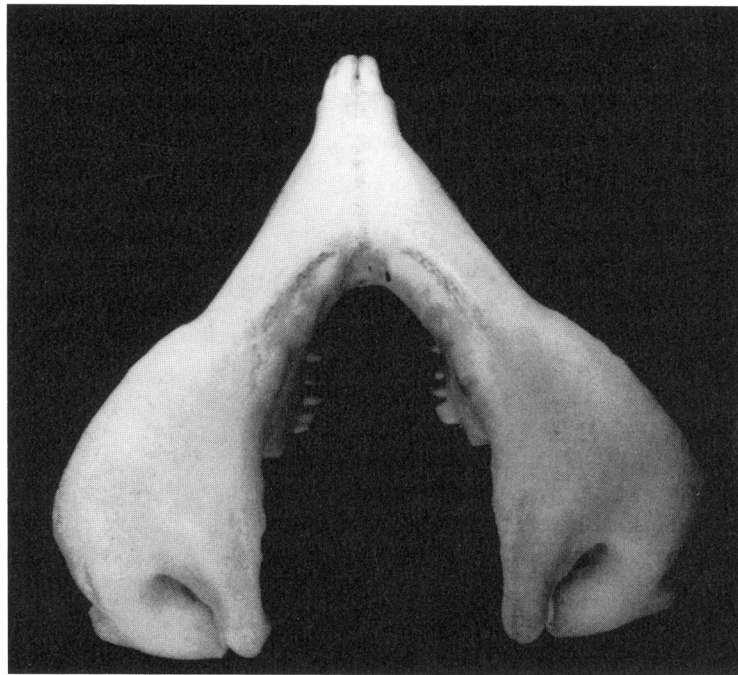


Fig. 9. Ventral view of the dentary of *Vombatus ursinus* (USNM-521059). Note how the medial most tip of the angular process extends particularly far posteriorly. Also, note the broad lateral expansion of the angle.

The Function of the Mandibular Angular Process in Marsupials and Placentals

If the variation in angular process form appears to correlate with presumed muscle function within marsupials and the dentary is consistently different between marsupials and placentals, the following question arises: Is there any fundamental difference between placentals and marsupials in the arrangement or function of muscles attaching to the angular process?

All published studies of the head muscles in both marsupial and placental mammals report that the masseter muscle attaches to the lateral side of the jaw and the medial pterygoid to the medial side (e.g., Schumacher, 1961; Saban, 1968; Turnbull, 1970). Both attachments extend to the angular region. Such an attachment has been reported for all marsupials for which we have found descriptions of head musculature: *Bettongia penicillata* (Parker, 1977), *Didelphis marsupialis* (Hiemae and Jenkins, 1969), *Caenolestes* sp. (Osgood, 1921), *Trichosurus vulpecula* (Barbour, 1963), *Echymipera* sp., *Isoodon* sp., and *Macrotis* sp. (Filan, 1990), *Phascolarctos cinereus* (Davison and Young, 1990), and *Sminthopsis* sp., *Acrobates* sp., and *Cercartetus* sp. (Rosenberg and Richardson, 1995). We have observed the same pattern in histological sections of the following taxa: *Dactylopsila* sp. (DUCEC-8323), *Petauroides* sp. (DUCEC-8412), *Petrogale* sp. (DUCEC-8325), and numerous stages of *Monodelphis domestica* and *Macropus eugenii*. Thus there appears to be no difference in the gross anatomy of muscle insertions on the angular process.

It is possible that the differences in the orientation of the angular process relate to consistent differences in the details of muscle attachment and function. In marsupials with an unfused symphysis the medially inflected angular process would probably increase the moment arm with respect to rotation of the jaw along its long axis. In marsupials with a fused symphysis, on the other hand, inversion of the lower border of each mandibular ramus along its long axis is impossible. Although it is tempting to relate the lack of an inflected angular process in the koala with the fused symphysis seen in this taxon, other marsupials with fused symphyseal regions retain a medially inflected angular process. For example, wombats and koalas are sister groups and both have fused symphyses, yet the wombat has a well-developed inflected angular process. Among macropodids there is also variation in the degrees of symphyseal fusion. For example, Flannery (1989) reported that, in his Sthenurinae (which includes *Lagostrophus*), the mandibular symphysis is strongly ankylosed (much more so than in potoroids, balbarines, and macropodines), yet there is little or no variation in degree of angular process inflection among these taxa.

No consistent differences in mastication have been reported that would distinguish marsupials from placentals. Crompton *et al.* (1977) found equivalent patterns of integrated movements of the jaw and hyoid in *Didelphis virginiana* and the placental *Tenrec ecaudatus*. *Didelphis* shows a four-stage chewing cycle with the same general profiles as seen in several placental groups (Kay and Hiemae, 1974; cf. Crompton *et al.*, 1977). The general profile of EMG activity for adductor and depressor muscles of *Didelphis virginiana* (Crompton *et al.*, 1977, p. 291, Fig. 17.2) and of *Tenrec ecaudatus* (Oron and Crompton, 1985, p. 172, Fig. 17) chewing soft food is quite similar. Further, although extensive movement at the symphysis is present in both *Didelphis virginiana* (Crompton and Hiemae, 1970) and *Tenrec ecaudatus* (Oron and Crompton, 1985), rota-

tion along the long axis appears to be particularly well developed in *Tenrec*, which does not have an inflected angular process. In *Tenrec* rotation continues through the power stroke. Mandibular rotation is a primitive mammaliaform (*sensu* Rougier *et al.*, 1996) feature, present in mammals of the Liassic period (Oron and Crompton, 1985; Crompton and Hylander, 1986). This mammalian feature is associated with unilateral occlusion, retained in insectivorous mammals (Oron and Crompton, 1985). Oron and Crompton (1985) suggested that such rotation in *Didelphis* is probably important primarily for the correct alignment of the molars and not so much for the breakdown of food.

Mellet (1980) attempted to explain the inflected angular process based on models of mastication. Mellett (1980) assumed that the medial inflection of the angular process was primitive for Theria and hypothesized that such inflection was an adaptation for particular masticatory requirements of early therians. He stated that “the inflected angular process arose sometime in the Mesozoic after the development of the protocone, to maintain occlusal relations between the buccally displaced stylar cusps, and the trigonid. Eutherians later reduced their stylar cusps and enhanced the development of conules between the protocone and paracone-metacone. With stylar cusps becoming less important in occlusion the inflected angular process was subsequently lost in eutherians.”

This hypothesis encounters many problems: (1) stylar cusps do not occlude with the trigonid (see Crompton, 1971; Maier, 1978); (2) several marsupial clades have lost their stylar shelves and have switched to an entirely different masticatory strategy (e.g., kangaroos) but retain a robustly inflected angular process; and (3) early placentals such as *Prokennalestes* and *Paranyctoides* have large stylar shelves and some well-developed stylar cusps, yet they have only a small and vertically oriented angular process (Szalay, 1994). Finally, as discussed above, an inflected angular process is not primitive in therians, but is instead a synapomorphy for marsupials. Thus there is little support for Mellett's hypothesis.

The Ontogeny of the Inflected Mandibular Angular Process in Marsupials and the Development of Hearing

Maier (1987, 1990) has discussed the question of the functional significance and origin of the medial inflection of the angular process in marsupials. He suggests that the ontogeny and role of the jaw in marsupial pouch young may explain the evolution of the medial inflection in the angular process in this group. Maier's (1987, 1990) work is notable because it addresses a usually neglected but important topic, the ontogeny of structure-function relations, in this case, sensory perception. Maier (1987, 1990) examined several marsupials but focused on a histological series of early postnatal ages of *Monodelphis domestica*. He recorded the relative position and architecture of the dentary, the ectotympanic, and the otic capsule during the first 4 weeks of development in this taxon. Maier (1987, 1990) found that during development, the dentary is initially quite horizontal, but during the second to fourth weeks of life it reorients from a horizontal to a vertical position. However, a medial projection remains, to form the medially inflected angular process. This angular process retains a very close relation to the ectotympanic bone (Fig. 8). Both Maier's and our work demonstrates that a close association between the angular process of the dentary and the ectotympanic is characteristic of all marsupial taxa examined.

Maier (1987) speculates that the association between the angular process and the ectotympanic represents a specific form–function complex for sound transmission. He proposes that at some time after birth, noises of the body and body vibrations from the mother become transmitted via the mandible to the middle ear of juveniles. This mechanism of sound transmission would occur at a time when the external auditory canal is not yet opened and the auditory ossicles are still purely cartilaginous. Since the publication of Maier's hypothesis considerable information on the maturation of the auditory system in *Monodelphis domestica* has appeared, which allows us to evaluate this hypothesis. The most critical data to test this hypothesis would be evidence that the auditory system is capable of processing sound in the inner ear and brain before the external auditory meatus opens and the ossicles have started ossification. These data are summarized in Table II. There appears to be no brainstem response to sound before PND-29, when the first brainstem auditory evoked potential (BAEP) in *M. domestica* is reported (Reimer, 1996). This physiological measure of the onset of auditory function would give an indication of when this species is ready to perceive sounds. Reimer (1996) found that initially, only very high-intensity signals with frequencies in the lower mid-range of the adult audiogram evoke responses. However, since the high-intensity stimuli that are necessary to evoke the earliest responses are unlikely to occur in the natural environment, it appears that these auditory evoked responses have been elicited before the time an animal would normally use its auditory system (see Cant, 1997). Willard and Munger (cited by Cant, 1997) found that the first responses to airborne sounds (which they established documenting the "acoustic startle reflex") occurred on PND-34. According to Willard and Munger (cited by Cant, 1997), by PND-34 the hair cells in the inner ear are mature, that is, they have obtained their adult cytological characteristics with darkly staining, heterochromatic nuclei.

We think it is unlikely that hearing "through the jaw" could take place in pouch young of *Monodelphis domestica*. Around PND-32 the external auditory meatus has opened, the ear ossicles have ossified, the malleus has detached from Meckel's cartilage

Table II. Timing of Different Events in the Development of *Monodelphis domestica*

Event	Day (PND) ^a	Source
Adult number of turns in cochlea	8	In Cant, 1997
Cartilage on dentary condyle	8	K. Smith, pers. obs.
Tunnel of Corti opens	10	In Cant, 1997
Onset of ossification malleus	11	Clark and Smith, 1993
Onset of ossification incus	17	Clark and Smith, 1993
Mature dentary/squamosal joint	19	K. Smith, pers. obs.
Onset of ossification stapes	25	Clark and Smith, 1993
First BAEP ^b	29	Reimer, 1996
Opening of EAM	32	In Cant, 1997
First "acoustic startle reflex"	34	In Cant, 1997
Alisphenoid tympanic process between angle and ectotympanic	34 ^c	This work

^aPostnatal day.

^bBrainstem auditory evoked potential.

^cThis event might take place sometime between PND-31 and PND-34; it is not observed in PND-30 *Monodelphis domestica*.

(Smith, 1994), and the cavum tympani has fully formed. Therefore by the time the inner ear and central nervous system are capable of responding to auditory stimulus, the adult middle and external ear apparatus is present. A similar correlation between the onset of hearing and the maturation of the external, middle, and inner ear and central nervous system has been reported for *Dasyurus hallucatus* (Aitkin *et al.*, 1996). Although we reject Maier's hearing hypothesis, we have no alternative explanation for the close relation of the angular process to the ectotympanic.

We agree with Maier (1987, 1990, 1993; see also Presley, 1993; Wake and Roth, 1989) on the importance of studying ontogeny in order to explain morphological features and innovations in mammalian evolution. The inflected angular process in marsupials appears to maintain a close relation to the ectotympanic through early ontogeny. The relation between the ectotympanic and the angular process and therefore an inflection of the angular process is present even in pouch young of individuals that lose the inflected angular process as adults (e.g., *Dactylopsila*, *Phascolarctos*). This constancy supports Maier's hypothesis that the explanation for the presence of an inflected angular process may lie in, as yet unexamined, developmental processes.

Conclusions

To conclude, we hypothesize that a medially inflected angular process is a marsupial synapomorphy. No placental mammal possesses a true medial inflection (nor does *Vincelestes*), but such an inflection is found in virtually all marsupials, including those known only as fossils. The few extant marsupials that lack an inflected angular process appear to have lost it secondarily, and most that do not have one as adults do have a medial inflection in the angular process as pouch young. There are two distinct issues in understanding the medial inflection. The first concerns the existence of such an inflection. We see no evidence of consistent differences between muscle morphology and chewing mechanisms to distinguish marsupials and placentals. Therefore no obvious aspect of masticatory function explains this difference. It is possible that the reason for the difference relates to ontogeny, although, again, the functional basis for a close association between the angular process and the ectotympanic is obscure. The biggest obstacle to formulating an explanation for the evolution of an inflected angular process in marsupials may be that it was a unique historical event; therefore it is impossible to test hypotheses using the comparative method as outlined by Kay and Cartmill (1977).

The second major issue is the variation in form of the angular process among extant marsupials. Here we show that the form is related in a general way to diet, with herbivorous marsupials possessing expanded areas for attachment of the medial pterygoid and masseter muscles on the angular process. Phylogeny and size also appear to be important in determining the patterns of variation of form. However, as size, diet, and phylogeny all are interrelated, it is likely that the explanation for the variation observed in extant marsupials is a complex mix of all these factors.

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LITERATURE CITED

- Abbie, A. A. (1939). A masticatory adaptation peculiar to some diprotodont marsupials. *Proc. Zool. Soc. London* **B109**: 261-279.
- Aitkin, L., Nelson, J., Martsi-McClintock, A., and Swann, S. (1996). Features of the structural development of the inferior colliculus in relation to the onset of hearing in a marsupial: The northern quoll, *Dasyurus hallucatus*. *J. Comp. Neurol.* **375**: 77-88.
- Archer, M. (1984). Origins and early radiations of marsupials. In: *Vertebrate Zoogeography and Evolution in Australasia*, M. Archer and G. Clayton, eds., pp. 585-624, Hesperian Press, Perth.
- Archer, M., Hand, S., and Godthelp, H. (1988). A new order of Tertiary zalambdodont marsupials. *Science* **239**: 1528-1531.
- Archer, M., Hand, S. J., and Godthelp, H. (1991). *Riversleigh. The Story of Animals in Ancient Rainforests of Inland Australia*, Reed Books, New South Wales.
- Atchley, W. R. (1993). Genetic and developmental aspects of variability in the mammalian mandible. In: *The Skull, Vol. 1*, J. Hanken and B. K. Hall, eds., pp. 207-247, University of Chicago Press, Chicago.
- Atchley, W. R., and Hall, B. K. (1991). A model for development and evolution of complex morphological structures. *Biol. Rev.* **66**: 101-157.
- Avis, V. (1961). The significance of the angle of the mandible: An experimental and comparative study. *Am. J. Phys. Anthropol.* **19**: 55-61.
- Barbour, R. A. (1963). The musculature and limb plexuses of *Trichosurus vulpecula*. *Aust. J. Zool.* **11**: 488-610.
- Baverstock, P. R., Richardson, B. J., Birrell, J., and Krieg, M. (1989). Albumin immunologic relationships of the Macropodidae (Marsupialia). *Syst. Zool.* **38**: 38-50.
- Cant, N. B. (1997). Structural development of the mammalian auditory pathways. In: *Development of the Auditory System*, E. Rubel, R. Fay, and A. Popper, eds., Springer-Verlag, New York (in press).
- Carroll, R. L. (1988). *Vertebrate Paleontology and Evolution*, W. H. Freeman, New York.
- Cifelli, R. L. (1993a). Early Cretaceous mammal from North America and the evolution of marsupial dental characters. *Proc. Natl. Acad. Sci. USA* **90**: 9413-9416.
- Cifelli, R. L. (1993b). Theria of metatherian-eutherian grade and the origin of marsupials. In: *Mammal Phylogeny. Mesozoic Differentiation. Multituberculates, Monotremes, Early Therians and Marsupials*, F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds., pp. 205-215, Springer-Verlag, New York.
- Clark, C. T., and Smith, K. K. (1993). Cranial osteogenesis in *Monodelphis domestica* (Didelphidae) and *Macropus eugenii* (Macropodidae). *J. Morphol.* **215**: 119-149.
- Clemens, W. A., and Kielan-Jaworowska, Z. (1979). Multituberculata. In: *Mesozoic Mammals. The First Two Thirds of Mammalian History*, J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds., pp. 99-149, University of California Press, Berkeley.
- Crompton, A. W. (1971). The origin of the tribosphenic molar: In: *Early Mammals*, Kermack, D. M., and Kermack, K. A., eds., *Zool. J. Linn. Soc.* **50** (Suppl. 1): 65-87.
- Crompton, A. W., and Hiiemae, K. (1970). Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. *Zool. J. Linn. Soc.* **49**: 21-47.
- Crompton, A. W., and Hylander, W. L. (1986). Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. In: *The Ecology and Biology of Mammal-like Reptiles*, N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth, eds., pp. 263-281, Smithsonian Institution Press, Washington, DC.

- Crompton, A. W., and Parker, P. (1978). Evolution of the mammalian masticatory apparatus. *Am. Sci.* **66**: 192–201.
- Crompton, A. W., Thexton, A. J., Parker, P., and Hiemae, K. (1977). The activity of the jaw and hyoid musculature in the Virginia opossum, *Didelphis virginiana*. In: *The Biology of Marsupials*, B. Stonehouse and D. Gilmore, eds., pp. 287–305, Macmillan, London.
- Darwin, C. (1859). *The Origin of Species*, John Murray, London.
- Dashzeveg, D., and Kielan-Jaworowska, Z. (1984). The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. *Zool. J. Linn. Soc.* **82**: 217–227.
- Davison, C. V., and Young, W. G. (1990). The muscles of mastication of *Phascolarctos cinereus* (Phascolarctidae: Marsupialia). *Aust. J. Zool.* **38**: 227–240.
- Ellis, W. A. H., Melzer, A., Green, B., Newgrain, K., Hindell, M. A., and Carrick, F. N. (1995). Seasonal variation in water flux, field metabolic rate and food consumption of free-ranging koalas (*Phascolarctos cinereus*). *Aust. J. Zool.* **43**: 59–68.
- Emmons, L. H., and Feer, F. (1990). *Neotropical Rainforest Mammals, A Field Guide*, University of Chicago, Chicago.
- Filan, S. L. (1990). Myology of the head and neck of the bandicoot (Marsupialia: Peramelemorphia). *Aust. J. Zool.* **38**: 617–634.
- Flannery, T. (1987). The relationships of the macropodoids (Marsupialia) and the polarity of some morphological features within the Phalangeriformes. In: *Possums and Opossums: Studies in Evolution*, M. Archer, ed., pp. 741–747, Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney.
- Flannery, T. F. (1989). Phylogeny of the Macropodidae; A study in convergence. In: *Kangaroos, Wallabies and Rat-Kangaroos*, G. Grigg, P. Jarman, and I. Hume, eds., pp. 1–46, Beatty & Sons Pty Ltd., New South Wales.
- Flannery, T. F. (1990). *Mammals of New Guinea*, Robert Brown & Associates, Carina, Queensland.
- Flannery, T. (1995). *Mammals of the South-West Pacific & Moluccan Islands*, Comstock/Cornell, Ithaca, NY.
- Flower, W. H. (1885). *An Introduction to the Osteology of the Mammalia*, MacMillan, London.
- Gambaryan, P. P., and Kielan-Jaworowska, Z. (1995). Masticatory musculature of Asian taeniolabidoid multituberculate mammals. *Acta Palaeontol. Pol.* **40**: 45–108.
- Goin, F. J. (1997). New clues for understanding Neogene marsupial radiations. In: *Vertebrate Paleontology in the Neotropics*, R. F. Kay, R. Cifelli, R. H. Madden, and J. Flynn, eds., pp. 185–204, Smithsonian Institution Press, Washington, DC.
- Herring, S. W. (1985). The ontogeny of mammalian mastication. *Am. Zool.* **25**: 339–349.
- Hiemäe, K., and Jenkins, F. A., Jr. (1969). The anatomy and internal architecture of the muscles of mastication in *Didelphis marsupialis*. *Postilla* **140**: 1–49.
- Howell, A. B. (1932). The saltatorial rodent *Dipodomys*: The functional and comparative anatomy of its muscular and osseous systems. *Proc. Am. Acad. Arts Sci.* **67**: 377–536.
- Kay, R. F. (1984). On the use of anatomical features to infer foraging behavior in extinct primates. In: *Adaptations for Foraging in Nonhuman Primates*, P. S. Rodman and J. G. H. Cant, eds., pp. 21–53, Columbia University Press, New York.
- Kay, R. F., and Cartmill, M. (1977). Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. *J. Hum. Evol.* **6**: 19–53.
- Kay, R. F., and Hiemae, K. M. (1974). Jaw movement and tooth use in recent and fossil primates. *Am. J. Phys. Anthropol.* **40**: 227–56.
- Kielan-Jaworowska, Z. (1975). Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. *Paleontol. Pol.* **33**: 5–15.
- Kielan-Jaworowska, Z., and Nessov, L. A. (1990). On the metatherian nature of the Deltatheroidea, a sister group of the Marsupialia. *Lethaia* **23**: 1–10.
- Kirsch, J. A. W., and Palma, R. E. (1995). DNA/DNA hybridization studies of carnivorous marsupials. V. A further estimate of relationships among opossums (Marsupialia: Didelphidae). *Mammalia* **59**: 403–425.
- Kirsch, J. A. W., Krajewski, C., Springer, M. S., and Archer, M. (1990a). DNA-DNA hybridisation studies of carnivorous marsupials II. Relationships among dasyurids (Marsupialia: Dasyuridae). *Aust. J. Zool.* **38**: 673–696.
- Kirsch, J. A. W., Springer, M. S., Krajewski, C., Archer, M., Aplin, K., and Dickerman, A. W. (1990b). DNA-DNA hybridisation studies of carnivorous marsupials I. The intergeneric relationships of bandicoots (Marsupialia: Perameleidae). *J. Mol. Evol.* **30**: 434–448.
- Kirsch, J. A. W., Lapointe, F.-J., and Springer, M. S. (1997). DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Aust. J. Zool.* (in press).
- Krajewski, C., Painter, J., Buckley, L., and Westerman, M. (1994). Phylogenetic structure of the marsupial family Dasyuridae based on cytochrome b DNA sequences. *J. Mammal. Evol.* **2**: 25–34.

- Krause, D. W. (1982). Jaw movement, dental function, and diet in the Paleocene multituberculate *Prilodus*. *Paleobiology* **8**: 265–281.
- Kuhn, H.-J. (1971). Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. *Abh. Senckenberg. Naturforsch. Ges.* **528**: 1–224.
- Lee, A. K., and Cockburn, A. (1985). *Evolutionary Ecology of Marsupials*, Cambridge University Press, Cambridge.
- Lillegraven, J. A. (1969). Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *Univ. Kansas Paleontol. Contrib.* **50**: 1–122.
- Lillegraven, J. A., Kielan-Jaworowska, Z., and Clemens, W. A. (1979). *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, University of California Press, Berkeley.
- Luckett, W. P. (1994). Suprafamilial relationships within Marsupialia: Resolution and discordance from multidisciplinary data. *J. Mammal. Evol.* **2**: 255–283.
- MacDonald, D. (ed.). (1984). *The Encyclopaedia of Mammals*, Facts on File, New York.
- MacPhee, R. D. E. (1981). Auditory regions of primates and eutherian insectivores: Morphology, ontogeny and character analysis. *Contrib. Primatol.* **18**: 1–282.
- Maier, W. (1978). Die Evolution der tribosphenischen Säugetiermolaren. *Sonderb. Naturw. Ver. Hamburg* **3**: 41–60.
- Maier, W. (1987). Der Processus angularis bei *Monodelphis domestica* (Didelphidae: Marsupialia) und seine Beziehungen zum Mittelohr: Eine ontogenetische und evolutionsmorphologische Untersuchung. *Gegenbaurs morphol. Jahrb.* **133**: 123–161.
- Maier, W. (1989). Morphologische Untersuchungen am Mittelohr der Marsupialia. *Z. zool. Syst. Evolut.-forsch.* **27**: 149–168.
- Maier, W. (1990). Phylogeny and ontogeny of mammalian middle ear structures. *Netherl. J. Zool.* **40**: 55–74.
- Maier, W. (1993). Cranial morphology of the therian common ancestor, as suggested by the adaptations of neonate marsupials. In: *Mammal Phylogeny. Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*, F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds., pp. 165–181, Springer-Verlag, New York.
- Marshall, L. G. (1978). *Dromictops australis*. *Mammal. Species* **99**: 1–5.
- Marshall, L. G. (1979). Evolution of metatherian and eutherian (mammalian) characters: A review based on cladistic methodology. *Zool. J. Linn. Soc.* **66**: 369–410.
- Marshall, L. G., and Kielan-Jaworowska, Z. (1992). Relationships of the dog-like marsupials, deltatheroidans and early tribosphenic mammals. *Lethaia* **25**: 361–374.
- Marshall, L. G., and Muizon, C. de (1995). Part II: The Skull. In: *Pucadelphys andinus* (Marsupialia, Mammalia) from the Early Paleocene of Bolivia, C. de Muizon, ed., *Mém. Mus. natn. Hist. nat. Paris* **165**: 21–90.
- Mellet, J. S. (1980). Function of the inflected mandibular angle in marsupials. Abstracts of papers and posters. Sixtieth annual meeting American Society of Mammalogists.
- Mellet, J. S., and Szalay, F. S. (1968). *Kennatherium shirensis* (Mammalia, Palaeoryctoidea), a new didymoconid from the Eocene of Asia. *Am. Mus. Novitates* **2342**: 1–7.
- Miao, D. (1988). Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata) and its implications to mammalian evolution. *Contrib. Geol. Univ. Wyo. Spec. Paper* **4**: 1–104.
- Murray, P., Wells, R., and Plane, M. (1987). The cranium of the Miocene thylacoleonid, *Wakaleo vanderleuri*: Click go to shears—a fresh bite at thylacoleonid systematics. In: *Possums and Opossums—Studies in Evolution*, M. Archer, ed., pp. 433–466, Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney.
- Nikolai, J. C., and Bramble, D. M. (1983). Morphological structure and function in desert heteromyid rodents. *Great Basin Nat. Mem.* **7**: 44–64.
- Norbury, G. L., Sanson, G. D., and Lee, A. K. (1989). Feeding ecology of the Macropodoidea. In: *Kangaroos, Wallabies, and Rat-kangaroos*, G. Grigg, P. Jarman, and I. Hume, eds., pp. 169–178, Surrey Beatty & Sons Pty. Ltd., New South Wales.
- Novacek, M. J. (1986). The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* **183**: 1–112.
- Novacek, M. J. (1995). New therian mammals from the Cretaceous of Mongolia. *J. Vert. Paleontol.* **15**: 46A.
- Novacek, M. J., Norell, M. A., Dingus, L., and Dashzeveg, D. (1996). Dinosaurs, mammals, birds, and lizards from the Late Cretaceous Ukhaa Tolgod Fauna, Mongolia. *J. Vert. Paleontol.* **16**: 56A.
- Nowak, R. M. (1991). *Walker's Mammals of the World*, The John Hopkins University Press, Baltimore.
- O'Connell, M. (1983). *Marmosa robinsoni*. *Mammal. Species* **203**: 1–6.
- Oron, U., and Crompton, A. W. (1985). A cineradiographic and electromyographic study of mastication in *Tenrec ecaudatus*. *J. Morphol.* **185**: 155–182.

- Osborn, D. J., and Helmy, I. (1980). The contemporary land mammals of Egypt (including Sinai). *Fieldiana Zool.* 1-579.
- Osgood, W. H. (1921). A monographic study of the American marsupial, *Caenolestes*. *Publ. Field Mus. Nat. Hist. Zool. Ser.* 14: 1-156.
- Parker, P. J. (1977). *Aspects of the Biology of Bettongia penicillata*, Ph.D. dissertation, Yale University, New Haven, CT.
- Pascual, R., Goin, F. J., and Carlini, A. A. (1994). New data on the Groeberiidae: Unique late Eocene-early Oligocene South American marsupials. *J. Vert. Paleontol.* 14: 247-259.
- Paula Couto, C. d. (1952). Fossil mammals from the beginning of the Cenozoic of Brazil. Marsupialia: Polydolopidae and Borhyaenidae. *Am. Mus. Novitates* 1559: 1-27.
- Pérez-Hernández, R., Soriano, P., and Lew, D. (1994). *Marsupiales de Venezuela*, Cuadernos Lagoven, Caracas.
- Presley, R. (1993). Development and the phylogenetic features of the middle ear region. In: *Mammal Phylogeny. Mesozoic Differentiation. Multituberculates, Monotremes, Early Therians and Marsupials*, F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds., pp. 21-29, Springer-Verlag, New York.
- Radinsky, L. (1985). Patterns in the evolution of ungulate jaw shape. *Am. Zool.* 25: 303-314.
- Reig, O. A., and Simpson, G. G. (1972). *Sparassocynus* (Marsupialia, Didelphidae), a peculiar mammal from the late Cenozoic of Argentina. *J. Zool. Lond.* 167: 511-539.
- Reimer, K. (1996). Ontogeny of hearing in the marsupial, *Monodelphis domestica*, as revealed by brainstem auditory evoked potentials. *Hear. Res.* 92: 143-150.
- Ride, W. D. L. (1959). Mastication and taxonomy in the macropodine skull. *Syst. Ass. Publ.* 3: 33-59.
- Rosenberg, H. I., and Richardson, K. C. (1995). Cephalic morphology of the honey possum, *Tarsipes rostratus* (Marsupialia: Tarsipedidae); An obligate nectarivore. *J. Morphol.* 223: 303-323.
- Rougier, G. W. (1993). *Vincelestes neuquenianus Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina*, Tesis doctoral, Universidad Nacional de Buenos Aires, Buenos Aires.
- Rougier, G. W., Wible, J. R., and Hopson, J. A. (1996). Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. *Am. Mus. Novitates* 3183: 1-38.
- Saban, R. (1968). Musculature de la tête. In: *Traité de Zoologie*, P.-P. Grassé, ed., pp. 229-471, Masson et Cie Éditeurs, Paris.
- Sánchez-Villagra, M. R., and Kay, R. F. (1995). A skull of *Proargyrolagus*, the oldest argyrolagid (early Miocene Salla Beds, Bolivia). *J. Vert. Paleontol.* 15: 51A-52A.
- Sánchez-Villagra, M. R., and Kay, R. F. (1997). A skull of *Proargyrolagus*, the oldest argyrolagid (Late Oligocene Salla Beds, Bolivia), with brief comments concerning its paleobiology. *J. Vert. Paleontol.* (in press).
- Schumacher, G. H. (1961). *Funktionelle Morphologie der Kaumuskulatur*. Veb, Gustav Fischer Verlag, Jena.
- Seebeck, J. H., Bennett, A. F., and Scotts, D. J. (1989). Ecology of the Potoroidae—A review. In: *Kangaroos, Wallabies and Rat-Kangaroos*, G. Grigg, P. Jarman, and I. Hume, eds., pp. 67-88, Surrey Beatty & Sons Pty. Ltd., New South Wales.
- Simpson, G. G. (1926). Mesozoic Mammalia. IV. The multituberculates as living animals. *Am. J. Sci.* XI: 228-250.
- Simpson, G. G. (1970). The Argyrolagidae, extinct South American marsupials. *Bull. Mus. Comp. Zool.* 139: 1-86.
- Smith, A., and Hume, I. (eds.) (1984). *Possums and Gliders*, Australian Mammal Society, Sydney.
- Smith, K. K. (1994). Development of craniofacial musculature in *Monodelphis domestica* (Marsupialia, Didelphidae). *J. Morphol.* 222: 149-173.
- Springer, M. S., Kirsch, J. A. W., Aplin, K., and Flannery, T. (1990). DNA hybridization, cladistics, and the phylogeny of phalangerid marsupials. *J. Mol. Evol.* 30: 298-311.
- Springer, M. S., McKay, G., Aplin, K. and Kirsch, J. A. W. (1992). Relationships among ringtail possums (Marsupialia: Pseudocheiridae) based on DNA-DNA hybridisation. *Aust. J. Zool.* 40: 423-435.
- Springer, M. S., Westerman, M., and Kirsch, J. A. W. (1994). Relationships among orders and families of marsupials based on 12S ribosomal DNA sequences and the timing of the marsupial radiation. *J. Mammal. Evol.* 2: 85-115.
- Strahan, R., (ed). (1995). *Mammals of Australia*, Smithsonian Institution Press, Washington, DC.
- Szalay, F. S. (1994). *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*, Cambridge University Press, New York.
- Szalay, F. S., and Trofimov, B. A. (1996). The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *J. Vert. Paleontol.* 16: 474-509.
- Tate, G. H. H. (1948). Results of the Archbold Expeditions No. 59. Studies on the anatomy and phylogeny of the Macropodidae (Marsupialia). *Bull. Am. Mus. Nat. Hist.* 91: 233-352.
- Tedford, R. H., and Woodburne, M. O. (1987). The Ilariidae, a new family of vombatiform marsupials from

- the Miocene strata of South Australia and an evaluation of the homology of molar cusps in the Diprotodontia. In: *Possums and Opossums: Studies in Evolution*, M. Archer, ed., pp. 401–18, Surrey Beatty and Sons and the Royal Zoological Society of New South Wales, Sydney.
- Thomas, O. (1888). *Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum*, British Museum, Nat. Hist., London.
- Thompson, S. D. (1987). Body size, duration of parental care, and the intrinsic rate of natural increase in eutherian and metatherian mammals. *Oecologia* **71**: 201–209.
- Turnbull, W. D. (1970). Mammalian masticatory apparatus. *Fieldiana Geol.* **18**: 149–356.
- Tyndale-Biscoe, H., and Renfree, M. (1987). *Reproductive Physiology of Marsupials*, Cambridge University Press, Cambridge.
- von Koenigswald, W., and Storch, G. (1992). The marsupials: Inconspicuous opossums. In: *Messel. An Insight into the History of Life and of the Earth*, S. Schaal and W. Ziegler, eds., pp. 155–158, Clarendon Press, Oxford.
- Wake, D. B., and Roth, G. (1989). The linkage between ontogeny and phylogeny in the evolution of complex systems. In: *Complex Organismal Functions: Integration and Evolution in Vertebrates*, D. B. Wake and G. Roth, eds., pp. 361–377, Wiley, Chichester.
- Wall, C. E., and Krause, D. W. (1992). A biomechanical analysis of the masticatory apparatus of *Prilodus* (Multituberculata). *J. Vert. Paleontol.* **12**: 172–187.
- Wilson, D. E., and Reeder, D. M., (eds.) (1993). *Mammal Species of the World*, 2nd ed., Smithsonian Institution Press, Washington, DC.
- Winge, H. (1941). *The Interrelationships of the Mammalian Genera. Vol 1. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata*, C. A. Reitzels Forlag, Copenhagen.
- Wood Jones, F. (1923). *The Mammals of South Australia. Part I. The Monotremes and the Carnivorous Marsupials*, E. E. Rogers, Adelaide.
- Zeller, U. (1989). Die Entwicklung und Morphologie des Schädels von *Ornitorhynchus anatinus* (Mammalia: Prototheria: Monotremata). *Abh. Senckenberg. Naturforsch. Ges.* **545**: 1–156.