

ORIGINAL ARTICLE

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Anatomy and development of the koala, *Phascolarctos cinereus*: an evolutionary perspective on the superfamily Vombatoidea

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Abstract Fifteen koalas (*Phascolarctos cinereus*) – 5 pouched young from 4 to 6.5 months and 10 adults from 5 to 16.5 years – were analyzed for functional parameters (body composition, limb segment and muscle mass, post-cranial skeletal characters) and developmental expressions (growth of body, brain, musculature). These data were compared with a convergent eutherian, the three-toed sloth, *Bradypus infuscatus*, and with the koala's distant (Macropodid; wallabies) and proximate (Vombatid; wombats) marsupial relatives. Musculoskeletal structures correlated with sitting and climbing; the growth of the young and the physiological demands of adulthood correlated with the low-quality diet of *Eucalyptus* foliage. The gestalt of the ancestral Vombatoids (pronograde quadrupeds, generalist browsers and social conservatives with low basal metabolism and attenuated development) provided the baseline essential for their locomotor and nutritional divergence into arboreal browsers, the koalas, and fossorial grazers, the wombats.

Keywords Locomotor anatomy · Life history · Lactation energetics · Brain and muscle growth · Wombats

Introduction

“With so many components contributing to the functioning biological system, it is for the working scientist a matter of strategy and interest to decide the study of which level would make the greatest contribution toward the full understanding of the system” (Mayr 1988, on ‘constitutive hierarchies’).

The koala, *Phascolarctos cinereus*, is an ideal subject for the holistic approach to multiple levels of adaptation. The complexity of its biology is reflected in four distinct but integrated themes: the functional anatomy of sitting

and climbing; the effects of *Eucalyptus* herbivory on maintenance metabolism; the patterns of growth and reproduction on a reduced energy and nutrient budget; and their evolutionary relationship to the other vombatoid marsupials, the wombats.

Functional anatomy

Despite numerous studies of gross structure (Forbes 1881; Young 1882; Mackenzie 1918a, b; Sonntag 1921, 1922; Flower 1966; reviewed Lessertisseur and Saban 1967), virtually no correlations have been made between muscles, bones, joints and locomotor repertoire. What attributes permit the koala to sit, climb, and feed among branch terminals barely large enough to support it? The koala also scampers substantial distances across open ground to travel between stands of trees. Adults have been reported to disperse up to 11 km and “one male...dispersed 48 km and another 29 km within 12 months...these long-distance movements...covered areas of unsuitable and often treeless habitat” (Martin 1985, pp 383–384). What is the “goodness of fit” between musculoskeletal form and total motor function?

Dietary preference, the driving force in their arboreality, resulted in a second cascade of structural modifications that include massive jaws and powerful masticatory muscles, sharp cutting molars, and an enormous cecum (Lee and Carrick 1989).

Eucalyptus herbivory

The *Eucalyptus* leaf itself, however, is the central problem – a low energy resource whose oils are toxic to some herbivores. The koala is by far the largest (4–15 kg) and most obligate of *Eucalyptus* consumers (Hindell and Lee 1990). It appears to select those leaves with more than 55% moisture, at least 2% essential oils, and a high proportion of nitrogen in relation to tannins and fiber (Hume and Esson 1993). The energy and nutrients available

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from this diet are limited by plant defenses, e.g., tannins, oils, lignin (Freeland and Janzen 1974; Foley et al. 1999) and the volume of fiber to be chewed, digested, and excreted. Thus, digestive efficiency constrains body size toward some lower limit; arboreal climbing acts upon some ill-defined upper limit. Water demand, against the backdrop of Australia's increasing aridity, is a third operative variable.

Growth and reproduction

The mother-young pair is the fundamental unit of social life and the object of intense selection. Within this dyad energy conservation is evident through the transfer of maternal nutrients and the growth demands of the joey. "Koalas had the lowest mass-specific daily milk-energy production at peak lactation so far recorded in a mammal, but the duration of reproduction was 58% longer than the combined marsupial and eutherian average...The prolonged lactation and low daily rate of energy transfer to the young by female koalas is an adaptation to...low energy availability...Energy requirements (field metabolic rates) of young koalas were lower than those expected for typical marsupials (only 60% at permanent pouch exit), which may be a necessary preadaptation that allows the low rate of maternal energy transfer" (Krockenberger 1998, p 45). What are the effects of dietary energy on brain and muscle growth, two of the body's most energy-expensive tissue systems? How do these patterns of development correlate with the joey's departure from the pouch at 7-8 months and physical independence from mother at 11 months?

Evolutionary relationship

The kinship of koala and wombats is suggested by a range of similarities: molecular data; microstructure of the head of the sperm; structure of the dentition; the presence of cheek pouches; a concentrated secretory patch on the stomach known as the cardio-gastric gland; a posteriorly directed marsupium; a vestigial tail; reduced supratragus (of the ear); adherence of the pericardium to the diaphragm; a distinct ossific nucleus in the inferior arch of the atlas (C1; Flower 1966; Lee and Carrick 1989). On the one hand, these characters in isolation offer no insight into adaptation or evolution. On the other hand, the fully isomorphic correspondence between the two species permits a coherent reconstruction of the vombatoid radiation. The ancestral gestalt is one of metabolic endurance and behavioral conservatism. The derived traits, largely post-cranial, correlate directly with physical habitat and diet; that is, trees and foliage for koalas, burrows and grasses for wombats.

The koala is compared and contrasted with species at varied phylogenetic distance: the convergent three-toed sloth, *Bradypus infuscatus*; the evolutionarily divergent common wombat, *Vombatus ursinus*; and as the locomo-

tor outgroup, Bennett's wallaby, *Macropus rufogriseus*. The anatomical methods were developed through studies of primates (Grand 1977), rodents and edentates (Grand 1978), didelphids (Grand 1983), macropodids (Grand 1990), and East African bovids (Grand 1997). Neural and musculoskeletal growth of the joey shed light on the effects of nutrient specialization.

Interpretations of faunal and floral evolution in Australia have been dominated by Old and New World models: American opossums with Australian possums, horses with kangaroos, European parklands (trees intermixed with grasses) with arid *Eucalyptus* woodlands. The koala was even called the New Holland sloth. At last, a cognitive revolution has emancipated the marsupials in general (Flannery 1998) and, as we will argue, the koalas in particular.

Materials and methods

The sample

During an 18 month period in 1993-1994 twelve koalas were euthanized at the San Diego Zoo (SDZ) for medical reasons. Three more adults were euthanized during 1995. The acute disease processes resulted in rather brief illness and thus, neither musculature nor other tissues were atrophied. Carcasses were frozen after post-mortem exam and shipped to the National Zoological Park (NZIP) for dissection (Appendix I). Wombat skeletons were obtained from the National Museum of Natural History (NMNH). Photos and radiographs of the post-cranial skeleton were taken of two representatives: a 10 year old male koala (7.3 kg, crown-rump length of 53 cm, ID 1652) and an adult female common wombat (unknown mass, but crown-rump of 94.0 cm, USNM 521059).

Analysis of the developing joey depends upon a careful estimation of conceptual age. Since a mother may have a young for several weeks before pouch distension is visible, each adult female's pouch was examined on a regular basis.

Dissection methods

Body composition was evaluated directly. The major tissues and organs (skin, muscle, skeleton, brain) were dissected and weighed (Appendix I). Each quantity, divided by body mass, gave its percentage of total body mass (%TBM). In order to quantify regional distribution the muscles were removed singly or in small groups and weighed. Muscles of the shoulder were included with the 'forelimb' category, those of the hip with the 'hindlimb.' The (dorsal) extensors of the back were removed along defined planes (see below). Two further categories, 'masticatory' and 'other' (obliques, intercostals, ventral flexors of the vertebrae), were dissected away individually and weighed (Appendix II). The sum of all groups equaled total muscle mass (TMM); the division of this quantity into each category gave a regional picture in %TMM. The back extensors were sectioned transversely at the following levels: nuchal crest, C7, Th8, L1, S1 (Appendix II). Each group, divided by the total back musculature (TBkM), gave their percentages along the entire vertebral column.

On the other side of the body the limb segments were disconnected along the major joint planes (shoulder, elbow, wrist, hip, knee, ankle). The weight of each segment, divided by total body mass, helped to quantify overall shape (limb proportions and mass) and to locate the center of gravity. The head was indirectly calculated, the sum of the individual weights of the skull and mandible, eyes, brain, masticatory muscles, and skin (Appendix I). Although the same side of the body was not selected in every dissection, bodily symmetries were confirmed periodically by compar-

ing the right and left side weights of muscles, muscle groups, and long bones.

Comparative methods

The koala is a "peak of adaptation," with neither extant relatives nor an adequate fossil record by which to reconstruct its ascent up Mount Improbable (Dawkins 1996). Other species, therefore, were chosen to cast their light and shadow upon it: **A** The three-toed sloth, *B. infuscatus*, is the perfect convergent – a tail-less deliberate climber of similar mass, an arboreal browser of relatively low basal metabolism. These similitudes in the sloth (of size, locomotor pattern, diet, etc.) 'stabilize' the less familiar koala because the perception of similarity is arguably less complex than that of difference (Inhelder and Piaget 1964; Arnheim 1971). **B** The wombats, *V. ursinus* and *Lasiorninus sp.*, massive fossorial grazers, are the closest living relatives of koala and the effects of this kinship were extraordinary. The 100% isomorphic correspondence between the two species means that every trait and characteristic must either be shared and ancestral or derived. Such a framework not only avoids the rigid, closed-end definitions of formal logic – opposites cannot be identical (Langer 1953), but also acknowledges the dynamic history of the species – change involves a continuity between opposites (Cohen 1959). Adaptations can be transformed: a pronograde quadruped can become an orthograde climber or a fossorial digger; a generalist browser can become a specialist browser or a grazer. **C** The Bennett's wallaby, *M. rufogriseus*, a distant diprotodont relative and completely modified for bipedal hopping, functions as the locomotor outgroup. Measures of koalas were compared with other species by one sample *t*-test with Bonferroni's adjustments (Engelman 1998).

Adult koalas were also compared with pouched juveniles. This permitted a cross-sectional evaluation of growth of the body, brain, muscle, and segmental masses. Life stages were compared by ANOVA with body mass or muscle mass as covariates (Wilkinson and Coward 1998). Segmental measures within each group were compared by *t*-test with Bonferroni's adjustments (Engelman 1998).

Results

Adult koala, sloth, wallaby: body composition

Figure 1A; Table 1; Appendix I. The percentage of skin was equal in the adult koala ($15.6 \pm 1.4\%$ TBM) and sloth (15%; $P > 0.1$) and significantly higher than that of wallabies (7% TBM; $P < 0.05$). The percentage of muscle mass in the adult koala ($34\% \pm 4.1\%$ TBM) was higher than that in the sloth (23%; $P < 0.05$; Beebe 1926; Britton and Atkinson 1938; Goffart 1971; Grand 1978) and lower than that in the wallaby (50%; $P < 0.005$). The ratio of muscle to bone in the hindlimb also reflected this spectrum: adult koala (4.2 ± 0.7) were intermediate to the sloth (2; $P < 0.05$) and the wallaby (6; $P < 0.05$).

Regional distribution of muscle mass

Figure 1B; Table 1; Appendix II. In the adult koala muscle mass was evenly distributed between the hindlimb ($33.2 \pm 2.2\%$ TMM) and the forelimb ($32.2 \pm 2.3\%$ TMM; $P > 0.05$). The hindlimb of the sloth carried one-third less muscle than the forelimb. Hindlimb muscle mass in the wallaby was 50% of total muscle mass (TMM), five to six times the mass of the forelimb. The wallaby tail accounted for 5% TMM. The back extensor muscles were lowest in the sloth (7% TMM), highest in the wallaby (22% TMM).

Table 1 Distribution of body mass (g) in adult and juvenile koala (mean \pm sd) compared by ANCOVA

Segment	Adult (n)	Juvenile (n)	Covariate	Life-Stage (P)	Covariate (P)
Age (y)	9.95 \pm 1.27 (9)	0.51 \pm 0.07 (5)			
Body mass	5974.5 \pm 920.36 (10)	285.0 \pm 100 (5)		0.000	
Skin	938.4 \pm 170.8 (10)	47.3 \pm 20.3 (5)	Body mass	n.s.	0.000
Head	358.2 \pm 127.2 (9)	30.5 \pm 5.6 (4)	Body mass	n.s.	0.003
Brain	18.6 \pm 2.3 (7)	7.0 \pm 1.2 (10)	Body mass	n.s.	0.023
Total muscle	1818.3 \pm 361.9 (10)	65.0 \pm 27.0 (5)	Body mass	n.s.	0.005
Hindlimb muscle	301.5 \pm 60.4 (10)	8.8 \pm 4.0 (5)	Total muscle	n.s.	0.000
Back extensors	116.8 \pm 25.5 (10)	4.3 \pm 1.9 (5)	Total muscle	n.s.	0.000
Forelimb muscle	294.4 \pm 62.8 (10)	12.6 \pm 5.4 (5)	Total muscle	n.s.	0.000
Sacral	14.3 \pm 3.4 (10)	0.3 \pm 0.1 (5)	Back extensor muscle	n.s.	0.004
Lumbar	57.1 \pm 13.4 (10)	1.6 \pm 0.8 (5)	Back extensor muscle	n.s.	0.000
Post-4	7.3 \pm 1.6 (10)	0.3 \pm 0.2 (5)	Back extensor muscle	n.s.	0.002
Thoracic	14.7 \pm 2.0 (10)	0.8 \pm 0.3 (5)	Back extensor muscle	0.000	0.000
Cervical	23.4 \pm 0.2 (10)	1.4 \pm 0.5 (5)	Back extensor muscle	0.003	0.000

Back extensor musculature

Figure 1C; Table 1; Appendix II. The cervical muscles were disproportionately large in koala, the lumbar and sacral muscles disproportionate in the wallaby. These differences correlated with regional functions. The head of the koala was larger ($6.1 \pm 1.6\%$ TBM) than that of the wallaby (2% ; $P < 0.05$). In the caudal region the contrast was vestigial versus massive tail.

Adult koala, wombat: skeletal attributes

The appropriate framework by which to describe and interpret bone and joint characters must be based upon the habitual posture of the species (Fig. 2). The trunk of the koala is orthograde, the head postured upon the neck to a degree of forward flexion. By contrast, the head of the wombat is in line with the pronograde trunk. The shoulders of the koala are directed laterad and craniad, those of the wombat forward and downward. The koala's palms and soles face medially (in supination and inversion, respectively), whereas the wombat's palms and soles are plantigrade (in pronation and eversion, respectively).

In resting position the vertebral border of the koala's scapula lies parallel to the spines of the upper thoracic vertebrae (Fig. 3). Since the glenoid cavity is directed laterad and craniad, the scapular spine lies at almost 90° to the vertebral border. The supraspinous fossa is small, the axillary border unremarkable. By contrast, the wom-

Fig. 1 **A** Body composition in the wallaby, sloth, and adult and juvenile koalas for skin and muscle as percentages of total body mass. **B** Regional distribution of muscle in the wallaby, sloth, and adult and juvenile koalas to tail, hindlimb, back extensors, and forelimb as percentages of total muscle mass. **C** Back extensor muscle groups in wallaby, adult and juvenile koalas as percentages of total back extensor muscle mass. Back extensor data unavailable for the sloth; all other data from Grand 1978, 1990; Britton and Atkinson 1938

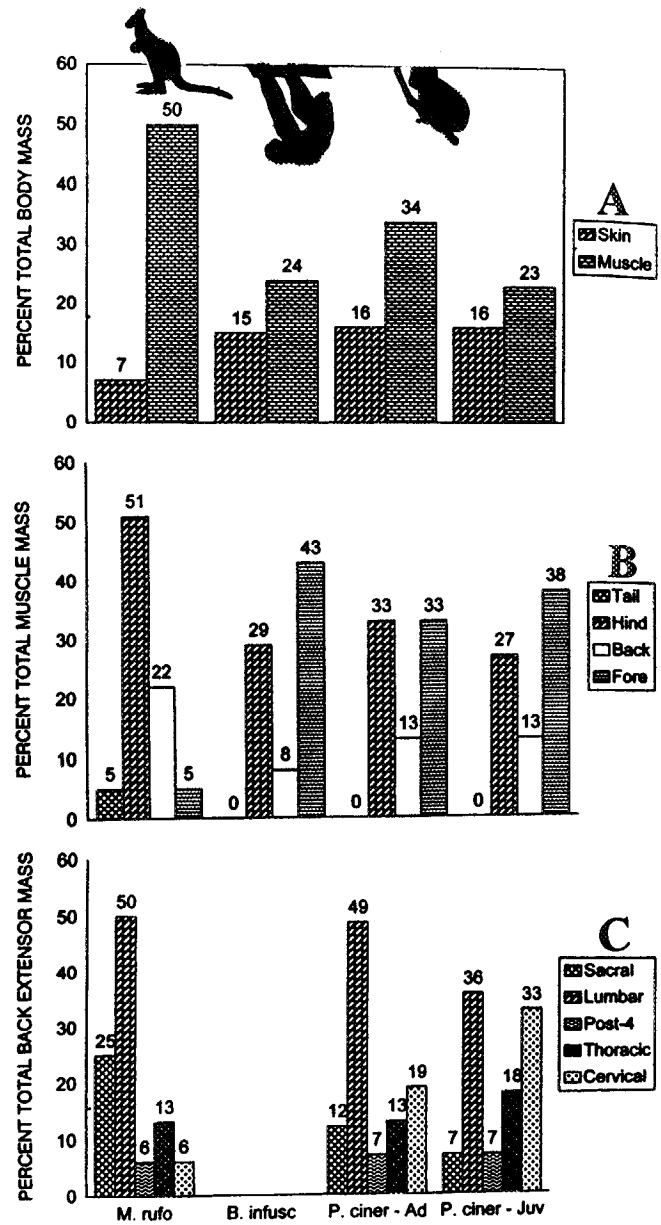
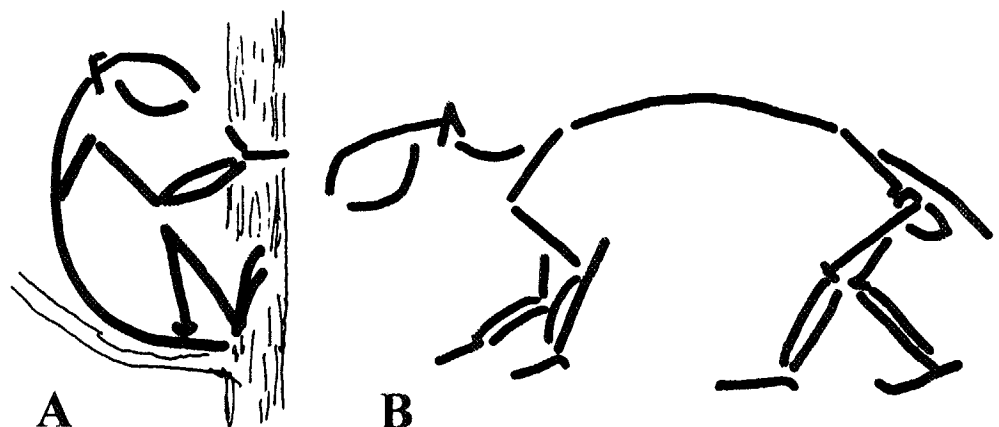


Fig. 2 Habitual body and limb postures in **A** koala and **B** wombat



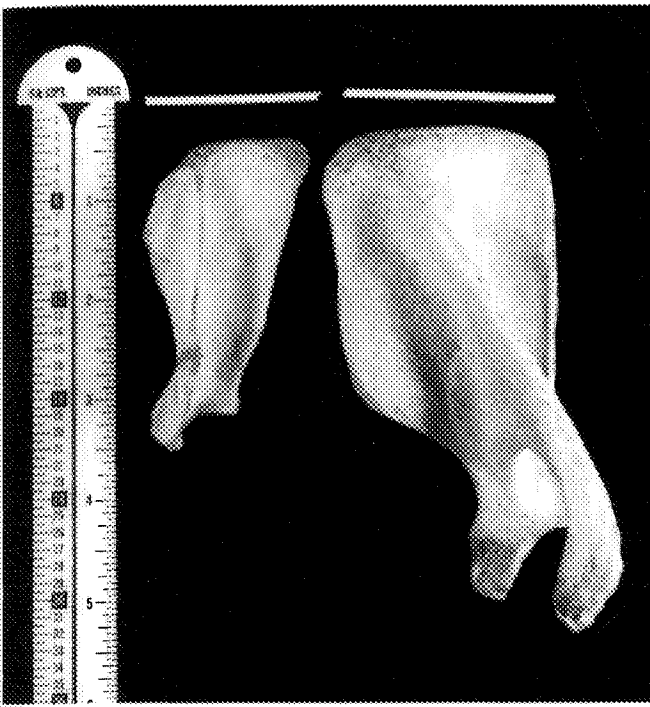


Fig. 3 Left scapulae of koala (left) and wombat (right). Vertebral borders in alignment with the spinous processes of the vertebrae (thick white lines). The marked differences in shape are largely the effect of positional differences in the glenohumeral cavity, the size of the supraspinous fossa, and the angulation of the scapular spine. Animals 1652 for *P. cinereus* and 521059 for *V. ursinus*

bat's scapula is rectangular and thickened overall. The glenoid cavity is directed forward (medially) and the scapular spine lies at 60° to the vertebral border. The supraspinous fossa is large and responsible for this 'shape' difference between the two species. The axillary border is robust.

The correspondence of landmarks between the humeri of koala and wombats is complete: greater tuberosity, deltoid ridge, and supracondylar prominences (Fig. 4). The two, nevertheless, are poles apart morphologically and functionally. The humerus of koala is elongate and slender; the greater and lesser tuberosities and the deltoid ridge are prominent, but not extreme. (The deltoid ridge marks the proximal third of the humerus.) The epicondylar ridges are moderate. The humerus of wombat is compact and robust; the attachments for the rotator cuff and deltoid muscles (greater and lesser tuberosities, deltopectoral ridge) are quite pronounced. The ridge extends to mid-shaft on the humerus. The epicondylar origins of the extensor and flexor muscles of the forearm are enormous. "In the burrowing wombat the humerus is stout, broad at the distal end, and with strongly developed deltoid and supinator ridges" (Flower 1966, p 279).

The limb joints have rotated in opposite directions in the two species. As measured by humeral torsion, from glenohumeral to humero-radio-ulnar joints, the koala elbow rotated internally, the wombat elbow externally. In

the koala the articular surfaces for the radius and ulna are antiflexed (straightened) so that the forearm may achieve full extension; in the wombat these joint surfaces have shifted to face more anteriorly. Relative to body size the koala's radius and ulna are long, the wombat's short (Fig. 5). The olecranon of the koala is abbreviated, that of the wombat robust and, as shown by radiograph, strongly reinforced with compact bone. The deep bow of the koala radius facilitates supination; the wombat radius is compact, so intimately joined to the distal ulna as to restrict supination. (This last conclusion about the wombat comes only from osteo-ligamentous preparations.)

The forepaw or manus is 'forcipate' (Lee and Carrick 1989) or schizodactylus, an axis running through the palm between digits II and III. This functional split is magnified because the metacarpals and phalanges of digits I and II have rotated on their long axes in opposition to those of digits III, IV, and V. These rotations, basically clockwise and counter-clockwise with respect to one another, and the deep crease in the skin facilitate grasping and closure through the palmar axis. The claws, long and curved, help secure the animal to a tree's surface bark. Although no split is evident in the wombat's palm, an illustration by Wells (1989) suggests that claws I and II are also slightly rotated in opposition to claws III, IV, and IV. Since schizodactyly is a character shared by the koalas and phalangers, the rigid palm and enormous claws of the fossorial wombat may hide vestiges of this ancestral pattern.

Koala joeys: size, body composition, and shape

The juvenile koalas in our sample were advanced in development (4 to 6.5 months), that is, toward the end of pouch life (5 to 7 months; Appendix I; Nowak 1991, p 64). Body mass explained most of the variation in segmental masses between juvenile and adult koalas (Table 1). However, the ability to resolve differences between juveniles and adults independent of body mass was weakened by small sample size and the large difference in body mass between the groups.

Muscle constituted only $22.7 \pm 4.1\%$ of total body mass in the juvenile koala (Fig. 1A; Table 1; Appendix I), significantly lower than that of adults ($P < 0.05$). Similarly, the ratio of muscle to bone in the hindlimb of juvenile koalas (2.0 ± 0.4) was lower than that of adults ($P < 0.05$). The head was large, but decreased in relation to body mass from the youngest (20% TBM) to the oldest (9.5% TBM) juvenile. During this window into early development brain mass increased in a linear fashion from 4.9 to 8.4 g (1.28 g/months; $P < 0.05$).

Regional distribution of muscle

The forelimb musculature ($38.4 \pm 2.9\%$ TMM) was disproportionate in comparison with the hindlimb

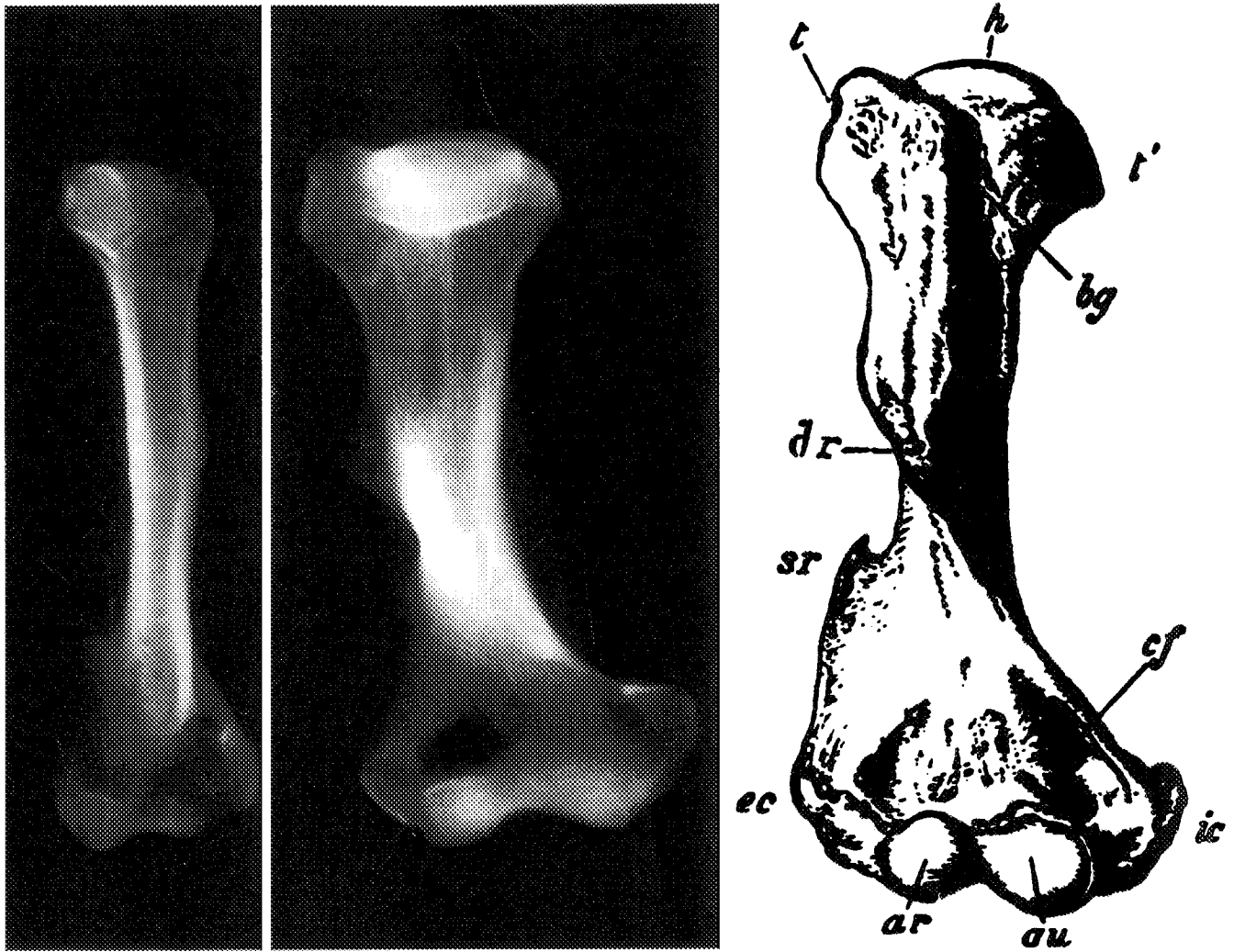


Fig. 4 Radiographs of the right humerus of koala (left) and wombat (center). Wombat humerus (right) from Flower (1966) identifies the isomorphic characters of the two species: *t* and *t'* greater and lesser tuberosities, *bg* bicipital groove, *dr* deltoid ridge, *sr* supinator ridge, *cf* supracondylar foramen, *ec* external and internal epicondyles, respectively, *ar* and *ic* articular surfaces for radius and ulna, respectively. Animals 1652 for *P. cinereus* and 521059 for *V. ursinus*

($26.5 \pm 2.0\%$ TMM) in the juvenile koala (Fig. 1B; Table 1; Appendix II). Although the proportion of total back extensor muscle was similar between juveniles and adults, cervical and thoracic extensors were larger in juveniles ($51.5 \pm 4.3\%$) than those in adults ($32.5 \pm 1.8\%$; Fig. 1C; Table 1; Appendix II).

Discussion

Functional anatomy

The paradigm of form and function correlates attributes of muscles, bones, and joints with the behavioral repertoire of the species. It is implicitly biased towards physi-

cal activity: acrobatic climbing by gibbons to feed among slender branch terminals (Grand 1972); high-speed evasion by various prey species from their usual predators (Howell 1965; Gambaryan 1974); agonistic encounters between male bovids in competition for females (Grand 1997). And whereas this assumption is reasonable, with so lethargic a species as the koala it is important to evaluate the entire spectrum of activities, passive as well as active, peripheral as well as central.

Climbing

The slow, deliberate koalas carry one-third less muscle (34% TBM) than high-speed wallabies (50% TBM), diprotodont relatives of similar mass. Branch resilience dissipates propulsive thrust, hence the reduction of muscle in koala; soil resistance optimizes thrust, hence its increase in virtually all macropodids. This trend was reversed, however, when tree kangaroos (*Dendrolagus*) reinvaded the canopy and their muscular mass decreased to 35% TBM (Grand 1990). Eutherian climbers and high-speed runners and hoppers exhibit a comparable spectrum in muscularity: a low proportion in sloths, lorises and pottos,

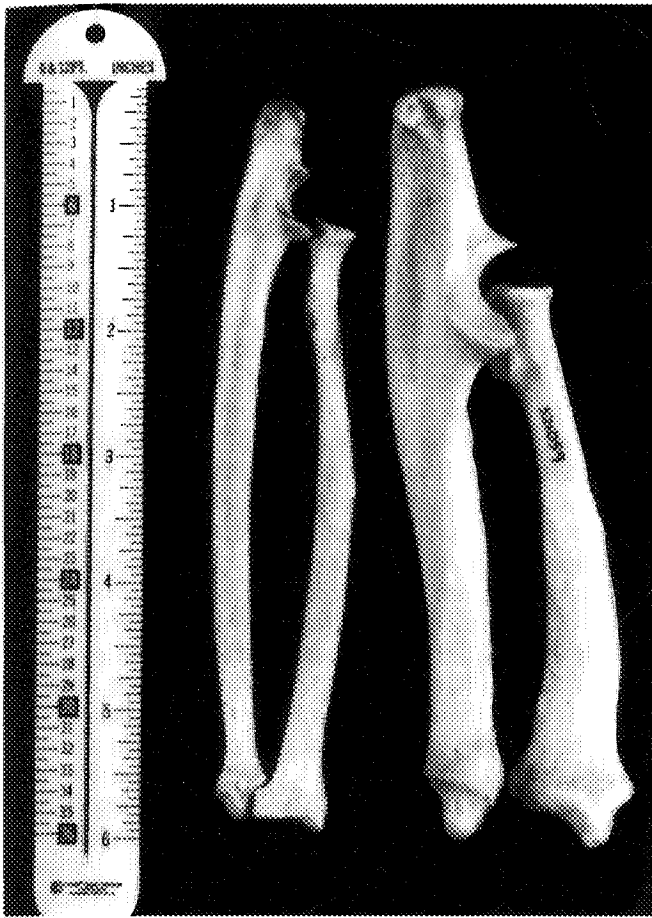


Fig. 5 Left radius and ulna of koala (left) and wombat (right). Animals 1652 for *P. cinereus* and 521059 for *V. ursinus*

red pandas, and prehensile-tailed porcupines (22–34% TBM), a high proportion in Patagonian mara, jackrabbits, greyhounds, and East African bovids (45–50% TBM; Grand 1997). Elevated muscle mass for power output is evident in burrowing aardvarks, moles, and pocket gophers (T.I. Grand, unpublished observations). Similarly, whole-body protein turnover reflects the large pool of muscle in wombats (Barboza et al. 1993).

Muscle in the adult koala's hindlimbs and forelimbs was equal (33% TMM), an index of the likely balance between pushing and hauling its body mass. Muscle in prehensile-tailed porcupines piled up posteriorly: the hindlimbs and tail carry 24% and 22.5% TMM, respectively, the forelimbs 16.5% TMM. Fifty percent of the musculature in the wallaby was concentrated in the hindlimbs, another 5% in the tail, but less than 10% in the forelimbs (Grand 1990). Along with its shift in propulsive requirements the tree kangaroo reduced the difference in muscle mass between hindlimbs (33%) and forelimbs (25%). In koala supinator, pronator teres, and pronator quadratus muscles are large, with extensive attachments (compared to the wombats); the deep bow of the radius increases the mechanical advantage of the manus from pronation through supination. In the lower leg popliteus and peroneo-

tibialis muscles have extensive attachments so that the fibula may rotate about the tibia. This allows the pes to invert and evert, a plane of movement not evident in the wombat.

The back extensors were reduced in koala, sloth, potos and lorises, reflecting the coordination of the trunk with the limbs during climbing and foraging. The prehensile tail literally 'draws' muscle mass posteriorly: in the porcupine 24.5% TBkM to the lumbar region, 33.5% to the sacrum (Grand and Eisenberg 1982). Similar displacements have occurred in the howler monkey (Grand 1978) and in the kinkajou (compared to their closest relatives; T.I. Grand, unpublished data). Muscle piled up in the lower back of the wallaby to accelerate the body mass and to control the tail. The cervical extensors in the koala were quite large. Not only was the head enormous, but it was flexed upon the neck and required muscular balance. In wallabies (and larger kangaroos) the cervical extensors were one-half this percentage and the head was less massive. The developing marsupial skull is a suckling mechanism (Smith 1999), which matures in the koala into a chewing machine housing a small brain (Radinsky 1987).

Sitting

Passive energy-conserving behaviors are certainly formative to species design. In Old World monkeys the skin (naked thickened epidermal pads) and lower pelvis (expanded ischial tuberosities, altered attachment sites for the hamstrings) correlate with sitting. This posture, which facilitates resting, feeding, and mutual grooming, revolutionized social life throughout the entire family (Washburn 1957).

In contrast to the monkeys, the koala is relatively quiescent and non-social. An adult spends a remarkable proportion of time (19 h/day) sitting, with only 4 min/day in active movement (Nagy and Martin 1985), further testimony to the intense pressures on energy conservation. The koala even uses the geometry of *Eucalyptus*, wedging itself between vertical and diagonal branch forks. The posture is complementary to open-branching trees such as *Eucalyptus* and perhaps also *Nothofagus*, a dominant of Australian forests during the marsupial radiations (Hume 1999). It is unsuitable for trees with simple horizontal, radiating limbs (e.g., conifers).

The skeletal attributes that adapt the koala to climbing are equally important to sitting: orthograde trunk, head flexed forward, shoulders directed craniad and laterad, elbows internally rotated, palms turned toward the midline, an axis of closure between digits II and III. The hindlimbs of koala and wombat are slightly more similar than the forelimbs, although differences in joint alignment, skeletal robusticity, and segment proportions are still obvious. The koala's hip joints tend to be flexed, the knees externally rotated, the soles turned toward the mid-line in inversion. The functional axis of the pes lies between the hallux and remaining four digits. Digits II and III are syndactylus, an ancestral character shared with the other diprotodonts. Syndactyly in the wombat has persisted, although overlaid

with modifications for rigidity (see figure in Wells 1989). The fused synsacrum in the wombat, stabilized for digging (Hildebrand 1985), also contributes to defense when an animal is pursued into its burrow (Barboza 1995).

Scampering

When a koala moves from one stand of *Eucalyptus* to another it may cross 10 km (or more) of open ground. The risks are considerable because it moves as an individual, not as the member of a troop as do most semi-terrestrial primates. In fact, a lactating female expresses its aversion to risk by reducing its home range, despite the increased energetic cost of milk production and thus, of food intake (Krockenberger 1993). In addition to the lack of social protection, their biomechanical inefficiency is striking: (1) the digits are so long, the claws so curved and talon-like that manus and pes are splayed at placement on the ground; (2) as a consequence of this and the alignment of the limb joints, forward swing (recovery) is not confined to the parasagittal plane; (3) the pelvis and hip appear to be inflexible and induce considerable side-to-side displacement of the hindquarters; (4) the thoraco-lumbar region is also rather immobile so that limb movements are not coordinated or 'fluid.' The structure of the lower body reveals still another puzzlement: the marsupium opens posteriorly, clearly maladaptive to an arboreal species with an upright sitting posture. The explanation, of course, goes back to the koala's terrestrial ancestry where the direction of pouch opening may have been somewhat less crucial. Every species is molded by the history and relative intensity of the selection pressures exerted upon it. This is what Gould and Lewontin (1979) missed in their confused and fatuous criticism of the form-function paradigm. Darwin got it just right: "Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence" (quoted by Mayr 1988, p 151). In modern koalas performance latitude and paradoxical structures have persisted because, prior to the human invasions, the disconnection of forest stands was more gradual and the level of terrestrial predation still moderate.

Eucalyptus herbivory

The koala is an energetic and nutritional conservative, what might be called a metabolic endurance species. Its maintenance requirement is estimated at $330 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ (Cork et al. 1983), similar to its field metabolic rate ($329\text{--}390 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) (Nagy and Martin 1985; Ellis et al. 1995). Resting rates for koalas are 74% of the marsupial average, including other folivores. Wombats expend $140 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ for maintenance (Barboza et al. 1993), 32% of the requirement for macropods. Energy reserves in fat stores estimated from live koalas and wombats range from 3–19% of body mass (Ellis et al. 1995; Ellis and Carrick 1992; Woolnough 1998). Even though energy ex-

penditure in koala varies between summer and winter, body water and fat content do not vary seasonally (Cork et al. 1983; Ellis et al. 1995). Neither Vombatoid relies upon accumulating fat reserves for reproduction but minimizes basal costs for maximum gains in growth and reproduction when plant growth can support these added expenses (Barboza 1995). Desert wombats (*Lasiorhinus*), for example, endure prolonged drought but reproduce successfully when the drought ends and plant growth resumes (Gaughwin et al. 1984).

The high proportion of fiber in *Eucalyptus* constrains its utilization. As the bulk (or volume) of the material handled by the gastrointestinal tract increases so does the indigestible fraction. The foliage may contain allelochemicals – tannins, which can limit protein digestion – and phenolics, which must be detoxified and excreted at additional metabolic cost (Foley et al. 1999). Much the same holds for the fiber content, bulk, and indigestibility of grasses. In addition, silicates abrade the teeth and increase the effort to triturate the food items.

Comminution, reducing particle size to increase the surface area of plant fibers, enhances degradation in the digestive tract. Chewing in the koala produces an array of small particles and hones the surfaces of the teeth to maintain cutting edges throughout life (Lanyon and Sanson 1986; Cork and Sanson 1990). This differs from other arboreal marsupials (Davison and Young 1990). Differential wear of dentine and enamel in wombats maintains the cutting edges of continuously growing teeth (Hume 1982; Ferreira et al. 1989). Indeed, chewing effort and dental structure probably reduce particle size in arid-zone wombats (*Lasiorhinus latifrons*) more than in forest species (*Vombatus ursinus*) when fed the same diets (Barboza 1993a).

Plant fiber has a peculiar influence on body size. Since bulky fiber matrices are most efficiently degraded by fermentation in large chambers with slow passage rates for digesta (Demment and Van Soest 1985), small animals must develop alternate strategies for fibrous diets (Justice and Smith 1992; Cork 1994). Among folivorous marsupials the enlargement of the cecum increases the capacity to digest fiber (Hume 1999) and accounts for gut volume in the koala (10% of body mass). Selective retention of the more digestible fine particles and fluids optimizes the energetic returns from fermentation in the cecum and proximal colon (Cork et al. 1983; Foley and Hume 1987). The smallest arboreal folivore, *Pseudocheirus*, employs a specialized form of coprophagy to salvage microbial products from the hindgut (Chilcott and Hume 1985); similar cecal products in koalas and sloths pass from mother to young to foster microbial colonization (Montgomery and Sunquist 1978; Osawa et al. 1993). The colon of the wombat de-grades grass fibers, but large particles are selectively retained for fermentation (Barboza and Hume 1992a, b; Barboza 1993a). Retention of the most bulky portion of the diet correlates directly with gut capacity (13–18% of body mass) and with food intakes that accompany low energy requirements (Barboza and Hume 1992a; Barboza 1993a).

Table 2 Maternal investment strategies, from Strahan (1983). * significant differences in male and female dispersal schedules

	Bandicoot	Ring-tail	Bennett's wallaby	Koala	Wombat
Age at Weaning (months)	2.5	6-7	9	11	12
Age at Dispersal (months)	3+	8-12	*	12-18	18
Females at First Reproduction (year)	1	1	1.2	2	2
Litter number	1-5 (3/year)	1-3	1	1	1

Water conservation is a pre-requisite for survival in the arid Australian landscape and the colon an important site for water resorption. Both koalas and wombats minimize fecal water loss by means of enlarged absorptive surfaces of the distal colon (Snipes et al. 1993; Barboza and Hume 1992a). Nevertheless, the physiological mechanisms that minimize water lost in urine and feces are modest in comparison with those of desert rodents (Lee and Carrick 1989; Barboza 1993b). Absolute water requirements are further reduced through conservative energy expenditure, low thermal demands, insulating pelage - koala, and burrowing - wombats (Degabrielle et al. 1978; Wells 1978). Renal concentration mechanisms are amplified in arid-zone wombats over their forest relatives (Barboza 1993b; McAllan et al. 1995). Postures and movements also regulate body temperature: three-toed sloths bask near the canopy surface to warm the body and descend when core temperature rises (Montgomery and Sunquist 1978); wombats bask at their burrow entrances, but cool down when they forage or withdraw to their subterranean chambers (Wells 1978; Brown 1984).

Thus, diet, water demand, and locomotor mechanism bracket species size. The lower limit is constrained by digestive capacity and fiber digestion, the upper limit by locomotion in trees and through soil. Koalas are the largest arboreal folivores and wombats the largest burrowing herbivores. For koalas the energy costs are vertical climbing within the canopy and the load strain on flexible branches; for wombats the costs are burrowing through resistant soils (Lovegrove 1989; Vleck 1979). The largest arboreal species, the binturong (>20 kg) and orang-utan (>100 kg), inhabit larger, more complex rainforests and as frugivores, consume higher quality foods than *Eucalyptus* foliage. Thus, for their habits and habitats the Vombatoids may be maximal in body size.

Vombatoid conservatism is also reflected in the low rates of social interaction and small home range (Johnson 1991, Taylor 1993). Scent marking and vocalization delimit feeding territory (McIlroy 1976; Russell 1982). Wombats share burrows but maintain exclusive feeding territories as do koalas with their home ranges (Eberhard 1978). Both species spend a large proportion of time at rest (in trees, in burrows), their movements intense, but generally brief.

Growth and reproduction

Maternal investment (Table 2) actually represents two sides of the coin of adaptation. On the mother's side, pro-

longed investment is partly reflected by a change in milk composition. The solid fraction, comprised primarily of fat, declines at permanent pouch exit when milk demand is greatest (Krockenberger 1996), a pattern similar to that of two other *Eucalyptus* folivores (*Pseudocheirus* and *Trichosurus*). This suggests how a foliage diet limits milk production by the mother even though daily weight gain of the joey (body mass/day) increases through the latter part of pouch life to weaning (Gemmell and Hendrikz 1993). Although milk solids are high late in lactation for the wombat (*Vombatus*; Green 1984), the total output of milk has not been measured. In any case, a low output of highly concentrated milk appears to be characteristic of reproductive investment in both vombatoids (Triggs 1988).

On the joey's side, energy demand is comparable to that of other mammals (19-29 MJ.kg⁻¹) but dispersed over a longer period than other species of similar mass. Peak lactation demand is reduced to 18-24% of the eutherian mean (Krockenberger et al. 1998), while energy expenditure is 40% lower than predicted. Thus, growth requirements are adjusted to maternal energy supply (Russell 1982). In fact, marsupial development represents a fundamental shift in the mammalian body plan (Nunn and Smith 1998; Smith 1999). The musculature and internal organs develop in advance of the brain, the facial portion of the skull becoming a pure suckling mechanism. The brain's growth rate was calculated to be 1.28 g/month. The consequent prolongation of weaning is consistent with milk's role as a dietary supplement to foliage until development is complete.

Evolutionary relationship

The climatologic and geologic background for modern Australia includes progressive desiccation of the continent, poor soils, and fire. These factors largely explain the dominance of the grasslands and the spread of sclerophyllous dicots such as the Eucalypti (Main 1989; Flannery 1998). To this mix during the past 100,000 years must be added human interference in the ecosystem and our particular forms of predation. For the diprotodont herbivores the result has been loss of species diversity and reduction in body size, condensations evident in every family: the Phalangeridae (small generalist browsers and arboreal folivores); the Phascolarctidae (medium sized arboreal folivores); the Macropodidae (small to medium sized generalist terrestrial browsers and grazers), and the Vombatidae (large fossorial grazers).

Within this radiation the koala stands out as an evolutionary 'outlier,' that is, an isolated taxon, remarkably disjunct from its closest relatives, the wombats, with no living species and no adequate fossil record to connect them. Such a void cries out for holistic reconstruction. "Historical narratives have explanatory value because earlier events in a historical sequence usually make a causal contribution to later events...The evolutionary biologist must always ask why questions when he attempts to analyze evolutionary causations" (Mayr 1988, p 72). "The answer to the question *why*, is always a reason that puts the fact to be explained into a system, so that knowing the nature of the system and certain data (or given existences), we can deduce or form a rational account of the events to be explained" (Cohen 1959, p 157, italics his).

When we work backward from koalas and wombats two clusters of attributes are identifiable, one ancestral, the other derived. Every character of maternal investment in the two species (Table 2) has been attenuated for metabolic endurance and the K end of the r-K spectrum: age at weaning displaced to 10–12 months, age of dispersal extended to 12–18 months, age at first reproduction to 2 years, and birth number from litter to single offspring. This makes concrete our proposition about metabolic conservatism in the Proto-Vombatoids. Furthermore, it is consistent with Parsons' hypothesis (1994) about environmental adversity; that is, either one of two conditions (a restricted availability of nutrients or a stable though resource-limited environment) would favor precisely those specializations found in koalas and wombats: low metabolism, low fecundity, long life.

By contrast, the locomotor adaptations are derived; every musculoskeletal attribute that distinguishes the two animals correlates directly with their diets and habits. How did this come about? The Proto-Vombatoid ancestor was an above-the-ground pronograde quadruped and generalist browser. Its juveniles, in the manner of young wombats (Triggs 1988), were playful explorers of their habitat and experimenters with novel food items. Ur-wombats remained pronograde, but shifted to grasses during the Miocene, part of the explosion of mammalian herbivores that occurred on every major landmass (Janis 1976; Stevens and Hume 1995). They also began to use crevices for thermal refuge and predator avoidance. The passive behavior of their descendants is consistent with this. Selection favored burrow excavation: power output through shortened levers, confined planes of limb action, rigid palms and soles, enormous claws. Accelerated fusion of the epiphyses to their diaphyses resulted in short, thickened long bone shafts and maximized leverages. Curiously, their burrowing technique is novel. They lie on one shoulder and dig with the free, up-side forelimb. Then, possibly to relieve fatigue, they roll over onto that side in order to dig with the other forelimb. Pelvis and hindlimbs brace the body, the legs and feet clear dirt to the rear of the advancing tunnel face.

Ur-koala juveniles began to climb trees as an arena for play and a refuge from interaction with adults and potential predators, and to experiment with *Eucalyptus*

browse. During the mid to later Tertiary – Miocene to Pleistocene – (Eberhard 1978), there were probably few competitors for *Eucalyptus* and no specialist predators. Even today, the other browsers are much smaller than the koala and insects, which are seasonal, do not consume the entire leaf. One herbivore of comparable mass, the tree kangaroo, is a foregut-fermenter. However, this "pre-existing condition" of the Macropodid gastrointestinal tract effectively precluded exploitation of *Eucalyptus* because of its bactericidal compounds (Hume 1999). The koala, as a hindgut-fermenter, could absorb many allelochemicals from the small intestine before the fibrous residues were exposed to cecal and colonic microbes (Hume 1999). Furthermore, youth and small size were clearly advantageous in this shift of ecology and behavior: the ratio of strength to body weight is more favorable; the limb joints are more flexible; smaller individuals could move farther out along branch terminals where leaf growth concentrates. Hand feeding favored extending the length of the forelimb. The joint capsules rotated with respect to their shafts, realigning palms and soles toward the midline for climbing and sitting (in contrast to the ancestral plantigrade orientation). Muscles at shoulder and hip converted from extensors to adductors; closure of the digits persisted along ancestral axes. The cumulative effect was that selection postponed epiphyseal closure, but capped body size.

Diprotodon, the gigantic Pleistocene vombatoid, represents a terminus of the original adaptive plateau, a pronograde terrestrial browser in a more resource-rich environment than the present. Interestingly, this picture of an extinct over-sized species with disjunct survivors (i. e., koala and wombat) is mirrored by two radiations of South American mammals. In one case, a lineage of semi-arboreal browsing rodents gave rise to the porcupines and to *Dinomys*, an enlarged, and now terrestrial, "quill-less porcupine" from highland Ecuador. The tip of the third branch, *Telicomys*, the size of a small rhinoceros, was also terrestrial, but driven to extinction by late Pliocene immigrants from North America (Grand and Eisenberg 1982). In the other case, the sloths, armadillos, and anteaters (the Xenarthra) descend from the most ancient eutherians of South America. They are linked by vertebral characteristics, but otherwise divergent as a result of their extreme nutrient, locomotor, and antipredator specializations: leaf browse for the arboreal sloths; ants and termites for the arboreal and terrestrial anteaters; worms and other invertebrates for the plated terrestrial and fossorial armadillos. Their extinct relatives include *Glyptodon* and two giant ground sloths (Eisenberg 1981).

This is a complete and parsimonious interpretation of koala evolution and offers a (What?, How?, Why?) scenario against which to interpret structural, physiological, and behavioral adaptation. The muscular anatomy of the wombat can be examined with respect to the transformation of its limbs for digging: joint stability in exchange for mobility, increase in muscle force along restricted planes of motion, rigidity of manus and pes. It is unfortu-

nate that a survey of the thoracic and abdominal viscera of marsupials (Mackenzie 1918a, b) tested no conjectures about the reorientation of the trunk from pronograde to orthograde. The author simply concluded that "Mechanical factors probably play a part in its (duodenal or right lateral fold) development in Koala, where we have a large right colon and caecum swung on the mesentery and supported at the pylorus" (GI tract, p 25). Our scenario even predicts a strong pre-dispersal resemblance in the two lineages, which there certainly is, followed by radical divergence (Triggs 1988). Since growth is indeterminate in some macropods, especially in the sexually dimorphic species, plasticity in bone growth is also possible in the living Vombatoids where overall growth is both slow and prolonged (Cockburn and Johnson 1988). Nevertheless, suspicion about superficial similarity (that "wombats are *achondroplastic dwarfs*," that "koalas are *paedomorphic*

or *neotenic* wombats") is justified. The fundamental problem with the terminology of heterochrony (*sensu* McKinney and McNamara 1991; Gould 1977) is that it displaces one's attention from the concrete processes of evolution to abstract products and pseudo-categories. Thus, it fails utterly to account for the shifts in structure, physiology, and behavior that we have identified.

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Appendix 1

Specimen identification and body composition data

Animal	Sex	Age (y)	Body mass (g)	Crown-rump (cm)	Skin (g)	Head (g)	Brain (g)	Total muscle (g)
1572	M	0.42	111.9	14.5	13.7	22.5	4.9	24.2
1635	F	0.50	246.8	17.7	44.2	31.6	7.5	61.2
1500	M	0.50	395.1	19.3	71.5	38.1	7.4	108.4
1508	M	0.50	310.6	19.0	64.8	29.8	6.8	71.8
1556	F	0.63	361.9	19.5	42.1		8.4	59.4
1511	M	14.60	6540	54.5	988.3	442.5	18.4	2252.6
1543	F	5.75	5125	51.0	733.1	249.1	17.8	1617.8
1549	F	6.33	5300	49.0	856.1	257.1	18.6	1670.8
1553	F	4.95	6525	48.0	1052.8	292.6	20.0	2278.2
1574	F	7.50	5680	50.0	873.8	289.7	16.2	1834.4
1636	F	15.66	4830	50.5	703.9	220.5		1543.4
1653	F	9.15	6125	54.0	1149.8	468.1	15.9	1432.2
1654	F	16.60	4850		741.6	369.8		1375.2
1651	M	8.00	7450		1168.2		23.0	2463.1
1652	M	10.15	7320	53.0	1116.8	634.3		1715.0

Appendix 2

Muscle masses by region

Animal	Hindlimb muscle (g)	Back extensors (g)	Forelimb muscle (g)	Sacral (g)	Lumbar (g)	Post-4 (g)	Thoracic (g)	Cervical (g)
1572	2.8	1.8	4.1	0.1	0.6	0.1	0.3	0.7
1635	7.9	4.0	12.6	0.3	1.4	0.2	0.8	1.3
1500	15.2	7.4	21.0	0.5	3.0	0.6	1.0	2.3
1508	10.3	4.9	13.1	0.2	1.9	0.4	1.0	1.4
1556	8.0	3.4	12.4	0.3	1.1	0.2	0.7	1.2
1511	327.9	147.8	379.0	18.0	68.8	9.7	16.4	34.9
1543	293.4	95.3	250.4	11.6	46.7	6.1	14.1	16.8
1549	273.3	112.2	260.3	13.2	57.9	5.7	14.1	21.3
1553	414.2	144.7	364.6	15.9	76.4	9.4	15.8	27.2
1574	322.2	119.6	287.9	10.0	62.2	8.0	15.4	24.0
1636	257.9	100.0	266.5	16.3	47.6	6.2	11.9	18.0
1653	235.0	80.0	225.4	10.8	35.3	6.4	12.7	14.8
1654	226.4	86.5	228.3	13.2	41.0	5.1	12.2	15.0
1651	395.5	157.7	411.3	21.3	75.3	7.4	18.3	35.0
1652	269.3	124.4	270.1	12.7	59.5	9.3	16.2	26.7

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