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Masticatory Motor Pattern in the Koala (*Phascolarctos cinereus*): A Comparison of Jaw Movements in Marsupial and Placental Herbivores

ALFRED WALTER CROMPTON[1]*, TOMASZ OWERKOWICZ[2], AND JAYNE SKINNER[2]
[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
[2]School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia, Australia

ABSTRACT Do closely related marsupial herbivores (Diprotodontia) conserve a common masticatory motor pattern or are motor patterns linked to the structure and function of the masticatory apparatus? We recorded the sequence and duration of activity of the individual jaw closing muscles during rhythmic chewing in koalas and then compared their motor pattern with that of their closest extant relatives, wombats, and their more distant marsupial relatives, macropodoids. These three lineages prove to have fundamentally different motor patterns and jaw movements during mastication. Each motor pattern represents independent modifications of an earlier motor pattern that was probably present in an ancestral diprotodontian. We show that koalas evolved a motor program that is in many aspects similar to that of placental herbivores with a fused mandibular symphysis (artiodactyls, perissodactyls, and higher primates) and almost identical to one artiodactyl, viz. alpacas. Anatomically, koalas are convergent on placental herbivores because they lost the inflected mandibular angle and large external part of the medial pterygoid muscle characteristic of other marsupials. We support the view that many different motor programs evolved for the control of transverse jaw movements, but identical motor programs for the control of transverse jaw movements can evolve independently in distantly related taxa. *J. Exp. Zool. 313A, 2010*. © 2010 Wiley-Liss, Inc.

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Mammalian Masticatory Motor Patterns

Mammalian masticatory cycles have some defining and ubiquitous features. In most mammals, jaw and tongue movements are linked and rhythmic; occlusion is unilateral; differential activities in both working- and balancing-side adductors control jaw movements during closing; and the orbit of movement of the jaw, when viewed from the front, is triangular or ellipsoid (Hiiemae, 2000). Weijs ('94) showed that in mammals with a primitive motor pattern (didelphid marsupials, placental insectivores, insectivorous bats, and basal primates) as well as in those with a transverse pattern (ungulates, lagomorphs, derived primates,

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*Correspondence to: Alfred Walter Crompton, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138.
E-mail: acrompton@oeb.harvard.edu

Tomasz Owerkowicz's present address is Ecology and Evolutionary Biology, University of California, Irvine, CA 92697.

Jayne Skinner's present address is University of South Australia, Adelaide, South Australia, Australia.

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and some marsupial herbivores), two groups of muscles control jaw movements during jaw closing, each group including muscles from both working and balancing sides.

Weijs ('94) referred to these muscle groups as "Triplet I" and "Triplet II". Triplet I muscles (balancing-side superficial masseter, balancing-side medial pterygoid, and working-side posterior temporalis) were defined as those that drew the working side of the jaw dorsolaterally. Triplet II muscles (working-side superficial masseter, working-side medial pterygoid, and balancing-side posterior temporalis) by definition drew it dorso-medially. In addition, Weijs ('94) claimed that in primitive mammals activity in another group of muscles preceded that of Triplet I muscles, referring to this group as "symmetric closers" (anterior temporalis, deep temporalis, and zygomaticomandibularis). He recognized at least five distinct mammalian motor patterns (primitive, carnivore symmetric, rodent symmetric, rodent alternate, and transverse) and showed that each of these specialized motor patterns constituted a unique modification of a primitive masticatory pattern. Weijs ('94) showed the temporal separation of activity between Triplet I and II muscles, and the extent of medially directed movements to be minimal during the power stroke in mammals with a primitive pattern, but much greater in those with a transverse pattern.

Bramble and Wake ('85) suggested that mammals retained the masticatory motor pattern of reptiles, and concluded that "the evolution of the complex mammalian masticatory system was accomplished through minimal changes in neuromotor mechanisms but relatively enormous alterations in the peripheral feeding structures (bones, muscles, and dentition)." Smith ('94) reviewed the literature on the conservation of masticatory motor patterns, and established criteria required to support or refute this hypothesis. She claimed that the hypothesis of a conservative pattern could not be corroborated "when the feeding cycle is placed in a broader phylogenetic context."

Since Weijs' classic 1994 paper, the masticatory motor pattern has been described for several placental and marsupial species that were not included in his review. The primitive pattern was revised and described in detail for tree shrews (Vinyard et al., 2006a), galagos (Hylander et al., 2000, 2005), and opossums (Hylander et al., 2005; Crompton et al., 2008b). Vinyard et al. (2006a,b) dismissed the concept of symmetric closers and demonstrated that the working side anterior temporalis drew the working side of the jaw dorsolaterally and therefore should be included with Triplet I muscles. The balancing side anterior temporalis, they argued, drew the jaw dorsomedially and therefore should be included with Triplet II. They also added the balancing side deep masseter to Triplet I and the working-side deep masseter to Triplet II. In contrast to Weijs ('94) who illustrated near synchronous timing of activity first in Triplet I muscles and later in Triplet II muscles (Fig. 1 in Weijs, '94), the later studies document significant differences in the timing of the onset, peak and offset of activity in individual Triplet I and II muscles. The sequence of adductor activity was shown to be basically the same in mammals with the primitive pattern.

In herbivorous mammals several different motor patterns have been described for the control of transverse jaw movements. These include some placental ungulates (de Vree and Gans, '75; Williams et al., 2007, 2008), higher primates (Hylander et al., 2000, 2005; Wall et al., 2006), and some marsupials (Crompton et al., 2008a,b). In some of these mammals certain muscles assigned to Triplet I in primitive mammals act as Triplet II muscles, and vice versa. The working- and balancing-side deep masseters, for example, are sometimes reversed from the primitive pattern. In macropodids both the balancing-side anterior and posterior parts of the temporalis act as Triplet I muscles; and in wombats there is only one Triplet I muscle (balancing-side medial pterygoid), the rest of their balancing-side muscles being silent and all the working-side muscles acting as Triplet II muscles. Williams et al. (2007, 2008) concluded that no single motor pattern contributes to transverse jaw movements in placental ungulates. The same is true for two marsupial herbivores (wombats and macropods, Crompton et al., 2008a,b).

Because the muscles assigned to Triplets I or II in primitive mammals can vary in herbivorous mammals with a transverse pattern, the continued use of the terms Triplet I and II is confusing. For this reason we suggest retaining the division of jaw adductors into two groups, but refer to them simply as Group I and Group II on the understanding that the muscles included in each group can be different in major groups of herbivorous mammals and that Group I muscles always draw the jaw dorsolaterally and Group II dorso-medially.

One Group I muscle usually peaks early during the Fast Close stage to draw the working-side jaw dorsolaterally. The remaining Group I and all the Group II muscles peak slightly later and contribute to the dorsal and transverse components of the power stroke.

Division of the Power Stroke

The power stroke of certain placental herbivores has been divided into two phases. Kay and Hiiemae, in a series of publications (Hiiemae and Kay, '72; Kay and Hiiemae, '74; Kay, '77), developed the concept of dividing the power stroke into Phases I and II. During Phase I the molars move dorsally and medially into centric occlusion that is reached when the protocone is firmly in contact with the talonid basin. During Phase II, occlusal contact is briefly maintained as the lower jaw moves medially and anteriorly before the onset of the opening stroke. Kay and Hiiemae (Hiiemae and Kay, '72; Kay and Hiiemae, '74; Kay, '77; Hiiemae, 2000) claimed that both phases contribute to effective food breakdown, but Hylander et al. ('87) and Wall et al. (2006) showed that in macaques and baboons effective bite force is restricted to Phase I. Only a minimal amount of food breakdown, they suggested, might occur during Phase II in those placental herbivores in which a Phase II has been reported to occur (primates: Kay and Hiiemae, '74; hyraxes: Janis, '79; perissodactyls: Fortelius, '85; Wall et al., 2006).

Phases I and II in placental herbivores are entirely different from the similarly named phases in marsupial herbivores. The power stroke in macropods is divided into a Phase I, when the jaw is drawn dorsally, and a Phase II, when the jaw moves medially (Sanson, '80). Food is actively broken down during both phases and a distinct pattern of adductor activity is associated with each phase (Crompton et al., 2008a). Using the same terms for different parts of the power stroke in placentals and marsupials is confusing. Since these terms are well established in the literature, we will modify the terms and suggest Phase Im and Phase IIm for marsupials, and Phase Ip and Phase IIp for placental herbivores.

Koala Mastication

Young and Robson ('87) and Lanyon and Sanson ('86a,b) have described occlusal function and transverse jaw movements that occur during mastication in the koala. Koala molars are quadritubercular and possess high, tightly interlocking cusps with opposing curved blades well suited for shearing eucalyptus leaves (Lanyon and Sanson, '86a). Lanyon and Sanson ('86b) discuss the effect of wear of the molars on chewing efficiency. Initial wear increases the length of the cutting edges of the molars and this results in the ingestion of a high proportion of small leaf particles. As the major cusps are obliterated by wear, particle size increases. At the end of the medially directed power stroke in koalas, the jaw moves slightly forward as it begins to open. Young and Robson ('87) proposed that this forward movement adds a crushing action and serves to clear the molars of leaf fragments. A powerful transverse movement followed by a weak forward movement at the beginning of opening is reminiscent of Phases Ip and IIp of placental herbivores (Janis and Fortelius, '88; Wall et al., 2006).

Davison and Young ('90) describe the anatomy of the masticatory apparatus of koalas, and point out that the relative sizes of the koala's adductor muscles differ from those of placental ungulates (Group II of Turnbull, '70). The dominant muscles of placental ungulates are the masseter and the medial pterygoid, while the temporalis is relatively small. Koalas have a large masseter and temporalis, but small medial pterygoid complex. Davison and Young determined that the masseter complex made up 52% of the total adductor muscle mass in the koala, 43% of the temporalis, and only 5% of the medial pterygoid.

Aims

The purpose of this paper is to describe molar occlusion and the masticatory motor pattern of the koala (*Phascolarctos cinereus*) and to compare the control of jaw movements in marsupial and placental herbivores. We wish to test two hypotheses concerning masticatory motor patterns in koalas:

Hypothesis 1 is that koalas and wombats share a similar masticatory motor pattern for controlling transverse jaw movements during the power stroke.

Hypothesis 2 is that the masticatory motor pattern of koalas resembles one of the placental herbivores with a fused mandibular symphysis.

Hypothesis I is based on the generally accepted sister–group relationship of koalas and wombats. This is supported by morphological criteria (Archer, '78, '84a,b; Harding and Aplin, '90; Horovitz and Sànchez-Villagra, 2003) and molecular phylogenetics (Aplin and Archer, '87; Kirsch, '97; Osborne et al., 2002; Amrine-Madsen et al., 2003; Meredith et al., 2008). Meredith et al. (2009) have concluded that the common ancestor of Vombatiformes was arboreal and that the separation of the two living families, Vombatiidae (wombats) and Phascolarctidae (koalas), probably occurred during the late Eocene (37 million years ago). Considerable time elapsed between this split and the first known representatives of each family (Long et al., 2002; Brewer et al., 2009) found in late Oligocene/early Miocene deposits (approximately 25 MYA). Marked differences in cranial and dental morphology between extant koalas and wombats reflect their long independent evolution. Hypothesis I suggests that both lineages conserved the motor pattern of their common ancestor.

The second hypothesis is based on morphologic features shared by koalas and placental herbivores. In most marsupials, the angular process is inflected and directed medially (Winge et al., '41; Sànchez-Villagra and Smith, '97). In koalas, as in placental herbivores, the angular process is vertical, deep, and uninflected. The medial pterygoids of placental herbivores and koalas do not divide into small deep and large superficial sections, in marked contrast to the clearly divided medial pterygoids in wombats and macropods. Sànchez-Villagra and Smith ('97) point out that a few distantly related marsupial taxa independently lost their inflected angular process, or retained it only in juveniles while reducing it in adults. Hypothesis 2 tests whether the motor pattern is strongly linked to the structure of the mandibular angle and division of the medial pterygoid. Deep and inflected mandibular angles are compared in Figure 7.

MATERIALS AND METHODS

Subjects and Specimens

Data were collected from two koalas captured on Kangaroo Island on August 4, 2004 and transported to the animal housing facility at the University of Adelaide. The animals were judged to be relatively young because their molars showed minimal amount of wear. Following the advice given by the staff of the Cleland Animal Park (Adelaide), a suitable environment was created in one of the University's animal rooms. The koalas were supplied with fresh eucalyptus browse daily. They settled in remarkably quickly and their feeding was not hindered by the presence of staff or recording equipment. Video recordings of feeding were made prior to surgery to determine the possible adverse effects of surgery on normal feeding. At the end of the experiment the animals were returned to the Cleland Animal Park. No attempt was made to repeat the experiment on either animal.

We attempted to acquire data from a third animal, but due to complications this was not possible. We recognize that data from two animals is a small sample, but consistent results were obtained and in view of the difficulty in obtaining data from additional animals, we feel justified in drawing conclusions from the limited data we acquired.

The figures of the cranial and dental structure of a koala were based on Specimen 29283 in the collections of the Museum of Comparative Zoology (Harvard University). In order to portray the orientation of the shearing crests extending from the principal cusps, casts of the molar rows were made. These were sectioned transversely in order to view anterior and posterior surfaces of individual molars.

Surgery

Prior to surgery the animals were sedated with Zoletil (1 mg/kg, IM) and then maintained at a surgical plane of anesthesia with Isoflurane administered through a facemask. The ventral surfaces of the lower jaw and neck were shaved and scrubbed with betadiene and ethyl alcohol. One midventral incision was made behind the jaw; and two additional incisions, each below the postero-lateral region of the lower jaw, were made on the left and right sides. Plastic tubes (3 mm internal diameter) were fed below the skin from the medial to the lateral incisions. Three bipolar electrodes made of 0.004 in enameled copper wire (California Fine Wire Co. Grover Beach, CA) were fed through each tube. Each pair of three electrodes was soldered to a 6-pin microconnector (Glenair, Glendale, CA). The tubes were then withdrawn, leaving the wires below the skin. Electrode tips were hooked into the bevel of an injection needle, which was then inserted into the muscle belly to a predetermined depth. Electrodes were inserted in the superficial masseter and medial pterygoid. One mid-dorsal incision was made in the neck, and two above the temporal fossae. Tubes were led below the skin from the median to the lateral incisions, wires for three electrodes were fed through each tube and the tubes were then withdrawn. Electrodes were placed in the anterior and posterior temporalis. In order to reach the deep masseter, a 3 in. long 20-gauge hypodermic needle together with an electrode wire was inserted vertically between the ascending process of the dentary and the zygoma until the needle contacted the masseteric ridge on the external surface of the mandible.

Wires from the four microconnectors were led to a 25-pin connector placed on each animal's back between the shoulder blades. The connectors and wires were held in place by a flexible Vetrap bandage loosely wrapped around the animal's neck and covered with a more substantial Elastoplast bandage. Once the animals had recovered, they were placed on the tree branches mounted in the animal room. They were not sacrificed at the end of the experiment, so it was not possible to check the placement of the electrodes. However, we have successfully practiced electrode insertion into each of the jaw adductors on koala cadavers prior to surgery, and feel confident about correct electrode placement. All surgical procedures received the approval of the Animal Ethics Committee of the University of Adelaide.

Recording

Several hours after surgery, the animals were given fresh eucalyptus browse. While the animals were feeding, the 25-pin connector on each animal's back was released from the flexible bandage and joined to a matching 25-pin connector. Long shielded and insulated wires (8 ft) led from the connector to 12 P511 amplifiers (Grass Inc., Quincy, MA) and amplified (X1000-X10000) with a 300 Hz to 3 kHz bandpass filter. All data were recorded digitally on a TEAC RD-145 DAT tape recorder (TEAC$^{\text{TM}}$ Corp., Tokyo, Japan). Amplification for each electrode was held constant during the course of each feeding sequence. Feeding behavior was recorded on a digital video recorder (DCR-TRV30, Sony Corporation, Japan). In order to synchronize the video and EMG data, a small light emitting diode (LED) was placed within the edge of the video field. Manually triggered short current pulses to the LED of varying duration and number were recorded synchronously with EMGs. Twenty-eight feeding sequences were recorded for Koala 1 and 19 were recorded for Koala 2. The raw data were played out on a 16-channel thermal array recorder (WR3600, Graph Tec America, Santa Ana, CA). This made it possible to match specific jaw cycles identified on video recordings with the paper printouts of EMG data. We were unable precisely to correlate jaw movements and the accompanying EMGs as the video recordings were too slow (30 fields/sec) and a fixed point on the lower jaw could not be identified in all the frames. In the absence of accurate jaw kinematics, the account of jaw movements given in this study is based primarily on the pattern of molar occlusion with additional information from the video recordings. The duration of adductor activity in each chewing cycle appears to be limited to the duration of jaw closure (from maximum gape to the end of dorso-medial movement of the jaw). Based on these estimates we speculated on the relationship between the sequence of activity of the individual adductors and the perceived jaw kinematics. In order to test the ideas presented in this study a more precise method such as videofluoroscopy is required more accurately to synchronize EMGs and jaw movements. For analysis, we chose four sequences for Koala 1 and two sequences for Koala 2 that included at least 20 rhythmic chewing cycles in which there was at least one change in the chewing side and which were also captured by video.

EMG Data Analysis

Electromyographic recordings of rhythmic molar chewing were sub-sampled at 6 kHz to reduce file size and transferred from the TEAC data recorder to a computer using TEAC's QuikView II program. Custom-written software (©David Hertweck) processed the raw EMG data in the following manner: it eliminated any offset, performed full-wave rectification, applied a 10 msec time constant, reset integration and rejected randomly-timed electrical activity (Thexton, '96). The software finally displayed the processed EMG signals together with the video synchronization pulses.

Within each feeding sequence, amplification of the EMG signals was held constant and the maximum EMG activity of each muscle scaled to 100 units. This equalized signal amplitude across electrodes despite inherent amplitude variations due to differences in the distance of electrodes from the nearest active muscle fibers. Igor Pro v.4.0 (Wavemetrics Inc., Lake Oswego, OR) displayed integrated and rectified EMGs. We calculated the median and standard deviation of peak EMG amplitudes; the median time of onset, offset and peak activity of each muscle relative to peak activity in the working-side superficial masseter; and the chewing cycle length, based upon the interval between peaks of activity in the working-side superficial masseter between consecutive chews. Peak activity levels of the working- and balancing-side muscles, regardless of when they occurred during the power stroke, were used to calculate working-to-balancing side ratios (*W*/*B*).

RESULTS

Occlusion

Video recordings of both experimental koalas and several uninstrumented animals in the Cleland Animal Park and the experimental animals indicate that, as the jaws begin to close, the lower jaw is drawn laterally until the lower molars on the working side appear to be directly below the upper molars, and the lower working-side incisor is positioned external to the upper I^2 (Fig. 1). During the power stroke, the mandible is drawn first dorsally and then medially when the lower incisor sweeps across and wears down the occlusal surfaces of I^2 and I^3. As the jaws open, the working-side incisors are drawn transversely beyond the sagittal plane of the skull. As seen in the occlusal view of an upper and lower molar (Fig. 2A), well-defined shearing crests, numbered 1 to 8, run in a labial direction from the paracone, metacone, protocone, and hypocone and in a lingual direction from the protoconid, hypoconid, metaconid, and entoconid. As the jaws close, matching surfaces shear past one another. This occlusal pattern is best shown in an anterior view of shearing surfaces 1 and 5 on the left upper molar with matching crests on the posterior surface of the protoconid and metaconid

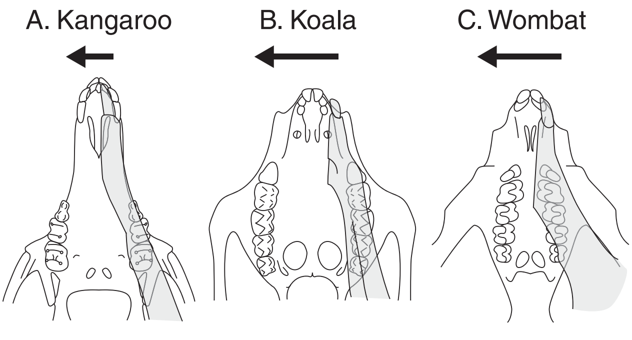

Figure 1. Ventral view of the upper dentition and lower jaw of a kangaroo (*Macropus rufus*), koala (*Phascolarctos cinereus*) and wombat (*Lasiorhinus latifrons*). The arrows indicate the relative amount of transverse lower jaw movement during the power stroke (based on the data from Crompton et al., 2008a,b).

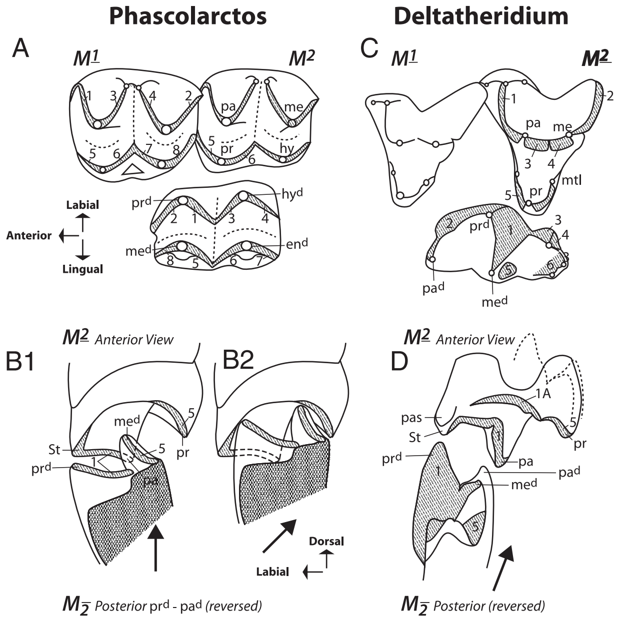

Figure 2. Molars of a koala (*Phascolarctos*) and a Cretaceous mammal, *Deltatheridium*. **A**: Occlusal view of upper molars M^1 and M^2, and lower M_2 **B_1**: Anterior view of right M^2 and posterior view of matching occlusal surfaces on M_2 (reversed) at the beginning of the vertically directed power stroke on the right side (vertical arrow). **B_2**: Position of M_2 during the medially directed power stroke (oblique arrow). **C**: Occlusal view of M^1, M^2 and M_2 of *Deltatheridium*. **D**: Anterior view of right M^2 and posterior view of M_2 (reversed) at the beginning and end of the power stroke when chewing on the right side (dotted outline indicates the position of the lower cusps at the end of the power stroke). Shearing surfaces are numbered 1–6 in *Deltatheridium* and 1–8 in *Phascolarctos*. BDM, balancing-side deep masseter; BMPt, balancing-side medial pterygoid; BPT, balancing-side posterior temporalis; BSM, balancing-side superficial masseter; en^d, endoconid; hy, hypercone; hy^d, hypoconid; LAT, left anterior temporalis; LDM, left deep masseter; LMPt, left medial pterygoid; LPT, left posterior temporalis; LSM, left superficial masseter; M, molar; me, metacone; me^d, metaconid; mtl, metaconule; pa, paracone; pas, parastyle; pr, protocone; pr^d, protoconid; RAT, right anterior temporalis; RDM, right deep masseter; RMPt, right medial pterygoid; RPT, right posterior temporalis; RSM, right superficial masseter; st, stylar cusp; WDM, working-side deep masseter; WMPt, working-side medial pterygoid; WPT, working-side posterior temporalis.

(Fig. $2B_1$ and B_2). In this view the leading edge of shearing crests 1 on the upper and lower molar are horizontally oriented and slightly concave. Food is trapped and sheared as the lower jaw moves vertically (Fig. $2B_1$, vertical arrow). This is also true for shearing crests 2, 3, and 4. Shearing crests 5 are also slightly concave, but more vertically oriented, and they shear past one another as the lower jaw moves medially rather than dorsally at the end of the power stroke (Fig. $2B_2$, oblique arrow). Shearing surfaces 6, 7, and 8 also contact one another as the jaw moves medially.

Adductor Activity Pattern

Dissection of specimens of koala heads allowed us to estimate the main orientation of individual adductor muscles and their likely action on mandibular movement. Group I muscles—the working-side deep masseter and temporalis (both anterior and posterior) together with the balancing-side superficial masseter and medial pterygoid—all have the potential to draw the working-side mandible dorsolaterally (Fig. 3A and C). Group II muscles—the working-side superficial masseter and medial pterygoid along with the balancing-side temporalis (anterior and posterior) and deep masseter—can potentially draw the working-side mandible dorsomedially (Fig. 3B and D). In vivo EMG recordings showed a sequence of muscle activity that confirmed jaw movements we had visually observed on video recordings (Fig. 4A and B). The order of the muscles in Figure 4 and later figures is based on the sequence of muscle activity in the opossum during the power stroke.

The length of chewing cycles in both koalas remained relatively constant (between 415 and 460 msec; see Table 1), despite side shifts, differing bite points, marked changes in EMG amplitude (see Table 2), and the presumed inclusion of swallow cycles within a chewing sequence (presumed because swallows

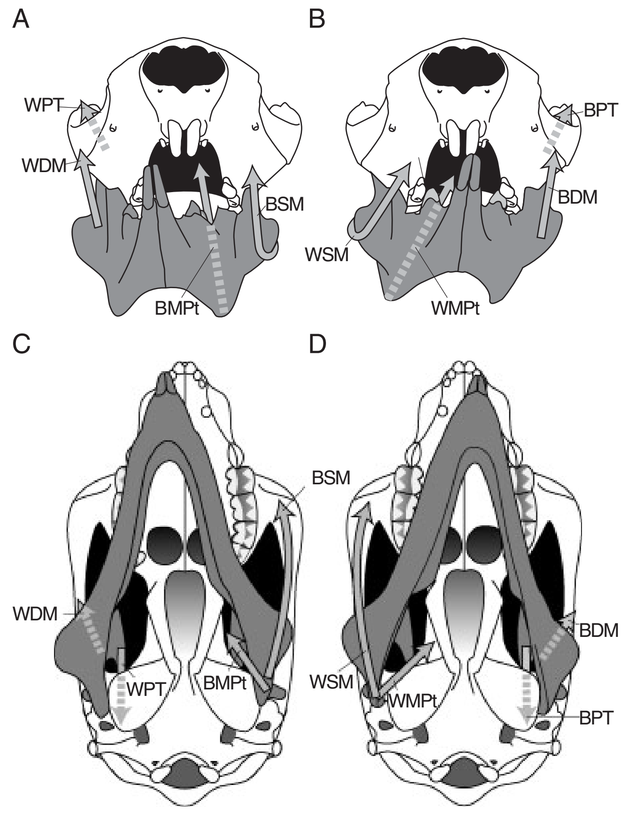

Figure 3. *Phascolarctos cinereus*. Anterior and ventral views of koala skull to show the position of the lower jaw at the beginning of the power stroke (**A**, **C**) and end of power stroke (**B**, **D**). Arrows indicate the approximate orientation of the adductor muscles. Dotted arrows indicate muscle orientation behind a bone surface. Group I muscles are indicated in A and B, and Group II in B, D.

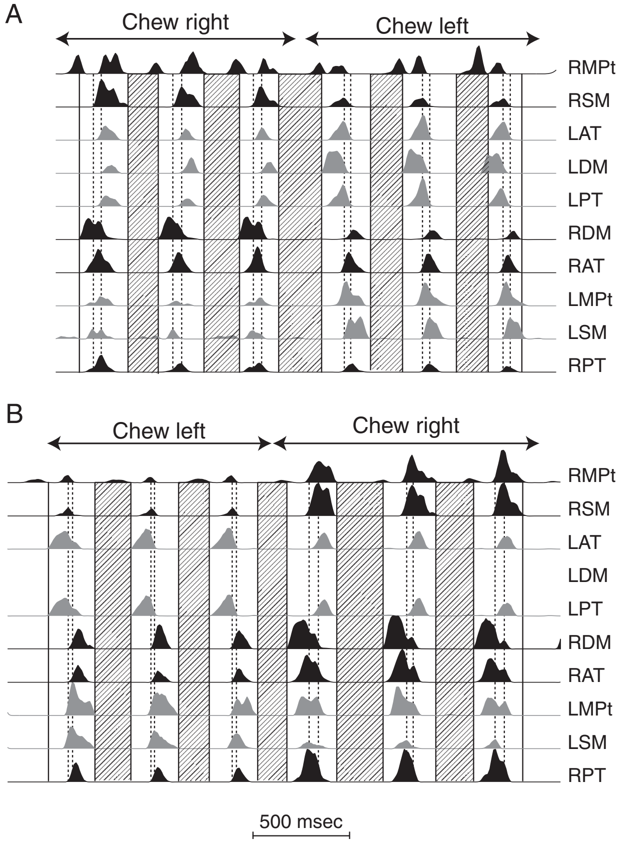

Figure 4. *Phascolarctos cinereus*. Integrated and rectified EMGs of selected adductor muscles recorded during three chewing cycles on one side followed by three on the opposite side in Koala 1 (**A**) and Koala 2 (**B**). Right-side muscles, solid black; left-side, solid gray. Solid vertical lines bracket adductor activity during closing and shaded columns indicate the opening phase. Dotted vertical lines pass through peak activity in the working and balancing-side superficial masseter. Levels of activity in the superficial and deep masseter clearly indicate the chewing side.

could not be identified from the adductor EMGs). (For a discussion of the factors governing the length of chewing cycles in mammals see Ross et al. (2007a,b). Synchronous recordings of video and EMG recordings confirm that the working side always has higher relative activity in the superficial and deep masseter than on the balancing side (Fig. 4 and Table 2). This is useful because the EMG pattern alone indicates the chewing side.

In the course of a chewing sequence, side shifts occur frequently, which means that each adductor acts alternately as a working- and balancing-side muscle. However, the timing of peak activity in right-side muscles when they are in a working or balancing phase may differ from that of matching left muscles during their own corresponding phase. This can probably be attributed to the position of electrodes within individual muscles (Herring et al., '79; van Eijden and Turkawski, 2001; German et al., 2008; Herrel et al., 2008). Based on the orientation of striations on occlusal facets, Young and Robson ('87) claimed that a slight forward movement of the mandible occurred at the end of the power stroke. However, we observed no such movement in our video recordings and our EMGs showed no activity that could be associated with such a change in the direction of jaw movement.

Despite the variation in amplitude and timing in the adductor muscles (Fig. 5; Table 3), there remains a consistent and

Table 1. Median cycle duration (±standard deviation) of five different chewing sequences in wild-caught koalas.

Animal	Sequence	*N*	Duration (msec)
Koala 1	1	19	460±17
Koala 1	14	23	430±14
Koala 1	26	20	460±33
Koala 2	21	17	450±15
Koala 2	25	25	440±31

Duration is in milliseconds; *N*, number of chewing cycles per sequence.

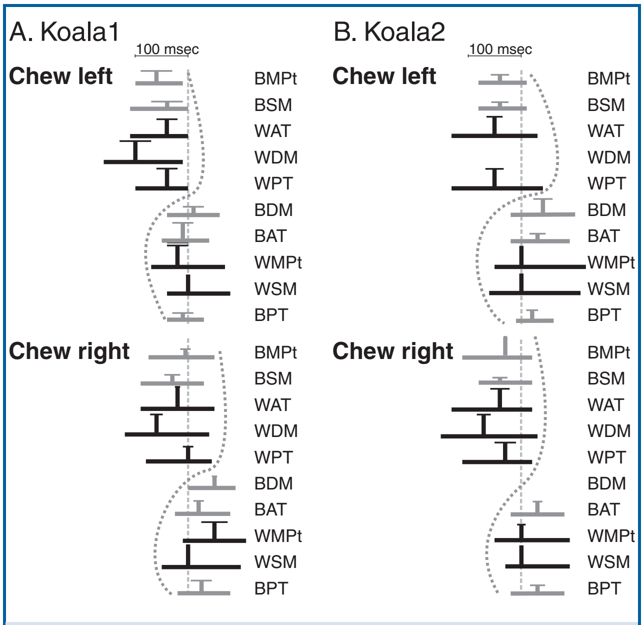

Figure 5. *Phascolarctos cinereus*. Comparison of median duration (heavy horizontal bar), time of peak activity relative to peak activity in the working-side superficial masseter (vertical bars) and standard deviation in the time of peak activity (light horizontal bar) when Koala 1 and 2 chew on the left and right. Heights of the vertical bars indicate the level of median peak activity (relative to a maximum value within each sequence). Working- and balancing-sides are indicated by black and gray bars, respectively. The heavy dotted line separates Group I (left) and Group II (right) muscles. The light dotted vertical line is drawn through the time of peak activity of the working-side superficial masseter. No recordings were obtained from the left side deep masseter. Figure based on the data given in Tables 2 and 3. Despite a fair amount of overlap in activity of Group I and Group II muscles, onset and offset of Group I muscle activity always precedes the onset and offset of activity Group II muscles, respectively.

Table 2. Median peak activity (±standard deviation) of individual working- and balancing-side adductor muscles for ten sequential chewing cycles in four chewing sequences of Koala 1, and two of Koala 2.

	N	WSM	BSM	WMPt	BMPt	WAT	BAT	WDM	BDM	WPT	BPT
Koala1a chew right	10	85±11	32±17	71±10	30±7	82±9	48±12	75±14	43±13	54±21	46±9
Koala1a chew left	10	71±10	27±5	79±11	48±13	64±4	67±4	78±7	29±5	74±13	28±5
Koala1b chew right	10	75±12	67±16	54±11	39±11	85±10	35±17	75±12	33±8	55±13	30±5
Koala1b chew left	10	77±10	49±19	86±8	56±20	81±15	73±24	74±9	21±5	82±15	28±13
Koala2 chew right	13	82±11	19±4	60±18	70±6	81±10	49±12	83±9		83±14	30±12
Koala2 chew left	13	73±15	25±12	78±11	29±9	74±14	30±8		58±8	74±14	42±18

The maximum peak activity during any time-point in the EMG recording was assigned the value of 100, and all other peaks of the analyzed chewing cycles were compared to this maximum. Electrodes placed in the left deep masseter of Koala 2 failed to provide decent EMG recordings. BDM, balancing-side deep masseter; BMPt, balancing-side medial pterygoid; BPT, balancing-side posterior temporalis; BSM, balancing-side superficial masseter; WDM, working-side deep masseter; WMPt, working-side medial pterygoid; WPT, working-side posterior temporalis

Table 3. Median time (±standard deviation) of adductor muscle peak activity relative to peak activity of the working-side superficial masseter, for ten chewing cycles in four chewing sequences of Koala1 and 13 chewing cycles in two chewing sequences of Koala 2.

	N	BMPt	BSM	WAT	WDM	WPT	BAT	WMPt	BPT	BDM
Koala 1a chew left	10	−60±17	−40±18	−40±13	−90±23	−45±12	−10±12	−30±13	−10±8	10±13
Koala 1a chew right	10	−5±12	−30±15	−20±6	−70±17	−40±8	20±7	35±23	25±8	45±5
Koala 1b chew left	10	−50±10	−50±16	−50±8	−60±10	−50±8	−10±5	−30±6	0±8	20±13
Koala 1b chew right	10	−15±8	−20±16	−20±7	−40±15	−10±8	20±7	20±18	30±8	50±7
Koala 2 chew left	13	−40±17	−40±16	−50±15		−50±17	30±14	0±17	20±11	40±18
Koala 2 chew right	13	−30±3	−40±14	−40±18	−70±13	−30±22	30±14	0±8	30±14	

In the course of each chewing sequence individual muscles alternate between working- and balancing-side roles. However peak activity timing often differs between the right and left sides of the same muscle. See text for explanation. Negative timing indicates adductor peak activity leading (preceding) WSM peak activity, positive timing indicated adductor peak activity lagging (following) WSM peak activity. Abbreviations given in Table 1.

Table 4. Ratio of working- to balancing-side (*W*/*B*) peak activity in adductors of Koalas 1 and 2 when chewing on both left and right sides.

	N	Superficial masseter	Medial pterygoid	Anterior temporalis	Deep masseter	Posterior temporalis
Koala 1a chew left	10	2.2±0.4	1.5±0.6	1.0±0.2	2.5±0.6	2.9±0.7
Koala 1a chew right	10	2.5±1.1	2.0±0.3	1.6±0.4	2.0±0.7	1.3±0.3
Koala 1b chew left	10	1.5±0.3	1.5±0.6	1.1±0.2	3.6±0.8	3.0±1.3
Koala 1b chew right	10	1.3±0.3	1.3±0.4	2.5±0.8	2.2±0.7	2.0±0.6
Koala 2 chew right	13	2.7±0.6	2.8±1.0	1.8±0.5		2.0±0.7
Koala 2 chew left	13	4.2±1.2	0.9±0.2	1.7±0.4		2.8±1.3

Mean values of the *W*/*B* ratio (±standard deviation) were obtained from ten chewing cycles in four chewing sequences from Koala 1 and 13 chewing cycles in two chewing sequences from Koala 2. Electrodes in the deep masseter of Koala 2 failed to give useful recordings. *W*/*B* ratio is consistently at or above unity in all muscles, suggesting the adductors generate more force when on the working side.

recognizable masticatory motor pattern. Early activity in the working-side deep masseter appears to initiate lateral movement of the mandible. Dorsal jaw movement that follows is associated with activity in the remaining Group I muscles (balancing-side medial pterygoid and superficial masseter, and working-side anterior and posterior temporalis). Peak activity in Group I muscles barely precedes peak activity in Group II muscles (balancing-side anterior and posterior temporalis, working-side medial pterygoid and superficial masseter, with the balancing-side deep masseter being the last muscle to peak). However, activity in the individual Group II muscles extends well beyond that of the Group I muscles, and activity of Group I muscles precedes that of Group II. Peak activity in Group I muscles occurs before any significant activity in Group II muscles move the jaw medially. Some variation in the activation sequence occurs between the two animals, or between left and right chews in the same individual (Table 3), but this does not affect the identification of either Group I or II muscles.

Almost without exception the amplitude of activity in working-side muscles exceeds that of corresponding muscles on the balancing side. The *W*/*B* side ratios of adductor amplitude are consistently high, 1.3–2.9 for Koala 1, and 1.7–4.2 for Koala 2, with the exception of the medial pterygoid that maintains a ratio close to unity when the animal chews on the right side (0.9±0.2) (Table 4).

DISCUSSION

Origin of Koala Molars

Koala molars appear to have retained the six shearing crests that occur on typical tribosphenic molars, for example, those present in *Deltatheridium*, an early Cretaceous metatherium (Rougier et al., '98) or in the oldest known Australian marsupial, *Djarthia murgonensis* from the Eocene (Godthelp et al., '99; Beck, 2008; Beck et al., 2008). Figure 2 is based on Figure 5 in Crompton and Kielan-Jaworowska ('78). In mammals with tribosphenic molars, the lower jaw moves vertically and slightly medially during occlusion (Fig. 2D, oblique arrow) and there is no division into distinct vertical and transverse components of movement (Crompton and Hiiemae, '70). Shearing occurs between the crests that extend labially from the upper cusps and lingually from the lower. Beck et al. (2008) suggests that *Djarthia* "may approximate the ancestral morphotype of the Australian marsupial radiation". All diprotodontids feature the loss or marked reduction of the paraconid (pa^d) and talonid basin, and the addition of a new cusp on the posteromedial edge of the upper molars, usually referred to as the "hypocone" (hy in Fig. 2A). Placental herbivores and diprotodonts independently evolved a well-defined cusp in this position. For this reason, Tedford and Woodward ('87) prefer to call this cusp an "enlarged metaconule" (mtl, Fig. 2C). Sànchez-Villagra and Kay ('96) disagree and claim that the cusp is correctly identified as a hypocone. In koalas, this cusp supports two shearing surfaces, 7 and 8, that match shearing surfaces on the anterior surface of the metaconid and posterior surface of the entoconid. Koalas added a transverse component of jaw movement that early marsupials with tribosphenic molars lacked. Their quadritubercular molars retained the six primitive shearing crests of their ancestors' tribosphenic molars and added new crests on the slopes of the "hypocone."

Comparison of the Masticatory Motor Pattern of Koalas and Placental Herbivores

Figure 6 compares the primitive motor pattern of opossums and tree shrews with that of three marsupial herbivores (koala, wombat, and kangaroo) and two placental herbivores (alpaca and goat). The motor pattern for the alpaca and goat is based on Figure 4 in Williams et al. (2007), which compares the motor patterns of a goat, alpaca, and horse. In Figure 6, Group I and Group II muscles are included within light gray and dark gray ellipsoids respectively. The essential differences of these patterns lie in the activation sequence of individual muscles, their amplitude, and the temporal separation of their periods of activity.

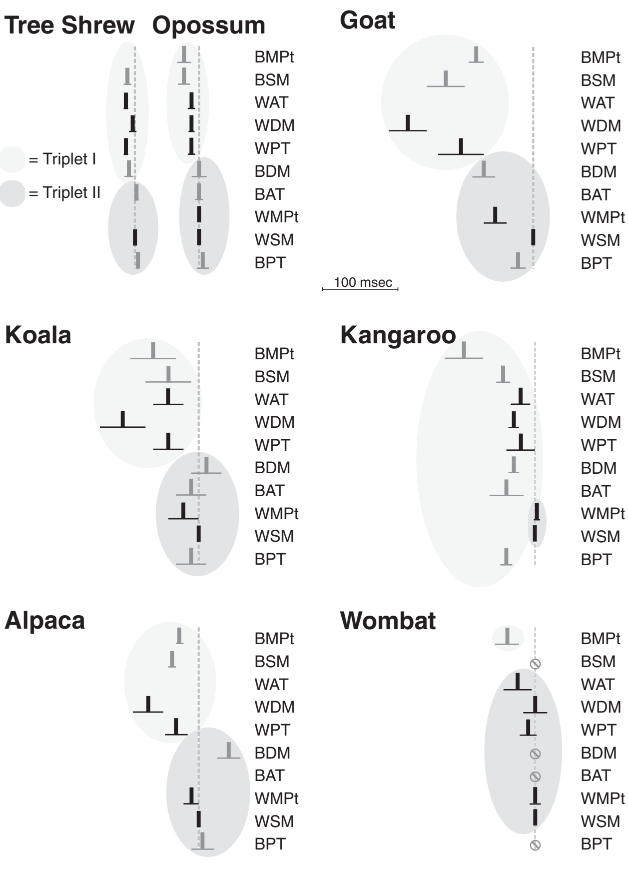

Figure 6. Comparison of the masticatory motor patterns (sequence of activity of the adductor muscles) in placentals and marsupials with a primitive pattern (tree shrew and opossum) and transverse pattern (koala, alpaca, goat, kangaroo and wombat). Time of activity is shown relative to the working-side superficial masseter (vertical dotted line). Scale for time (horizontal axis) is the same for all figures. Group I muscles are included in light gray and Group II muscles in dark gray ellipsoids. The order in which the muscles are listed is the same in all figures and is based upon the sequence of activity of the muscles in the American opossum.

The masticatory motor pattern of the koala is similar to that of the alpaca, which like the koala has a fused mandibular symphysis (Williams et al., 2007). However, Louys et al. (2009) has shown that early phascolarctids of the Oligo-Miocene age had unfused mandibular symphyses and concluded that they had a smaller transverse component to the power stroke than do extant koalas. In alpacas and koalas, the muscles assigned to Groups I and II and their activation sequences are almost identical. For example, in both, the working-side deep masseter is the first muscle to peak and the balancing-side deep masseter is the last. Horses (Williams et al., 2007) and higher primates have a similar pattern. According to Hylander and Johnson ('94), a fused mandibular symphysis in higher primates seems designed to resist "wishboning" caused by the medially directed force the balancing-side deep masseter generates toward the end of the power stroke. Hylander et al. (2000, 2005) correlate the late firing of the balancing-side deep masseter with the presence of a fused mandibular symphysis. Williams et al. (2007, 2008) suggest that the fused symphysis in alpacas may serve to resist twisting of the symphysis around a transverse axis. Either explanation may account for the presence of a fused mandibular symphysis in koalas and alpacas.

Alpaca molars have no obvious morphological features such as those present in the molars of koalas, which engage first as the jaw moves vertically, and second as the jaw moves medially. Nevertheless, the similarity in the order of firing of Group I muscles in the alpaca and koala suggests that jaw movements during the early part of the power stroke in the alpaca may also be vertically oriented, and precede the onset of medially directed movement.

The transition from a primitive motor pattern to the transverse pattern of koalas and alpacas involves a great increase in the time over which the adductors are active during the power stroke as well as an increase in the duration of activity of the individual muscles. The working-side deep masseter fires well before and the balancing-side deep masseter after the other adductors. Although the other adductors' duration and temporal separation change, their firing sequence remains much the same as in the primitive pattern.

Mandibular Angle

An interesting feature common to koalas and placental ungulates is the presence of a deep mandibular angle. Figure 7 compares the posterior views of goat, koala, and wombat mandibles. In both the goat and koala, the medial pterygoid and masseter muscles are directed dorso-medially and dorso-laterally respectively, holding the jaw in a muscular sling (Becht, '53). An inflected angle was almost certainly present in early diprotodontians but secondarily deepened in the koala lineage. The deep mandibular angle and a decrease in the size of the external part of the medial pterygoid appear to be associated with the acquisition of a masticatory motor pattern convergent on that of some placental herbivores.

Comparison of Koala and Wombat Occlusion and Motor Programs

Wombat dentition has adapted to a diet of dry, tough vegetation (Finlayson et al., 2005). The rows of the hypsodont's ever-growing molars are isognathous and relatively closer to the midline than in koalas (Fig. 1C), but molar wear patterns indicate unilateral occlusion. The molars are quadritubercular but lack high cusps supporting shearing crests. The cusp pattern of freshly erupted wombat molars is rapidly worn away and most of the occlusal surface except for a layer of enamel on the lingual surface of the uppers and labial surface of the lowers consists of dentine. Ever growing, these molars compensate for their rapid attrition. At the beginning of occlusion, wombats' working-side lower molars lie externally to the uppers (Murray, '98; Crompton et al., 2008b). As the working-side molars draw medially at the beginning of the power stroke, the leading lingual edge of the lower molars meets the labial edge of the uppers to shear food. Since both surfaces consist of dentine the occlusal surfaces are rapidly worn away. During the remainder of the power stroke food continues to be sheared and ground until dentine on the lingual surface of the lowers meets the enamel ridge on the lingual surface of the uppers and the dentine on the labial surface of the uppers meets the enamel ridge on the labial surface of the lowers (Murray, '98).

In contrast to koalas the power stroke in wombats is not divided into two phases, but consists of a single medially directed linear movement. Figure 6 compares the masticatory motor pattern of the wombat with that of the koala. In the wombat, the balancing-side medial pterygoid draws the working side laterally rather than the working-side deep masseter as it does in koalas. During the power stroke only the working-side adductors are active. Working-side muscles that in koalas and primitive mammals are part of the Group I complex (working-side anterior and posterior temporalis and deep masseter) act together with Group II muscles (working-side medial pterygoid and superficial

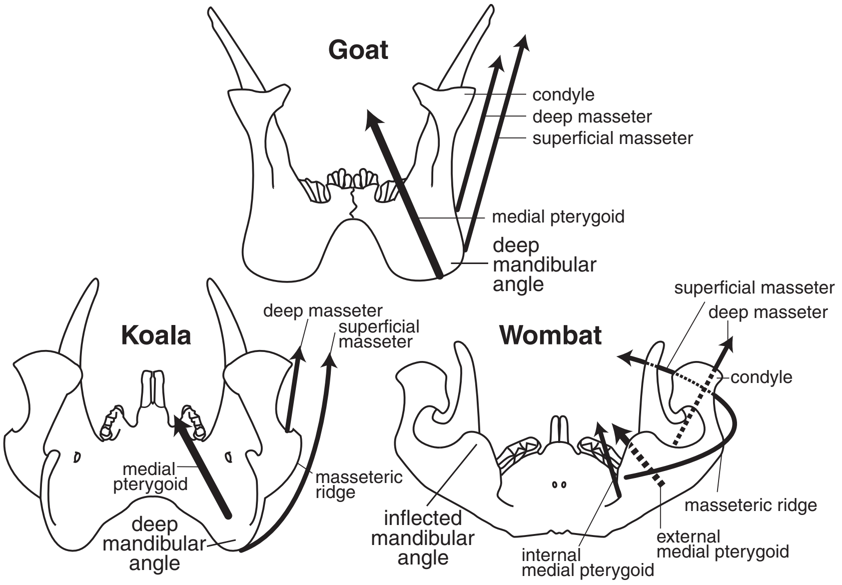

Figure 7. Posterior view of the lower jaws of a goat (*Capra hircus*), koala (*Phascolarctos cinereus*) and wombat (*Lasiorhinus latifrons*). Notice the differences in the orientation of the mandibular angle—deep in the goat and the koala, and inflected in the wombat. Arrows indicate the approximate vector of the masseter and medial pterygoid muscles. Notice that the medial pterygoid is undivided in the goat and the koala, but has two distinct parts (internal and external) in the wombat. Dashed arrow indicates muscle position behind a bone surface.

masseter) to draw the jaw medially (Crompton et al., 2008b). The balancing-side muscles (superficial masseter, deep masseter, anterior and posterior temporalis), active during the power stroke in all other mammals, are silent during the power stroke in wombats.

The presence of a wide inflected mandibular angle in wombats profoundly affects the organization of the adductor muscles (Fig. 7). In contrast to koalas and placental herbivores, the wombat's lower jaw is not held in a muscular sling. From its origin on the anterior surface of the zygoma, which lies medial to the condyle, when viewed from behind the superficial masseter passes obliquely backwards and wraps around the masseteric ridge and then directs medially to its insertion on the internal region of the inflected angle. The action of this muscle is to twist the whole mandible around its longitudinal axis (condyle to symphysis). The large external part of the wombat's medial pterygoid inserts on the dorsal surface of the inflected angle and is more horizontally oriented than the medial pterygoid in either koalas or placental herbivores. The deep masseter is directed dorso-medially. The skull of the wombat is wide and shallow, and its adductor muscles, relative to molar dentition, lie farther laterally than in koalas and macropods (see Fig. 5.11 in Crompton et al., 2008b). This contributes to the rotation of the mandible around its longitudinal axis and helps to separate the balancing-side molars during the power stroke. Any significant adductor force on the balancing side at this time would bring the balancing-side molars into occlusion, preventing transverse movement of the working-side molars.

The motor pattern controlling transverse jaw movements in wombats differs fundamentally from that of koalas and placental herbivores. Their unique masticatory apparatus probably evolved during the transition from an arboreal to terrestrial life style (Meredith et al., 2009). Brewer et al. (2009) concluded that the molars of the earliest wombats were "… poorly adapted to a diet consisting of leaves or grass, but would have been perfectly capable of coping with ingested grit as a result of masticating rhizomes and tubers or abrasive plant material such as barks and stems." It is not possible to derive the masticatory apparatus of wombats from that of extant koalas because wombats have retained the primitive marsupial inflected angle whereas koalas lost it. Subsequent to the koala-wombat split both animals' masticatory regions underwent major changes and their motor programs appear to be independent modifications of a primitive program.

Comparison of the Motor Patterns of Koalas and Macropods

Macropods have modified the tribosphenic molar in ways very different from those seen in koalas. Rather than retaining shearing crests on the mesial and distal surfaces of principle cusps, they have developed high transverse lophs that join the paracone to protocone, metacone to hypocone, protoconid to metaconid, and hypoconid to entoconid. In addition, mesio-distal ridges or links join the bases of the lophs. Macropod molar occlusion can be divided into two distinct phases, a vertical (Phase Im) followed by a medial (Phase IIm). As occlusion begins, the working-side lower molars are positioned directly below the uppers. Food is sheared between the transverse lophs as the jaw closes in a dorsal direction and crushed as the lophs meet the links. Food is broken down further as the upper and lower lophs are drawn across the links on the matching molar (Sanson, '80, '89). The narrow upper incisal arcade into which the large lower procumbent incisors fit (see Fig. 1A) restricts transverse movement (Janis and Fortelius, '88; Crompton et al., 2008a).

The transition from vertical to medial jaw movement during the power stroke is abrupt in macropods (Crompton et al., 2008a), whose motor pattern reflects the direction change during the power stroke (Fig. 6). The principal muscle drawing the working side laterally in macropods is the balancing-side medial pterygoid rather than the working-side deep masseter as in koalas and placental herbivores. In macropods, the balancing-side deep masseter and balancing-side anterior and posterior temporalis fire as the jaw moves vertically, rather than medially as in placental herbivores and koalas. Consequently, more muscles are active during Phase Im when the jaw moves vertically, and only two muscles—the working-side medial pterygoid and superficial masseter—are available to draw the working-side hemi-mandible medially (Phase IIm). This suggests that a higher bite force may be generated during the vertical Phase Im than during the transverse Phase IIm of the power stroke. In macropods and goats, the balancing-side deep masseter reaches peak activity before the other Group II muscles (Fig. 6) and does not generate a transversely directed force at the end of the power stroke. This may be associated with the presence of a highly mobile symphysis in both (Williams et al., 2007).

Evolution of Masticatory Motor Patterns

Jaw movements during mastication are basically the same among all mammals possessing tribosphenic molars (opossum and tree shrew, Fig. 6), but they vary in terms of the sequence of activity in their adductor muscles. For example, in tree shrews, galagos, and opossums, Hylander et al. (2005) and Vinyard et al. (2006a) report that the deep masseter on the balancing side fires before that of the working side. In some tree shrew recordings, this pattern is reversed. In our recordings of opossum mastication both patterns are encountered, but the order of activity of the other adductors appears to be identical to that of tree shrews. These differences may be due to electrode placement. In all cases peak activity in these muscles are within five to ten milliseconds of one another, suggesting that a single primitive motor pattern was common to early placentals and marsupials with tribosphenic molars. Mammals with a transverse motor pattern have no such unified pattern. Williams et al. (2008) have shown that there is no single transverse masticatory motor pattern for placental herbivores and our results extend this premise to marsupial herbivores.

In placental herbivores the lower jaw is held in a muscular sling formed by the masseter and medial pterygoid muscles. The sequence and duration of activity of the adductors effecting transverse jaw movements appear to be subtle modifications of the primitive pattern. In ungulates with a mobile mandibular symphysis, peak activity of the adductors increases in duration and in the time separating them compared to the primitive pattern. In placental herbivores with a fused mandibular symphysis, a notable difference lies in the late activity of their balancing-side deep masseter (Hylander et al., 2000, 2005).

Modifications to the primitive pattern are more profound in macropods and wombats, as is the difference in the sequence of motor activity. Differences between the motor patterns of marsupial and placental herbivores may be due to the presence of an inflected mandibular angle. There is a marked contrast in the superficial masseter and medial pterygoid configurations between macropods and wombats on one hand and placental herbivores on the other. In the former, the superficial masseter wraps around the inflected angle and the external portion of the medial pterygoid is more horizontally oriented and enlarged. In the latter, the superficial masseter orients vertically and the medial pterygoid inserts on the placental herbivores' deep mandibular angle (Fig. 7). Wombats rely only on working-side muscles to move the jaw medially. Macropods have reduced the number of muscles involved in moving the jaw medially and increased the number of muscles involved in moving the jaw dorsally during Phase Im. Figure 8 shows the relationships of the taxa discussed in this paper. It also illustrates how the anatomical and kinematic features that are associated with a primitive masticatory motor pattern are modified in selected placental and marsupial herbivores.

The view that the inflected and vertical mandibular angles are associated with different muscle activity patterns to control transverse jaw movements could explain the convergence of the motor patterns of koalas with those of some placental herbivores, although a more thorough evaluation of mastication in koalas and placental herbivores would be necessary to confirm such a relationship. As in placental herbivores, the reversal of an inflected to deep mandibular angle in the koala lineage resulted in placing the angle in a muscular sling. This suggests that koalas and some placental herbivores modified their ancestral motor patterns in similar ways, whereas macropods and wombats modified it in unique and different ways.

Although mandibular angle (inflected or vertical) appears to be related to the activity pattern of the adductor muscles that affect medially directed jaw movements, this does not explain the origin of two types of mandibular angles. The primitive pattern is associated with tribosphenic molars and a near vertical jaw movement during the closing stroke. The sequence of firing in the working- and balancing-side deep masseters may represent the only significant difference between the primitive pattern of marsupials (opossums) and placentals (tree shrews). In order to determine the significance of an inflected mandibular angle,

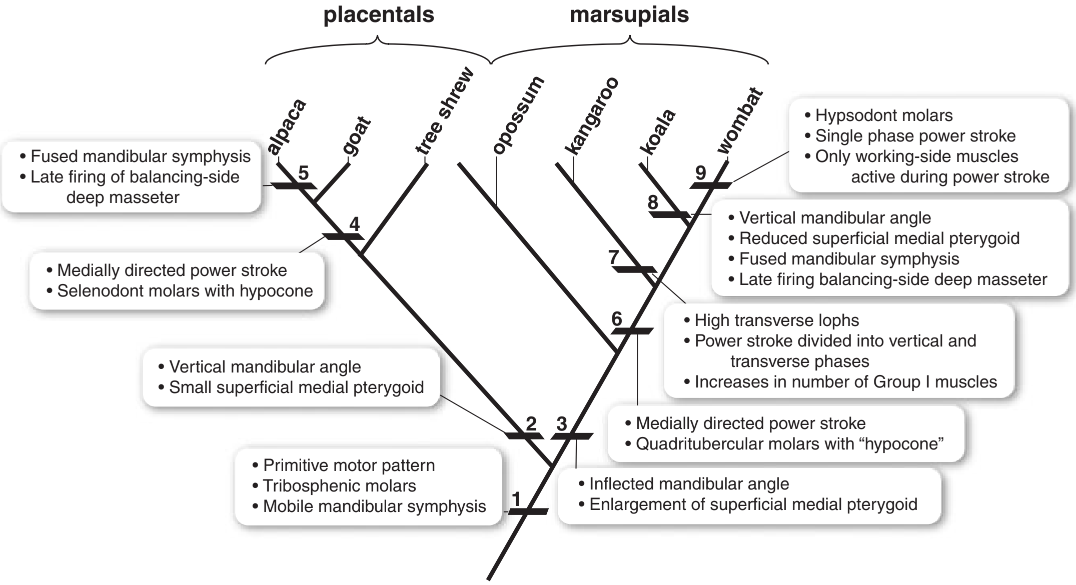

Figure 8. Relationships of the taxa discussed in this paper. The sequence of acquisition and a brief description of characteristic features of the masticatory system of these taxa is shown.

experiments that more accurately monitor the position of electrodes and jaw movements are required.

Conclusions

Despite the close relationship of koalas and wombats, *Hypothesis 1* is not supported. Each taxon has modified an ancestral motor pattern in unique ways. *Hypothesis 2*, however, is supported. Despite the vast phylogenetic distance between koalas and alpacas, they have evolved similar masticatory motor patterns.

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