Chapter 5
Motor Control of Masticatory Movements in the Southern Hairy-Nosed Wombat *(Lasiorhinus latifrons)*

Alfred W. Crompton, Daniel E. Lieberman, Tomasz Owerkowicz, Russell V. Baudinette*, and Jayne Skinner

Contents

Abbreviations **AT** and **a tem** anterior temporalis, **as ram** ascending ramus, **bdm** balancing-side deep masseter, **bmpt** balancing-side medial pterygoid, **btem** balancing-side temporalis, **bsm** balancing-side superficial masseter, **bu** buccinator, **ca** transverse orientation of condyle, **cran cav** cranial cavity, **DM** and **dm** deep

---

A.W. Crompton
Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge MA, 02138, USA
e-mail: acrompton@oeb.harvard.edu

* We regret to note that in the time period between completing this work and publication that Dr. Baudinette died on March 17, 2004.

C. Vinyard et al. (eds.), *Primate Craniofacial Function and Biology*,
DOI: 10.1007/978-0-387-76585-3_5, © Springer Science+Business Media, LLC 2008

masseter, **d mas** deep masseter, **DMPt** and **d mpt** deep part of the medial pterygoid, **ex s mas** external part of the superficial masseter, **fc** fibrous cartilage disc, **in rt** incisor tooth, **in s mas** internal part of the superficial masseter, **inf ang** inflected mandibular angle, **lpt** lateral pterygoid, **mas r** masseteric ridge, **MPt** medial pterygoid, **NC** nasal cavity, **o smas** origin area of superficial masseter, **o mpt** origin of medial pterygoid, **or** orbit, **ps** direction of jaw movement during the power stroke, **PT** and **p tem** posterior temporalis, **s** sinus, **SM** and **sm** superficial masseter, **SMPt** and **s mpt** superficial part of the medial pterygoid, **t** tendinous sheet, **tem** temporalis, **wdm** working-side deep masseter, **wmpt** working-side medial pterygoid, **wsm** working-side superficial masseter, **wtem** working-side temporalis **z** zygoma.

5.1 Introduction

Placental and marsupial herbivores have independently developed similar masticatory mechanisms to break down plant material. In both groups, chewing is accomplished by drawing the lower molars of the working side medially across the upper molars. The patterns of adductor muscle activity that controls jaw movement and generates strain in the mandibular corpus and symphysis are well documented in many placental mammals (Hogue and Ravosa, 2001; Hylander et al., 1998, 2000, 2004, 2005; Hylander and Johnson, 1994; Ravosa and Hylander, 1994; Vinyard et al., 2006; Weijs and Dantuma, 1981; Williams et al., 2003a, b, c, 2004). However, with the exception of the American opossum (*Didelphis virginiana*) (Crompton and Hylander, 1986; Crompton, 1995; Lieberman and Crompton, 2000), this information is not available for marsupials, including herbivorous taxa. The purpose of this paper is to describe the control of jaw movements in a marsupial herbivore, the Southern hairy-nosed wombat (*Lasiorhinus latifrons*), a large (22–24 kg), burrowing mammal from semi-arid South Australia, and to test the extent to which these patterns resemble those of placental herbivores.

In her extensive review of oral activity during feeding, Hiiemae (1978) stated: “the pattern of EMG activity was broadly similar in all mammals studied so far (1976) despite the differences in their profile of jaw movement.” Hiiemae (1978, 2000) recognized numerous themes common to all mammals in jaw and tongue movements and activity patterns of the adductor, supra- and infrahyoid muscles, and suggested that a basic mammalian pattern was established early on in their evolution. The review of the mammalian masticatory motor patterns by Weijs (1994), based upon the timing of the activity patterns of the jaw adductors during rhythmic chewing, expanded on these generalizations and proposed that the variations evident in jaw adductor patterns within extant mammals were modifications of an ancestral pattern.

Weijs divided the adductor muscles into three functional groups:

1. Symmetric closers (zygomaticomandibularis, and vertical fibers of the anterior temporalis) that fire early during the fast close phase (FC);

2. Triplet I (working-side temporalis and balancing-side masseter and medial pterygoid) that moves the working side of the jaw laterally during FC;
3. Triplet II (balancing-side temporalis and working-side masseter and medial pterygoid) that moves the working side of the jaw medially during the power stroke (PC). For convenience, we will continue to use the terms Triplet I and II despite the fact that more than three muscles are involved in controlling transverse jaw movements.

While details of how the adductor triplets function have yet to be worked out, it is important to note that several adductor timing patterns are evident among mammals. In the "primitive" motor pattern exemplified by the American opossum (Weijs, 1994; Lieberman and Crompton, 2000) and the treeshrew (Vinyard et al., 2005), the time differential between the onset and the offset of the muscle activity in Triplets I and II is relatively short, and consequently their respective periods of activity overlap considerably (Fig. 5.1). In the opossum, peak activity in the first muscle to fire (WDM) is only separated from that of the last (WSM) by 20–30 ms.

Primitive mammals have a highly mobile symphysis. In the opossum (Lieberman and Crompton, 2000) and the tenrec (Oron and Crompton, 1985), the hemi-mandibles rotate around their longitudinal axes. During the power stroke, the ventral border of the working-side hemi-mandible is everted (Fig. 5.1, bold arrow marked PS). As the molars lie above the axis of rotation (symphysis to jaw joint), medially directed transverse movement of the molars is effected by a combination of rotation and transverse movement of the whole hemi-mandible. Weijs (1994) demonstrated how in more specialized mammals the "primitive" motor pattern was altered by changing the timing of the onset, offset, and duration of the activity periods of the two triplets. For example, in carnivorous mammals that accentuate vertical jaw movements during the power stroke, Triplets I and II fire symmetrically. In ungulates like the goat (Fig. 5.1) that accentuate transverse movement of the working-side jaw, the time between peak activity in the first Triplet I muscle to fire (WDM) and the last Triplet II muscle to fire (WSM) is considerably longer than in primitive mammals. Depending on the food type, this may last between 150 and 250 msec. In the goat (Williams et al., 2003b, c), galagos (Hylander et al., 2005), ring-tailed lemurs (Hylander et al., 2003, 2004, Vinyard et al., 2006), and opossums (Lieberman and Crompton, 2000), the balancing-side deep masseter reaches peak activity before that of the working-side superficial masseter. In the goat, Triplet II muscles draw the working side hemi-mandible dorso-medially (bold arrow marked PS in Fig. 5.1) during the power stroke (Becht, 1953). The symphysis in the goat is slightly mobile. Some hemi-mandibular rotation can occur during opening and the beginning of closing in the goat, but not during the power stroke (Lieberman and Crompton, 2000). A mobile symphysis is capable of transferring vertically directed forces from one hemi-mandible to the other (Crompton, 1995), but appears to be poorly designed to transfer transversely directed forces.

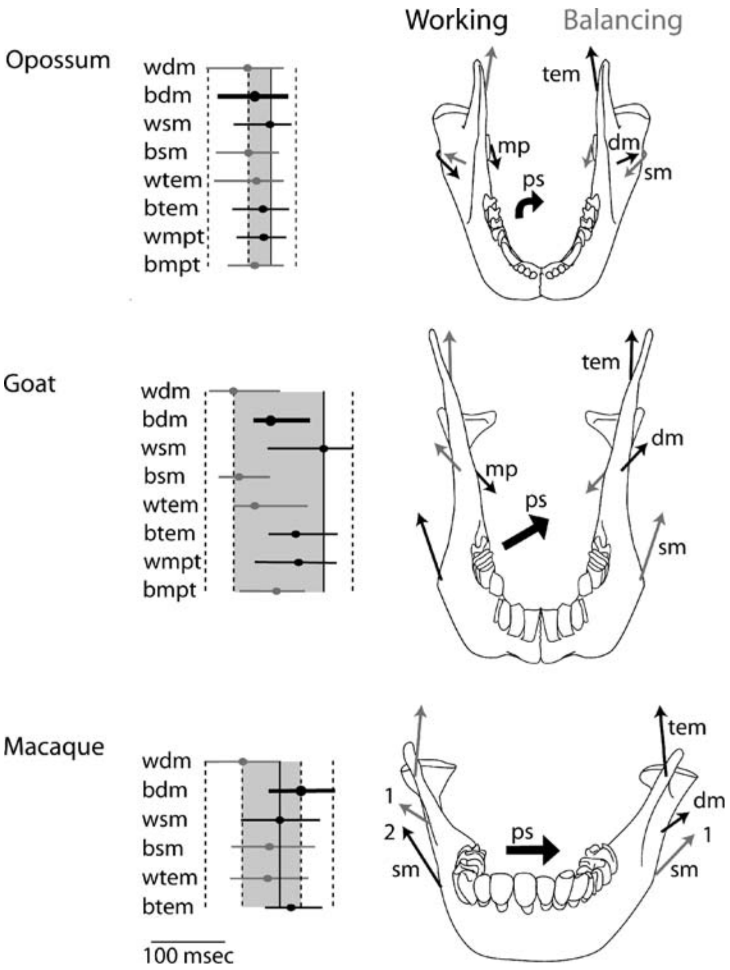

Fig. 5.1 Control of jaw movements in an opossum, goat, and macaque. On the left, the duration (indicated by horizontal lines) and time of peak activity (indicated by dots in the horizontal lines) in working- and balancing-side adductor muscles. On the right, the vectors of these muscles are shown on an oblique dorsal view of their lower jaws. Triplet I muscles are shown in gray and Triplet II muscles in black. The solid vertical line on the left is drawn through peak activity of the working-side superficial masseter. The shaded areas indicate the time between peak activity in the first and last muscles to fire. In the macaque there is a shift in the timing of activity in the balancing-side deep masseter

In animals with a fused symphysis (anthropoids, Hylander et al., 2000; Ravosa et al., 2000; sifakas, Hylander et al., 2003; and alpacas and horses, Williams et al., 2003b, c), the balancing-side deep masseter peaks after the working-side superficial masseter (Fig. 5.1). Hylander and colleagues suggest that the working- to balancing-side (W/B) EMG ratios and the muscle firing pattern of anthropoids support the hypothesis that symphyseal fusion and transversely directed muscle force are functionally linked (Hylander, 1984; Hylander and Johnson, 1994; Hylander et al., 2000, 2003, 2005).

In fused symphyses of placental mammals, the late firing of the balancing-side deep masseter generates lateral transverse bending, or "wishboning," of the mandibular symphysis in anthropoids (Hylander and Johnson, 1994). The fusion of the symphysis permits the complete transfer of a horizontal force from the balancing to the working side in order to draw the working side medially on a horizontal plane. Transverse movement early in the power stroke is generated by Triplet II muscles such as the working-side superficial masseter, working-side medial pterygoid, and balancing-side temporalis, but continued transverse movement toward the end of the power stroke is generated by the balancing-side deep masseter.

In placentals, a fused symphysis appears directly related to a shift in the timing of activity in the balancing-side deep masseter. In another placental, the alpaca, however, Williams et al. (2008) have shown that despite the late firing of the balancing-side deep masseter, the symphysis is fused and strengthened in order to resist twisting as opposed to any transversely directed forces. Strains associated with transverse masticatory forces in alpacas are small, it turns out. Williams et al. (2008) hypothesize that the fused symphysis functions to support the deep roots of the mandibular incisors.

While the general organization of the adductor muscles in marsupials and placentals is broadly similar (Turnbull, 1970; Abbie, 1939), the most striking difference between these two major groups is the presence of an inflected mandibular angle in marsupials and a deep non-inflected angle in placental herbivores. Sánchez-Villagra and Smith (1997) have shown that the inflected angle represents a synapomorphy of marsupials, but they could point to no consistent differences in mastication between marsupial and placentals that could be attributed to its presence.

Murray (1998) discussed the anatomy of the masticatory apparatus in the common wombat. He compared the mastication of wombats, rodents, and placental ungulates, and pointed out that the three groups exhibit different patterns of jaw movement: rodents emphasize propalinal jaw movements; ungulates emphasize wide translational movements of the mandible, slung between large medial pterygoids and superficial masseters; and wombats emphasize a more limited translational, but a more powerful compressive stroke during mastication. He concluded that the key attribute of the wombat's masticatory complex is an ability to exert extremely high occlusal forces as the lower molars are drawn medially in the horizontal plane, enabling the animal to grind down highly abrasive foods such as the fibrous perennial grasses and sedges typical of its diet (Finlayson et al., 2005). The anatomy of the masticatory apparatus in wombats differs from placental herbivores in many other respects, as well. Therefore, before presenting data on the kinematics and motor control of jaw movement during wombat mastication, we will begin with a review of the anatomy of wombat's teeth, mandible, cranium, and adductor muscles.

Transverse jaw movements and high occlusal forces are the hallmark of mammalian herbivores, but the anatomical features and neuro-muscular patterns commonly associated with transverse jaw movements are based entirely on placentals.

Wombats are ideal animals to test whether the models proposed for placentals are also true for marsupials.

5.2 Anatomy of the Wombat Masticatory System

5.2.1 Dentition

One of the most distinguishing features of the wombat is the postcanine dentition, characterized by tall, continuously growing, and semi-lophodont molars, well described by Murray (1998) and Ferreira et al. (1985, 1989). The height of the molar roots is illustrated in the transverse sections through the skull (Fig. 5.2, Sections 1[M^1], 2, 3). The upper and lower molars, as seen in these sections, form a sigmoid curve so that the exposed crowns of the upper molars are directed slightly laterally, and those of the lowers slightly medially. In occlusal view (Fig. 5.3B), the molars are bilobate with a deep embayment in the lingual aspect of the uppers and buccal aspect of the lowers, and smaller embayments on the opposite side. The enamel is thick on the buccal aspect of the lowers and lingual aspect of the uppers, and absent or extremely thin on the opposite sides. Most of the occlusal surface consists of dentine with the enamel forming a low ridge on the edge of the molar (Murray, 1998; Ferreira et al., 1985, 1989). The lower molars are positioned slightly anterior to the uppers (Fig. 5.3C).

In contrast to other herbivorous Diprodontia, such as the Phascolarctidae (koalas: Davison and Young, 1990) and macropodidae (kangaroos and wallabies: Sanson,

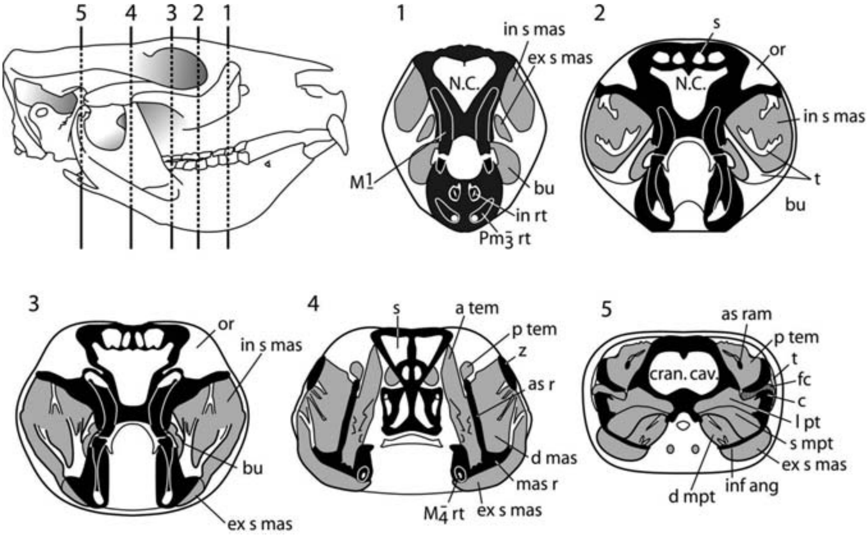

Fig. 5.2 *Lasiorhinus latifrons*. Five sections through the adductor musculature. The position of the sections is shown on a lateral view of the skull

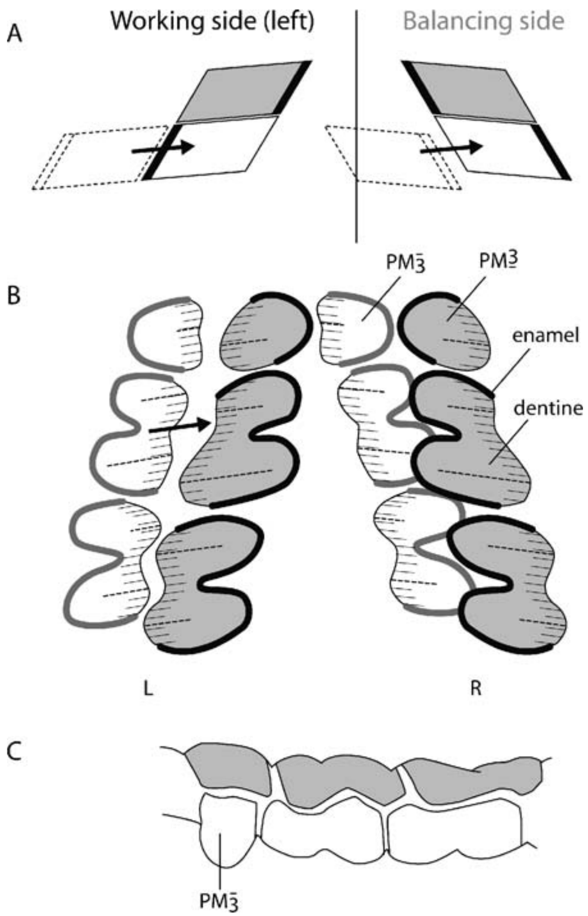

Fig. 5.3 *Lasiorhinus latifrons.* (**A**) The parallelograms represent schematic coronal (transverse) sections through the right- and left-side upper (*shaded*) and lower (*unshaded*) molars on either side of the midline (vertical line). The working side is on the left. At the beginning of occlusion, the positions of the lower molars are represented by parallelograms with dashed outlines and the end of occlusion with solid outlines. A thick black line represents the thick enamel on the lingual side of the uppers and buccal side of the lowers. (**B**) View of the occlusal surfaces of upper (*shaded*) and lower (*unshaded*) molars at the beginning of occlusion on the left side. Lingual enamel is indicated on the uppers by a thick black line and on the lowers by a thick gray line. (**C**) Lateral view of upper and lower PM3 and M1 and M2 to illustrate the position of the lower molars relative to the uppers

1980, 1989), who retain shearing crests on the sides of the main cusps of the molars, wombats rapidly wear down the occlusal surfaces of the molars leaving no remnant traces of the cusp pattern. In particular, the occlusal surfaces of the molars wear down heavily in the horizontal plane to produce low, rounded transverse ridges that fit into shallow valleys of the occluding tooth (Fig. 5.3C). The worn surfaces of the molars dip slightly in a ventral direction from lingual to buccal (Fig. 5.3A) so that the lingual edges of the molars are higher than the buccal edges. Judging from the observed lateral position of the lower incisors at the beginning of medially directed movement of the working-side mandible, the lingual edge of the posterior lower molar row meets or lies just lateral to the buccal aspect of the occluding uppers at the beginning of the power stroke. During transverse chewing movements, the exposed edges of dentine on the buccal edges of the upper molars and lingual edges of the lower molars rapidly wear down to form sharp cutting edges. Shallow transverse grooves are gouged out of the dentine on the lingual aspect of the lowers and buccal aspect of the uppers. Because of the orientation of the occlusal plane of the molars (Fig. 5.3A), the balancing-side molars do not contact each other at the beginning of the power stroke (dotted outline) and probably only come into full contact when centric occlusion is reached at the end of the power stroke. As Murray (1998) pointed out, food is trapped and broken down between the more resistant enamel ridges on the lingual side of the uppers and buccal side of the lowers. The wear pattern on the molar surfaces indicates that occlusion is unilateral.

Transverse jaw movement during the power stroke in wombats is probably achieved through the rotation of the jaw around the working-side condyle and the movement or translation of the balancing-side condyle in a posterior direction. However, as the molar rows are isognathic (the distance separating upper and lower molar rows are identical) and because transverse movement of the lower jaw as a whole does not exceed the transverse width of the upper molars, condylar translation during the power stroke is minimal. In wombats, the lower molars lie directly below the occluding uppers at the end of the power stroke. This limited medial movement contrasts with artiodactyls in which the narrower lower molars shear across the wider upper molars. At the end of the occlusal stroke in artiodactyls, both the active and the balancing-side lower molars lie internal to the matching upper molars (Crompton et al., 2005).

Another distinctive feature of the wombat dentition is the single pair of procumbent lower incisors (Figs. 5.2, 5.4). In the Southern hairy-nosed wombat (but not in the common wombat), the lower incisors shear past the posterior surfaces of the slightly larger upper incisor pair to produce a sharp apical cutting edge and beveled posterior surface on the uppers (Scott and Richardson, 1987). In order for the apices of the upper and lower incisors to meet, the lower jaw must be drawn slightly forward during opening and retracted as the jaw closes.

5.2.2 Skull

Several derived aspects of the wombat's skull are probably related to mastication. In general, wombat crania are broad and low with zygomatic arches that extend far laterally from the dentition (Figs. 5.2, 5.5), thereby extending the adductor musculature far laterally to the tooth row and increasing the leverage around the tooth row (Murray, 1998). The mandible is also large and broad. The mandibular symphysis, which houses the long roots of the lower incisors, is immobile because of a tightly interdigitating or partially fused suture that completely fuses in older individuals.

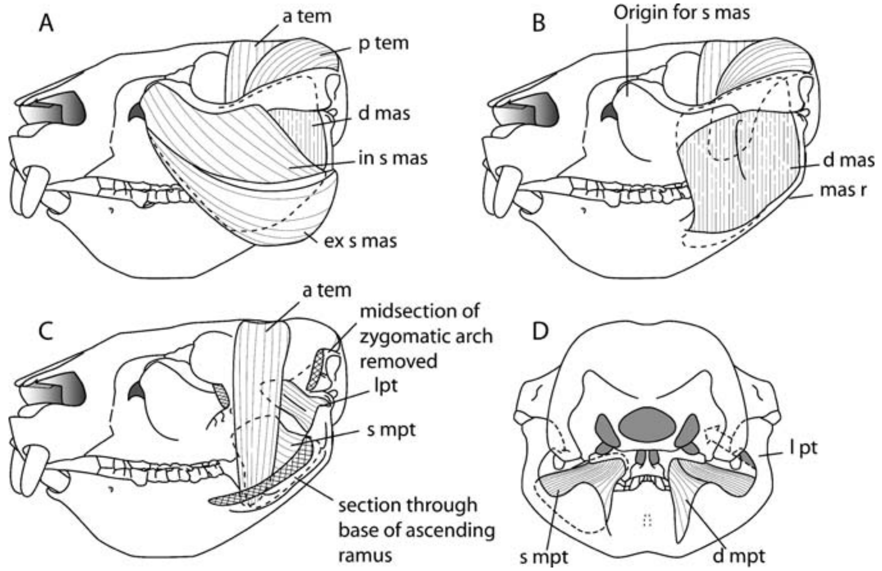

Fig. 5.4 *Lasiorhinus latifrons*. Lateral and posterior views of the adductor musculature. (**A**) shows the lateral view of the superficial masseter. In (**B**) this muscle is removed to expose the lateral surface of the deep masseter. In (**C**) the zygomatic arch and ascending ramus of the lower jaw has been removed to illustrate some of the deeper adductors. (**D**) is a posterior view.

Independent movement of the hemi-mandibles is therefore not possible. A large inflected mandibular angle extends internally far beyond the medial edge of the condyles (Fig. 5.5B, inf ang). The ventral surface of the angle forms a broad, thin, horizontal sheet (Fig. 5.2, Section 5.5). The massenteric ridge (Fig. 5.2, Section 5.4 and Fig. 5.5A, C, D: mas r) extends laterally so that a shallow depression separates it from the external surface of the ascending ramus.

The wombat temporomandibular joint (TMJ) is narrow antero-posteriorly, wide medio-laterally, and transversely oriented (Fig. 5.5A, C, D) in contrast to the long diarthroidal glenoid of the TMJ joint of placental ungulates. The axis of the narrow condylar head is oblique so that the medial edge lies posterior to the lateral edge (Fig. 5.5B, ca). In anterior and posterior views, the articular face of the mandibular condyle is convex and is separated from the concave and narrow glenoid (formed by both the squamosal and jugal) by a thick, tough fibrous disc (Fig. 5.2, Section 5.5, fc). A massive set of ligaments binds the temporal, the articular disc, and the condylar process of the mandible, restricting extensive antero-posterior movement of the mandibular condyle. Medially, a tendon of the lateral pterygoid muscle inserts on the medial aspect of the condyle and disc. In the common wombat, the medial aspect of the glenoid is buttressed by a prominent entoglenoid eminence. Murray (1998) suggests that the medial aspect of the condyle is forced against this structure, which acts as the point of rotation for the jaw as it moves in the horizontal plane.

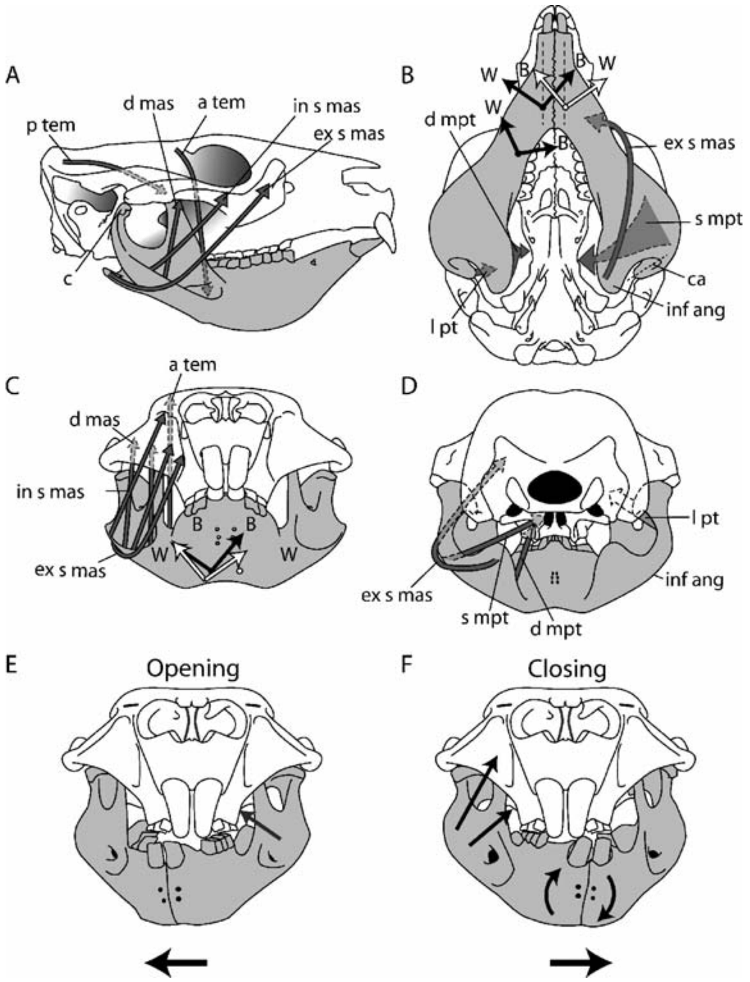

Fig. 5.5 *Lasiorhinus latifrons.* Average orientation of muscle fibers within the principal adductor muscles as seen in lateral (**A**), ventral (**B**), anterior (**C**), and posterior (**D**) views. The orientation of the principle strains (ε_1) on the ventral surface of the symphysis and ventral surface of the right hemi-mandible are indicated in **B**. The bold black arrows indicate strain orientation when chewing on the right side and the open arrows when chewing on the left side. Arrows labeled W indicates orientation of strain on the working side and those labeled B orientation of strain on the balancing side. Note that the orientation of working- and balancing-side strain orientations on each side are parallel to one another and shift through about 90° when the chewing side changes. In **B** and **C**, the orientation of principal strains is shown in ventral and anterior views, respectively. (**E**) At the end of opening and beginning of closing, the working side of the jaw (on the right side of this figure) is moved laterally by unilateral activity in the balancing (*left*) superficial medial pterygoid. (**F**) The working-side mandible is shifted in a medial direction by the synchronous activity of the working-side adductors. The working side of the jaw (*right*) is rotated clockwise (when viewed from the front) around its long axis (condyle to symphysis). Because of the tightly sutured mandibular symphysis, the balancing (*left*) side of the jaw is also rotated clockwise

5.2.3 Muscles

The jaw adductor musculature in wombats was described briefly by Murray (1998), and is illustrated in Fig. 5.4. The internal architecture of the muscles is complex and includes numerous intramuscular tendinous sheets, as shown in Fig. 5.2 (t). Figure 5.5 illustrates the principle directions of the muscle fibers within each muscle. The fibers of different muscle groups tend to interdigitate, and clear borders between muscles cannot be easily recognized. Weights and percentages of the total mass for the Southern hairy-nosed wombat (based on dissection of one specimen) appear in Table 5.1. These muscle ratios, specifically the relative dominance of the masseter, are similar to those in the common wombat (masseter, 65%; temporalis, 20%, pterygoid, 15%) (Murray, 1998). The masseter has a complex architecture. The superficial masseter is comprised of an external (ex s mas, Figs. 5.2, 5.4, 5.5) and an internal part (in s mas). The external part of the superficial masseter originates antero-ventrally on the root of the zygoma and inserts on and covers the ventral surface of the broad inflected mandibular angle. The internal part (in s mas) has a wide area of origin that extends posteriorly along the ventral edge of the anterior part of the zygoma, and it inserts on the massenteric ridge. The deep masseter (d mas) originates from the medial aspect of the zygoma and inserts in the basin formed between the massenteric ridge and the ascending ramus. The fibers of the two parts of the superficial masseter are oriented obliquely, while those of the deep, vertically. The anterior temporalis (a tem) originates on the exposed surfaces of the temporal fossa and inserts at the base and medial face of the ascending ramus; and the posterior temporalis inserts on both sides of the tip of the ascending ramus.

Although the pterygoid muscles are short and comprise a small percentage of the total adductor mass (Table 5.1), they have a large cross-sectional area. The wombat's medial pterygoid is divided into two: a deep part (d mpt) originates on the ventral edge of the pterygoid bone and inserts on the medial edge of the inflected angle of the mandible. A larger superficial part (s mpt) originates in a deep, concave pocket on the lateral surface of the alisphenoid above the pterygoid hamulus, and inserts on an extensive area that is bounded ventrally by the inflected angle and laterally by

Table 5.1 Weight and percentage of the total weight of the adductor muscle, in *Lasiorhinus latifrons*

Muscle	Weight	Percentage of total Weight
External Superficial Masseter	25.6 g	19.03
Internal Superficial Masseter	34.0 g	25.3
Deep Masseter	10.1 g	7.5
Total Masseter		51.8
Temporalis	42.1 g	31.3
Medial Pterygoid	16.0 g	11.9
Lateral Pterygoid	6.7 g	5.0
Total	134.5 g	

the medial surface of the ascending ramus and articular process (Fig. 5.4C, D and Fig. 5.2, Section 5.5). The fibers of the superficial medial pterygoid vary between horizontal and oblique, whereas those of the deep medial pterygoid are more vertical in orientation. The lateral pterygoid (l pt) has an insertion area on the medial aspect of the condyle and articular disc, and originates from the lateral aspect of the squamosal medially to the glenoid and above the origin of the superficial medial pterygoid.

5.3 Hypotheses to be Tested

5.3.1 General Hypothesis

The general hypothesis tested here is that the wombat, a grazer with molars designed to break down food by transverse movement of the lower teeth relative to the uppers, will, as Weijs (1994), Hiiemae (2000), and Kalvas (1999) all implied but did not explicitly state, resemble placental grazers in terms of the neuromuscular control of jaw movements. This hypothesis is tested via two more specific hypotheses:

3.1.1. The masticatory motor pattern for the control of jaw movements in wombats is predicted to resemble that of placental grazers such as goats and horses, wherein Triplet I muscles move the working-side jaw laterally and, during the power stroke, Triplet II muscles move the jaw medially. Both Triplet I and Triplet II muscles will also have a superior component of force. A substantial time difference is predicted to separate the activity periods of the two muscle groups.

3.1.2. The tightly sutured mandibular symphysis in wombats is predicted to transfer transversely directed forces from the balancing to the working side, as it does in placental herbivores with a fused symphysis. It is further predicted that these forces are generated early in the power stroke by Triplet II muscles and late in the power stroke by the balancing-side deep masseter muscle.

5.3.2 Alternate Hypothesis

The first two hypotheses do not take into consideration the fact that herbivory in Australian mammals developed independently and in isolation from the evolution of herbivory in placental mammals. The masticatory apparatus of wombats, despite superficial similarities such as a fused symphysis and transverse jaw movements, differs fundamentally from that of placental herbivores. Examples of these differences include the wombat's large inflected mandibular angle, the enlarged superficial part of its medial pterygoid muscle, the narrow transversely oriented mandibular condyle, and the position of enamel on its molars. Based upon these differences, it is predicted that the masticatory motor control pattern is also fundamentally unlike that of placental herbivores.

5.4 Material and Methods

5.4.1 Subjects

Data were collected from six mature hairy-nosed wombats (see Table 5.2) housed at the animal facility on the Waite campus of the University of Adelaide.[1] Data were collected from nine experiments: initially on six animals between September and November 2001 and then on three of the same animals in June 2004. The animals were housed in pens, 3/4 m in size, in which a stainless steel mesh was buried 1 m below the ground surface to prevent the animals digging deep tunnels and escaping. Each animal was provided with an artificial underground burrow that was covered with a removable roof.

The animals were given a daily diet of lucerne (alfalfa), oats, pellets, and freshly cut grass. Fresh water was provided daily. For the collection of data, the animals were housed temporarily in the animal quarters of the University of Adelaide.

Table 5.2 Data collected on nine hairy-nosed wombats

Animal	Electrode placement	Rosette strain gauge position
2001		
Wombat 1	r & l superficial masseter and medial pterygoid	r & l symphysis and ventral mandibular surface
Wombat 2	r & l superficial masseter and medial pterygoid	r & l symphysis and ventral mandibular surface
Wombat 3	r & l superficial masseter and medial pterygoid	r & l symphysis and ventral mandibular surface
Wombat 4	r & l anterior & posterior temporalis, deep masseter, superficial masseter and medial pterygoid	none
Wombat 5	r & l anterior & posterior temporalis, deep masseter, superficial masseter, and medial pterygoid	none
Wombat 6	r & l anterior & posterior temporalis, deep masseter, superficial masseter and medial pterygoid	none
2004		
Wombat 7	r & l temporalis, superficial masseter and deep &superficial medial pterygoid	r & l symphysis
Wombat 8	r & l temporalis, deep masseter, superficial masseter, and medial pterygoid	r & l symphysis
Wombat 9	r & l deep masseter, superficial masseter and deep & superficial medial pterygoid	r & l symphysis

---

[1] These animals were part of a wombat colony being studied by Glen Shimmin (Shimmin et al., 2001).

5.4.2 Surgery

In Wombats 1, 2, and 3 (Table 5.1), strain gauges were placed on either side of the suture on the ventral surface of the mandibular symphysis and onto the ventral surface of the right hemi-mandible below M_1. Six EMG electrodes were placed in the medial pterygoid and superficial masseter. In Wombats 4 through 6, 12 electrodes were implanted in the medial pterygoid, masseter, and temporalis muscles, but data could only be collected from six electrodes at any one time. In Wombats 7, 8, and 9, two strain gauges were positioned on the ventral surface of the symphysis. Twelve electrodes were implanted in the medial pterygoid, masseter, and temporalis muscles, but data could only be collected from ten electrodes at a time.

Prior to surgery, all the animals were sedated with Zoletil (1 mg/kg) and then maintained on a surgical plane of anesthesia with isoflurane administered through a facemask. All incision sites (skin as well as periosteum) were infused with a local analgesic Bupivacaine (diluted 1:10 v/v). In Wombats 1, 2, and 3, the ventral surface of the jaws and neck of all the animals were shaved and sterilized. Under sterile surgical conditions, an incision was made ventral to the mandibular symphysis and in the midline below the posterior region of the lower jaw. A plastic tube with an external diameter of 6 mm was inserted below the skin between these two incisions. Three insulated FRA-1-11 rosette strain gauges (Sokki Kenkyujo, Tokyo, Japan) of 120 ± 0.05 Ω resistance and their leads, together with six electrode wires, were led forward through the tube that was subsequently removed, leaving the leads and wires below the skin. The surface of the bone at each gauge site was prepared by cutting a small window in the periosteum, cauterizing any vessels in the bone and degreasing with chloroform. Gauges were bonded to the bone using methyl-2-cyno-acrylate glue and the orientation of the A-element of each gauge relative to the longitudinal axis of the symphysis was measured. Enameled copper wire (0.125 mm) was used to prepare the EMG electrodes. The tips of the electrodes were inserted in the ends of either a 2- or 3-in, 20-gauge hypodermic needle. The needle was inserted through the posterior portion of the medial incision into a selected muscle and then withdrawn, leaving the hooked tips of the electrodes in place. Electrodes were inserted in the superficial masseter on both sides just below the inflected mandibular angle. An attempt was made to insert one electrode in the deep and one electrode in the superficial portions of the medial pterygoids on both sides of the skull. The incisions were closed and the leads from the strain gauges and the electrodes led to two 25-pin connectors (one for strain gauges and one for EMG electrodes) on the animal's back.

In Wombats 4 through 6, a similar procedure was followed to place six electrodes in the medial pterygoid and superficial masseter. In addition, electrodes were placed in the temporalis muscle. The skin over the temporal and neck region was shaved and sterilized. A medial incision was made in both regions and a plastic tube was led subcutaneously between the two incisions. Wires for six electrodes were passed through the tube and inserted in the anterior and posterior temporalis. An attempt was made to reach the deep masseter with the aid of a 3-in, 20-gauge needle inserted vertically, lateral to the ascending ramus of the dentary. EMGs were collected first from the six ventrally placed electrodes, then from the six dorsally placed electrodes, and finally from all six electrodes on the right side.

For Wombats 7 through 9, the same procedure was followed to place two rosette gauges on the symphysis and twelve electrodes in the masseter, temporalis, and medial pterygoid complexes. Leads from the electrodes and strain gauges were led to a 37-pin connector on the animal's back. The connectors were positioned between the shoulder blades and together with the superficial wires held in place by flexible bandages loosely wrapped around the animal's neck and chest. Strain and EMG data were first collected approximately 6 h after surgery and again 24 h after surgery.

5.4.3 Recording

During recording sessions, the strain gauges were connected via insulated wires to Vishay 2120A amplifiers (MicroMeasurements Inc., Raleigh, NC, USA) to form one arm of a Wheatstone bridge in quarter bridge mode; bridge excitation was 1 V. Voltage outputs were recorded on a TEAC$^{\text{TM}}$ RD-145T DAT tape recorder (TEAC$^{\text{TM}}$ Corp, Tokyo, Japan). Gauges were periodically balanced to adjust for zero offsets during the experiment and calibrated when the animal was stationary. EMG electrodes were connected to P511J amplifiers (Grass Inc., Quincy, MA, USA) and amplified (X1000–X10000) with a 300 Hz–3 kHz bandpass filter. All data were recorded digitally on the TEAC tape recorder. Amplification of each EMG electrode was held constant during the course of each feeding sequence.

Feeding behavior was recorded with a digital video recorder (DCR-TRV30 Sony). Because wombats eat with their heads directed downward, they were fed on a 3/4 in glass plate and filmed from below in order to document the chewing side. In order to synchronize the video, strain, and EMG data, a small diode was placed within the edge of the video field. Manually triggered short pulses, of varying duration and number, illuminated the video and generated a 5-V signal that was recorded synchronously with the EMG and strain data on the tape recorder.

5.4.4 EMG and Strain Gauge Analysis

Sections of EMG data that corresponded to video recordings of rhythmic molar chewing were sub-sampled at 6 kHz using TEAC's QuikVu II program. A program written by D. Hertweck processed the EMG data. This program eliminated any offset, fully wave-rectified the raw EMG signals, applied constant time (10 ms) reset integration, rejected randomly timed activity following Thexton (1996), and graphed the resultant EMG signals together with any other associated mechanical measure (strain, synchronization pulse, etc.). EMG records chosen for analysis were limited to feeding sequences in which the chewing side shifted several times. Final analysis of all data was carried out using Igor Pro^{TM} 2.01 (WaveMetrics, Inc., Lake Oswego, OR). In order to determine working-to-balancing-side ratios, peak EMG activity for the recording of each muscle was scaled to 100 units and total activity calculated by totaling the activity levels at 10-msec intervals, that is, the area under the curve.

Selected sequences of strain data were sampled from the tape recorder on a Macintosh G4 computer using an Ionet^{TM} A-D board (GW Instruments, Somerville, MA, USA) at 250 Hz. A Superscope 3.0^{TM} (GW Instruments, Somerville, MA, USA) virtual instrument, written by D.E.L., was used to determine the zero offset and calculate strains (in microstrain, $\mu\varepsilon$) from raw voltage data using shunt calibration signals recorded during the experiment. For each gauge, principal tension (ε_1), compression (ε_2), and the orientation (ϕ) of the principal tensile strain relative to the longitudinal axis of the symphysis were calculated following equations in Biewener (1992). Processed EMG and strain data were then correlated with the synchronization signal.

5.5 Results

5.5.1 Muscle Activity

Figure 5.6 illustrates EMGs of muscles from which successful recordings were obtained in the nine wombat experiments. Sequences chosen for analysis include frequent shifts in the chewing side with right-side muscles in black and left-side muscles in gray; bars beneath the graphs indicate the working side (black for right, gray for left). Vertical lines (labeled in Fig. 5.6, W1) divide each cycle into two periods. Period 1 is the power stroke; during Period 2 the jaw opens and begins to close. The lengths of the masticatory cycle (measured from the time of onset of adductor activity of one cycle to the time of onset of activity of the next cycle) vary between 395 ± 12 msec and 600 ± 83 msec (Table 5.3). The cycle lengths are governed by food type: longer cycles are associated with lucerne, medium lengths with pellets, and the shortest with rolled oats. Adductor activity occupies about 50% of the cycle length (Table 5.3).

The most striking feature of wombat mastication is that, with the exception of some parts of the medial pterygoid, muscle activity during the power stroke is virtually restricted to the working side. Unilateral adductor activity in the wombat contrasts with all other placental herbivorous mammals in which both the working- and the balancing-side muscles are active during the power stroke. In several recordings, it is possible to compare the ratio of the level of activity of muscles on the working side with those on the balancing side. We only compared ratios of sequences that included a side shift. The maximum level activity in each muscle was scaled to 100 units, and the total activity during the power stroke of a single cycle was based on the area below the curve rather than peak values. We divided the value associated with each working-side muscle by that of a matching balancing-side muscle value to

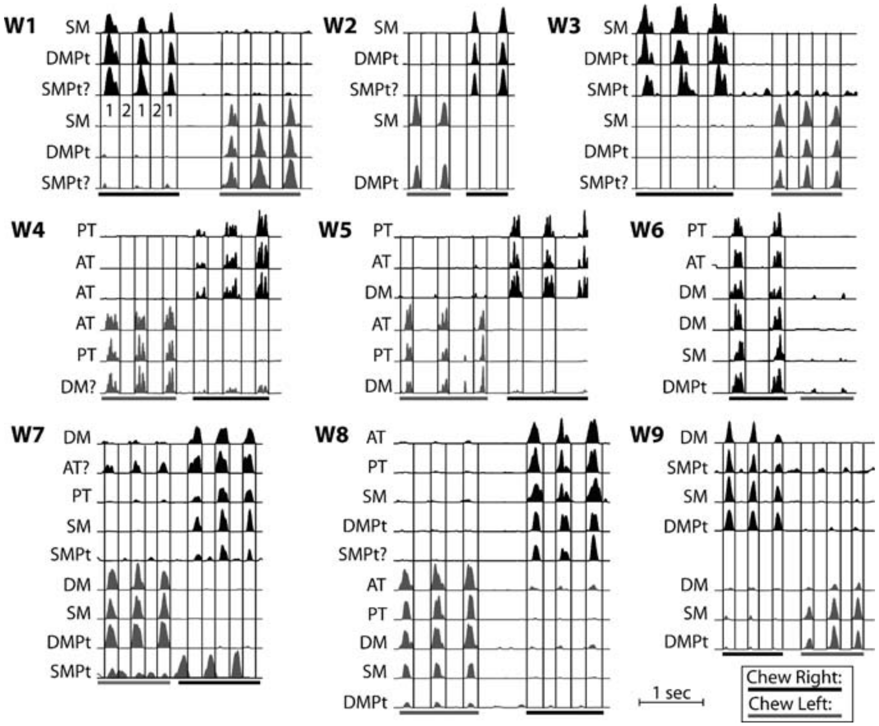

Fig. 5.6 *Lasiorhinus latifrons*. EMGs of a selection of adductor muscles during shifts in the chewing side in nine different wombat experiments. EMGs of muscles on the *right* are shaded black and those on the *left*, gray. The black bar *below* the EMGs indicates that the animal was chewing on the *right*, the gray bar, chewing on the *left*. Chewing cycles are divided into two periods by vertical lines. Period 1: adductor activity is on the working side when the working side of the jaw is drawn medially. Period 2: there is no activity in the working-side adductors

Table 5.3 Summary of cycle length and percentage of cycle with active adductors in six wombats feeding on different foods

	Animal	*n*	Median cycle length in ms	SD	Duration power stroke as % cycle length	SD
Oats	W9	5	395	12.9	49.4	4.4
	W7	10	402	19.3	54.5	3.4
	W2	10	432	38.2	49.9	7.5
Pellets	W1	10	458	45.6	50.9	4.3
	W4	10	467	23.6	49.5	5.1
	W3	10	497	52.7	49.6	5.7
	W8	10	507	52.5	46.9	6.4
Lucerne	W5	10	591	86.5	45.1	6.7
	W6	8	600	83.1	44.7	6.1

Table 5.4 Working-to-balancing side ratios of adductor activity during the power stroke in different adductors of *Lasiorhinus latifrons*

	AT	PT	DM	SM	MPt
W1				>50	>50
W2				>50	>50
W3				>50	>50
W4	>50	>50			
W5	>50		>50		
W7			>50	>50	34
W8	14	22	12		>50
W9			19	>50	>50

determine the working-to-balancing (W/B) side ratio (Table 5.4). In those instances where it was possible to record simultaneously from the same muscle on both the working and balancing sides, the lowest ratio was 12:1; however, the W/B ratio was highly variable and usually greater than 50:1 because the levels of most balancing-side muscles were either zero or extremely small. Muscles that tended to register the smallest ratios included the temporalis and deep masseter. In some cases, simultaneous recordings of working- and balancing-side muscles were not obtained. In these cases, we compared the levels of activity in the same muscle during a side shift when it was first on the balancing side and then on the working side. In two such cases, the deep masseter in Wombat 4 and the anterior temporalis in Wombat 7 (Fig. 5.6), the W/B ratio varied between 2.5 and 5.7. For these recordings, the electrodes had been placed deep in the muscles and it could not be determined whether they were in the intended locations.

In Wombats 1, 2, 3, 7, 8, and 9, the medial pterygoid was accessed from the ventral surface of the jaw. An attempt was made to place electrodes in both the superficial and deep parts of this muscle, but the actual position within the muscle could not be confirmed because the animals were not sacrificed at the end of the experiment. In Wombats 1, 2, 3, 7, 8, and 9, the superficial part of the medial pterygoid is active during the power stroke when it is on the working side. However, in Wombats 3, 7, and 9 (Fig. 5.6), the right-side superficial medial pterygoid (SMPt) is also active during the opening stroke when it is the balancing-side muscle and active during closing when it is a working-side muscle. In Wombat 7, major activity in the left superficial medial pterygoid occurs during opening when it is a balancing-side muscle. In Wombats 7 and 9, the working-side superficial medial pterygoid is active both during opening and closing, whereas the balancing-side superficial medial pterygoids in these two wombats are active during opening and silent during closing. In most instances (Wombat 1, 2, 3, 6, 7, and 9), the deep medial pterygoid (DMPt) is only active during the power stroke when it is on the working side and silent when it is on the balancing side. A plausible explanation for this variability, which needs further testing, is that in some experiments the electrodes that were originally intended to be placed in the superficial part moved or partially withdrew, so that they ended up in the deep part or between the deep and superficial parts.

5.5.2 Strain

Figure 5.7 shows the recordings of strain on either side of the symphyseal suture, together with five EMGs on the right and five on the left. Figures 5.8, 5.9, and 5.10 show strains both at the symphysis and on the ventral surface of the right mandible below M_1, along with the EMGs of selected muscles during a chewing-side shift. As in the case of adductor muscle activity, there is a clear change in the strain pattern of the jaw as the animal shifts chewing sides. Peak strain (Figs. 5.9, 5.10) occurs at the end of activity in the superficial masseter and medial pterygoid.

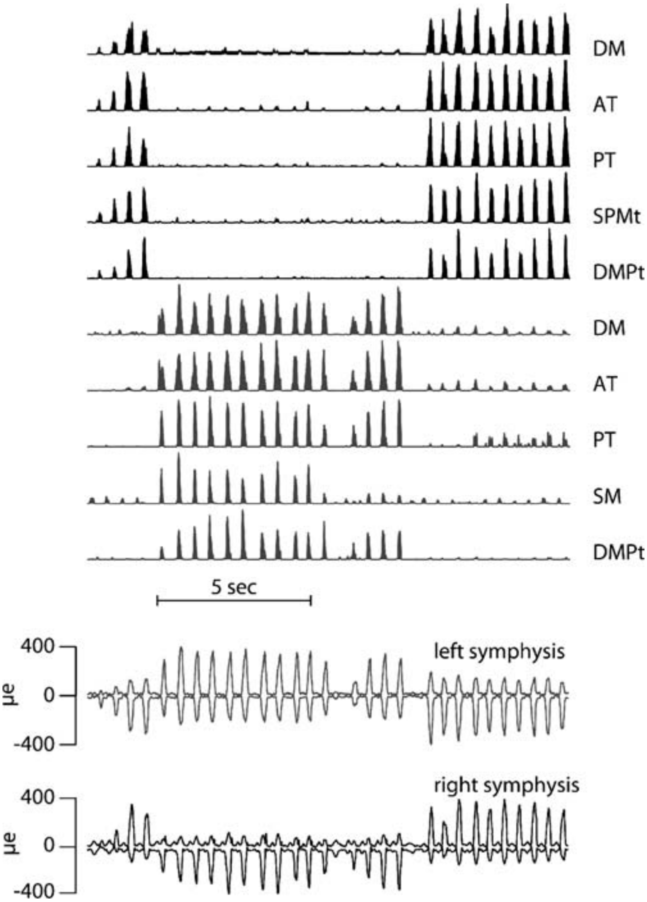

Fig. 5.7 *Lasiorhinus latifrons*. EMGs of adductor muscles during rhythmic chewing on lucerne, first on the right, then on the left, and finally on the right together with synchronous strain on the right and left sides of the ventral surface of the mandibular symphysis. EMGs and strain on the right are shown in black and those on the left in gray. There is a marked change in both the EMG and the strain pattern when the chewing side changes

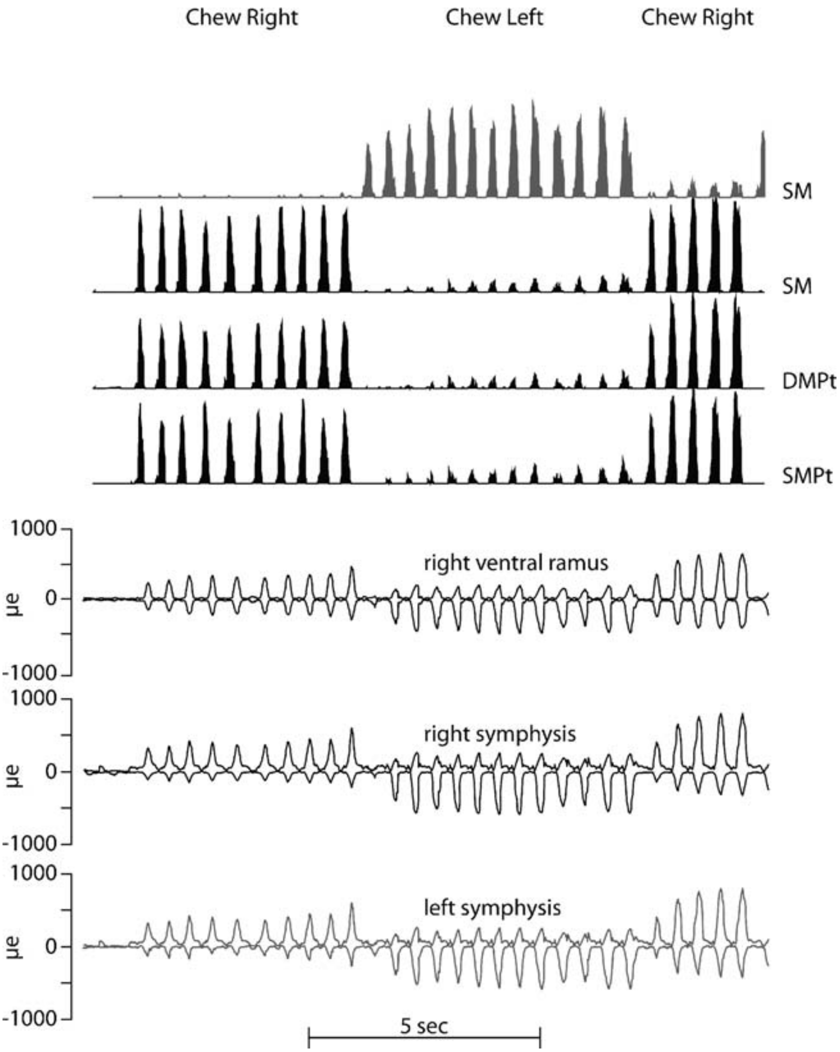

Fig. 5.8 *Lasiorhinus latifrons.* Synchronous EMGs of four adductors and strain on the ventral surface of the mandible on both sides of the symphyseal suture and ventral surface of the right mandibular ramus to illustrate the change in the muscle activity and strain as the animal shifts the chewing side, first from right to left and then back to right

Table 5.5 shows average tension (ε_1), compression (ε_2), and the angle of principle strain ($\varepsilon_1\phi$) relative to the sagittal plane, for 10–15 consecutive right- and left-side chewing cycles.

Figure 5.5B illustrates the orientation of principle strains on the working and balancing sides.

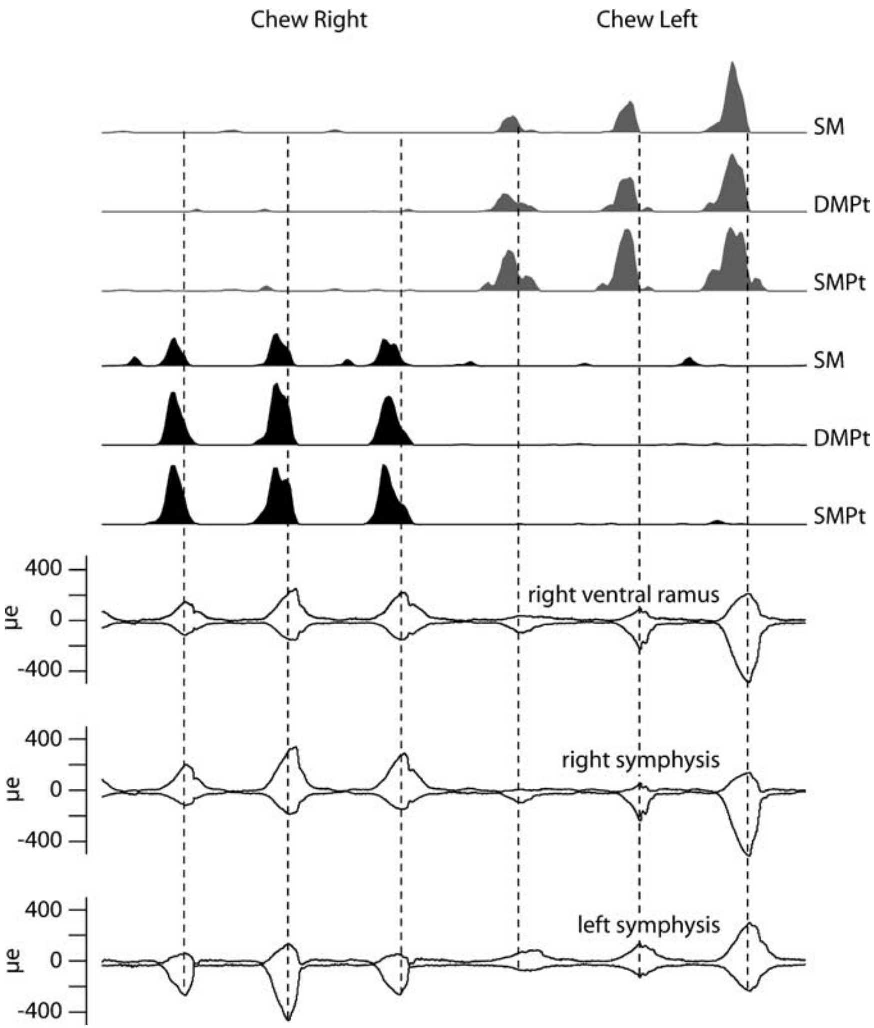

Fig. 5.9 *Lasiorhinus latifrons.* Synchronous EMGs and strain of three chewing cycles on the right, followed by three on the left, to illustrate the relation between muscle activity and mandibular strain. Vertical dotted lines indicate relationships between peak strain and the timing of adductor EMGs

With each change of chewing side, the angle of principle strain ($\varepsilon_1\phi$) on the ventral surface of the symphysis shifts approximately 90°. The $\varepsilon_1\phi$ on working and balancing sides are parallel to one another. For the gauge on the ventral surface of the right dentary, the shift is slightly greater (106–116°) (Fig. 5.5B). When an animal chews on the right side, $\varepsilon_1\phi$ on the right side of the symphyseal region (working side) varies between $-32°$ and $-55°$ relative to the long axis of the symphysis, while that on the left (balancing side) varies between $-41°$ and $-60°$. When the

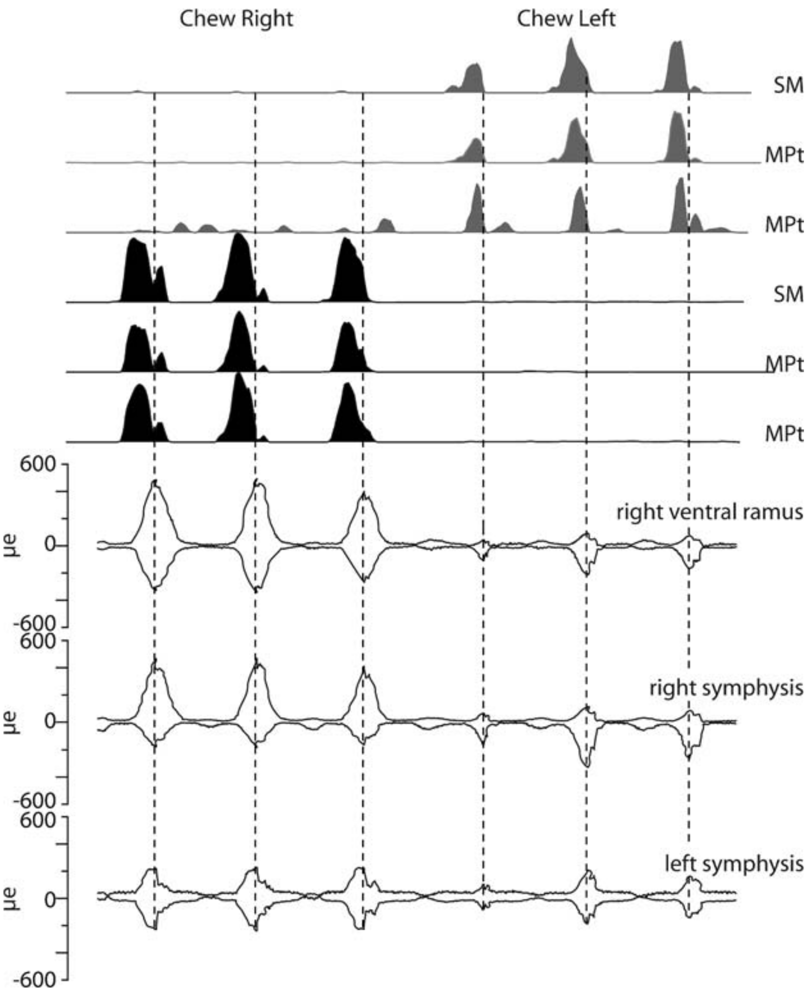

Fig. 5.10 *Lasiorhinus latifrons.* Synchronous EMGs and strain during three chewing cycles on the right, followed by three on the left

animal chews on the left, the angle on the left (working) side varies between 33° and 53° while that on the right (balancing) varies between 25° and 35°. The principle strain angle of a gauge on the ventral surface of the right mandibular ramus varies between $-25°$ and $-37°$ when it is on the working side, and 79° and 91° when it is on the balancing side. The parallel orientation of the angles of principal strain on the working and balancing sides suggests that the whole symphyseal region is twisted in the same direction. It acts as a single unit, and only one side generates all the torque force at any one time.

Table 5.5 Descriptive statistics for peak principal strains (ε_1 and ε_2) and angle of peak tensile strain ($\varepsilon_1\phi$) (standard deviation) on the ventral margin of the right hemi-mandible and ventral surface of the mandibular symphysis on either side of the midline during left- and right-side chews. $\varepsilon_1\phi$ is relative to the mid-sagittal plane

	n	Chew right			Chew left		
		ε_1	ε_2	$\varepsilon_1\phi$	ε_1	ε_2	$\varepsilon_1\phi$
Ventral Margin:							
W3	15	409.1 ± 46.9	−282 ± 42.6	−25.6 ± 1.1	91.9 ± 18.3	−259.7 ± 46.4	80.4 ± 4.9
W2	15	320 ± 52.7	−214 ± 37	−24.8 ± 1.3	184.4 ± 46.9	−460 ± 35.1	91.2 ± 2.1
W1	15	231.4 ± 27.9	−127.2 ± 18.9	−36.9 ± 2.5	140.2 ± 32.5	−314.6 ± 68.6	79.4 ± 1.5
Right Symphysis:							
W3	15	395 ± 56	−160 ± 18.8	−55.0 ± 0.63	109.3 ± 34	−394.6 ± 85	35.7 ± 0.5
W2	15	403 ± 75.3	−137.7 ± 30	−55.5 ± 1.0	225.2 ± 31.4	−536.6 ± 43.2	33.9 ± 0.3
W8	10	331 ± 50	−81 ± 9.4	−32 ± 1.4	112.5 ± 14.3	−222 ± 39.4	25.1 ± 0.35
Left Symphysis:							
W3	15	236.6 ± 44.1	−249.9 ± 37.4	−55.9 ± 0.8	284.2 ± 77.3	−292.9 ± 77.3	39.4 ± 1.7
W2	15	412.6 ± 76.3	−155.9 ± 47.2	−55.3 ± 1.3	226.5 ± 34.4	−532.1 ± 43.1	41.0 ± 1.3
W1	10	106.3 ± 20.2	−274.6 ± 33.2	−54.6 ± 0.5	254.6 ± 38.5	−148.5 ± 29.9	32.7 ± 1.3
W8	10	143.5 ± 18.4	−337 ± 37.2	−41.5 ± 0.96	363.5 ± 36.5	−224 ± 23.3	53.2 ± 0.98

5.6 Discussion

All herbivores (marsupial and placental) generate a transverse force to drag the lower molars in a medial direction across the uppers during the power stroke of mastication. In placentals, this movement involves the transfer of some force from the balancing to the working side. Placental herbivores with fused symphyses and those with unfused symphyses accomplish transverse movements in slightly different ways. For example, in an artiodactyl with an unfused symphysis, the working side is drawn medially by Triplet II muscles in which the activity in the balancing-side deep masseter precedes that of the working-side superficial masseter (Williams et al., 2003c). In anthropoids and ungulates with fused symphyses (Hylander et al., 2000, Williams et al., 2008), the timing of the firing of Triplet II muscles is changed so that the balancing-side deep masseter is the last muscle to fire. In the Southern hairy-nosed wombat, transverse jaw movements during the power stroke are generated almost entirely by the working-side adductor muscles. Forces are transferred from the working to the balancing and not, as in placentals, from the balancing to the working side. During the initial stages of jaw closure, transverse movements to draw the working side of the jaw laterally are generated by the balancing-side superficial medial pterygoid. It is not possible to divide the adductor muscles in wombats into Triplet I and II muscles. On rare occasions, low levels of activity were noted in the balancing-side temporalis and masseter during the power stroke. Judging from video recordings recorded synchronously with EMGs, this activity occurs when the incisors manipulate food. At such moments, the working- to balancing-side ratio

(W/B) of adductor muscles may drop to 12:1. In all other chewing cycles, the ratio is greater than 50:1.

In placental herbivores, bite force along the molar row can be increased by raising the level of activity in the working-side muscles, while at the same time recruiting increasing amounts of activity in the balancing-side muscles and W/B ratio may approach 1:1 (opossum: Crompton, 1995; anthropoids: Hylander et al., 2000; goats: Lieberman and Crompton, 2000). In wombats increased bite force is accomplished by recruiting increasing amounts of working-side musculature. In wombats the masseter muscle complex lies far lateral to the molar row, and because it is so wide medio-laterally, it has a large cross-sectional area presumably to generate high occlusal forces without the involvement of balancing-side muscles.

Another distinctive feature of wombats is the greatly enlarged superficial medial pterygoid that inserts on the wide and horizontally oriented inflected angle of the mandible. In contrast to placental herbivores that have a deep mandibular angle, the insertion of both parts of the medial pterygoid muscle in wombats is close to the condyle. As a result, the fibers of the superficial part of the medial pterygoid muscle are nearly horizontal. The superficial medial pterygoid has a large cross-sectional area and, together with the working-side superficial masseter, it plays an important role in drawing the working side of the mandible medially during the power stroke.

The activity pattern of the medial pterygoid muscle is complex in wombats. The deep medial pterygoid on the working side appears to be active during the power stroke and silent on the balancing side. This is the typical pattern reported for the medial pterygoid in placental herbivores (Herring and Scapino, 1973; Hylander and Johnson, 1994; Lieberman and Crompton, 2000). The firing pattern of the superficial part is more variable. During opening and the beginning of closing it is active on the balancing side; whereas on the working side it can be active during both closing and opening. In placental herbivores such as artiodactyls and perissodactyls (Nickel et al., 1986), and primates (Gray, 1858 [35th edition published 1973]), the medial pterygoid is also divided into two parts: a larger rostromedial part and a smaller superficial slip or caudolateral part. These divisions may be homologous to the two parts of this muscle in wombats, but this possibility still needs to be established. The presence of two parts of the medial pterygoid in placental herbivores may account for the atypical firing pattern reported for the medial pterygoid in primates (macaque, Hiiemae and Crompton, 1985) and artiodactyls (goat, Lieberman and Crompton, 2000). In both of these species, activity in the medial pterygoid is biphasic with activity during both the opening and the closing phases, and sometimes only during opening or closing. In goats, synchronous activity in the medial pterygoid, digastric, and geniohyoid during opening helps pull the lower jaw forward; during closing, synchronous activity of the medial pterygoid and the other adductors adduct the jaw vertically (Crompton et al., 2005). It must be noted that this variable pattern may simply reflect the positions of the electrodes within the medial pterygoid muscle complex. Nevertheless, it appears that in all marsupial herbivores, with the exception of koalas (Davison and Young, 1990), the superficial part of the medial pterygoid has been enlarged to become the dominant part of the medial pterygoid. The inflected angle provides an area of insertion for this muscle (Crompton and Lieberman, 2004a, b).

Recordings from strain gauges placed on the ventral surface of the massive, tightly sutured symphysis of wombats indicate that the whole symphyseal region is twisted clockwise (when viewed from the front) while chewing on the right. When the skull is viewed from the front, the symphysis is twisted clockwise when chewing on the right (Fig. 5.5F) and counter clockwise when chewing on the left. Torque is probably generated primarily by the superficial masseter, because the force vector of this muscle lies lateral to the working-side condyle. Because the mandibular symphysis is stiff and immobile, the torque force generated by the working side will be transferred to the balancing side and will tend to rotate the whole lower jaw around the working-side condyle (which rotates in the coronal plane), placing the balancing-side TMJ under tension. It was not possible to determine the magnitude of the twisting force, but the shear strains on the ventral surface of the symphysis are seldom in excess of 500 microstrain. Balancing-side condylar distraction is apparently resisted by the massive set of ligaments around the TMJ. Manipulation of the wombat skull shows that only a very small amount of rotation is necessary to prevent the balancing-side molars from coming into contact when the lower working-side molars are dragged across the uppers. Because wombat molars are isognathic, even low levels of activity in the balancing-side adductors would result in balancing-side occlusion. The wear pattern of the molars in wombats confirms that occlusion is unilateral.

There appear to be multiple reasons for developing a fused or immobile mandibular symphysis. In anthropoids the fused symphysis resists lateral transverse bending; but this is not the case in alpacas, where it is twisted rather than bent (Williams et al., 2008). Williams et al. (2008) suggest that the alpaca symphysis is fused in order to support long incisor roots. This could also be true for the wombat, since it has long incisor roots that extend the entire length of the symphysis. On the other hand, as kangaroos also have long incisor roots that extend the length of a highly mobile symphysis, there may be an alternative reason for the development of an immobile symphysis in wombats.

In contrast to wombat molars, those of the kangaroo molars are adapted for shearing rather than crushing and grinding. As Sanson (1989) pointed out, they have not evolved common adaptations to resist heavy wear of the molars such as hypsodonty and molar crown patterns that are not changed significantly by wear. Medially directed transverse movement of the whole working-side hemi-mandible in kangaroos is severely limited by the narrow upper incisal arcade. Kangaroos are only mildly anisognathic, and consequently there is not sufficient space between the upper molar rows to permit extensive transverse movements as in the case of most placental ungulates. However, because the occlusal surfaces of kangaroo lower molars lie above the axis of rotation of the hemi-mandible, rotation alone contributes to the transverse movements of the lower molars relative to the uppers (Lentle et al., 1998, 2003; Ride, 1959). Our as yet unpublished data on kangaroo mastication indicate that, as in wombats, only the working-side muscles move the hemi-mandible medially while simultaneously rotating it during the power stroke.

This suggests that the common ancestor of kangaroos and wombats possessed a similar masticatory motor pattern that has been modified in different ways in wombats and macropods. Wombats evolved a masticatory system designed to deal with tough, abrasive foods that require high occlusal forces to be broken down. However, the masticatory motor control pattern of wombats appears to rule out the possibility of recruiting balancing-side musculature to generate large bite forces. Wombats have increased the mass of the adductor muscles by moving the zygoma laterally, and further increasing the space for adductors by moving the molar rows closer to one another.

Figure 5.11 compares the areas of origin for the superficial masseter and medial pterygoid in a kangaroo and a wombat. This comparison is not to suggest that wombats arose from kangaroos, but to show the adaptations required to increase the bite force across the molars. Moving the origin of the adductors laterally increased the torque force acting on the working-side mandible. To deal with a tougher and more abrasive diet, wombats evolved ever-growing hypsodont molars. A tightly sutured symphysis prevents the balancing-side molars from coming into contact, because the torque force generated by the working side separates the molars on the balancing side. The whole mandible rotates around the long axis of the working side.

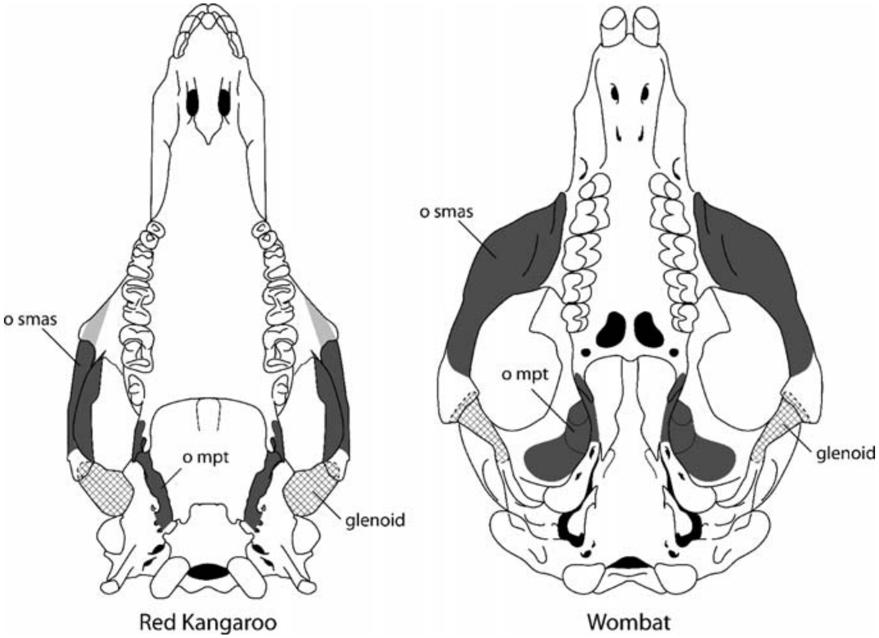

Fig. 5.11 Ventral view of the skulls of the red kangaroo and Southern hairy-nosed wombat, comparing the areas of origin (*shaded in gray*) of the superficial masseter (o smas) and the medial pterygoid (o mpt) muscles. (Light gray shading indicated a part of the origin of the superficial masseter that is not visible in ventral view). The hatched areas indicate the glenoid of the TMJ

This hypothesis is based upon the neuromuscular control of jaw movements of a single species, and with reference to unpublished data on the red kangaroo: as such it is still tentative and speculative. It does, however, establish that the masticatory motor pattern of wombats and kangaroos are fundamentally different from that of placental herbivores, and that the masticatory motor patterns in mammals are far more varied than the current literature suggests (Weijs, 1994; Hiiemae, 2000; Langenbach and van Eijden, 2001). This study stresses the fact that the ubiquitous feature of mammalian herbivores, viz. transverse jaw movements, can be generated and controlled in several different ways and accomplished with fundamentally different biomechanical systems. In order to understand the function, origin and, evolution of the diverse feeding mechanisms of Australian marsupials, it will be necessary to broaden the scope of this study to include, at a minimum, representatives of the major groups of Australian mammals, and then to integrate these findings with the known fossil record.

Acknowledgments This work was carried out with the aid of a grant from the Putman Fund of the Museum of Comparative Zoology, Harvard University, and a grant from the University of Adelaide.

References

Abbie, A. (1939) A masticatory adaptation peculiar to some diprotodont marsupials. *Proc Zool Soc Lond* 109: 261–279.

Becht, G. (1953) Comparative biologic-anatomical researches on mastication in some mammals. *Proc K Ned Akad Wet Ser C Biol Med Sci* C. 56: 508–527.

Biewener, A. (1992) In vivo measurement of bone strain and tendon force. In: Biewener, A. (ed.) *Biomechanics – tructure and systems: A practical approach*. Oxford University Press, Oxford, England pp 123–147.

Crompton, A. W. (1995) Masticatory function in nonmammalian cynodonts and early mammals. In: Thomason, J. (ed.) *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge pp 55–75.

Crompton, A. W., Hylander, W. L. (1986) Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. In: Hotton III, N., Mchean, P., Roth, J., Roth, E. (eds.) *The ecology and biology of mammal-like reptiles*. Smithsonian Institute, Washington pp 263–282.

Crompton, A.W., Lieberman, D.E. (2004a) Motor control of mastication in mammals: Marsupials and placentals compared. *Int Comp Biol* 44: 541.

Crompton, A. W., Lieberman, D. E. (2004b) Functional significance of the inflected mandibular angle. *J Vert Paleo* 24: 49A.

Crompton, A. W., Lieberman, D. E., Aboelela, S. (2005). Tooth orientation during occlusion and the functional significance of condylar translation in primates and herbivores. In: Carrano, M., Blob, R., Gaudin, T., Wible, J. (eds.) *Amniote paleobiology* pp 367–388.

Davison, C., Young, G. (1990) The muscles of mastication of *phascolarctos cinereus* (phascolactidae: Marsupiala). *Aust J Zool* 38: 227–240.

Ferreira, J. M., Phakey, P. P., Palamara, J., Rachinger, W. A., Orams, H. J. (1989) Electron microscopic investigation relating the occlusal morphology to the underlying enamel structure of molar teeth of the wombat vombatus-ursinus. *J Morphol* 200: 141–150.

Ferreira, J. M., Phakey, P. P., Rachinger, W. A., Palamara, J., Orams, H. J. (1985) A microscopic investigation of enamel in wombat*(vombatus ursinus). Cell Tissue Res* 242: 349–355.

Finlayson, G. R., Shimmin, G. A., Temple-Smith, P. D., Handasyde, K. A., Taggart, D. A. (2005) Burrow use and ranging behaviour of the southern hairy-nosed wombat (lasiorhinus latifrons) in the murraylands, south australia. *J Zool* 265: 189–200.

Gray, H. (1858) *Gray's anatomy*. W. B. Saunders, Philadelphia. (1471).

Herring, S. W., Scapino, R. P. (1973) Physiology of feeding in miniature pigs. *J Morphol* 141: 427–460.

Hiiemae, K. M. (1978) Mammalian mastication: A review of the activity of the jaw muscles and the movements they produce in chewing. In: Butler, P., Joysey, K. A. (eds.) *Development, function and evolution of teeth*. Academic Press, London pp 359–398.

Hiiemae, K. M. (2000) Feeding in mammals. In: Schwenk, K. (ed.) *Form, function and evolution in tetrapod vertebrates*. Academic Press, San Diego pp 399–436.

Hiiemae, K. M., Crompton, A. W. (1985) Mastication, food transport and swallowing. In: Hildebrand, M., Bramble, D., Liem, K., Wake, D. (eds.) *Functional vertebrate morphology*. Belknapp Press, Harvard University Press, Cambridge pp 262–290.

Hogue, A. S., Ravosa, M. J. (2001) Transverse masticatory movements, occlusal orientation, and symphyseal fusion in selenodont artiodactyls. *J Morphol* 249: 221–241.

Hylander, W. L. (1984) Stress and strain in the mandibular symphysis of primates a test of competing hypotheses. *Am J Phys Anthropol* 64: 1–46.

Hylander, W. L., Johnson, K. R. (1994) Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *Am J Phys Anthropol* 94: 523–547.

Hylander, W. L., Ravosa, M. J., Ross, C. F., Johnson, K. R. (1998) Mandibular corpus strain in primates: Further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. *Am J Phys Anthropol* 107: 257–271.

Hylander, W. L., Ravosa, M. J., Ross, C. F., Wall, C. E., Johnson, K. R. (2000) Symphyseal fusion and jaw-adductor muscle force: An emg study. *Am J Phys Anthropol* 112: 469–492.

Hylander, W. L., Vinyard, C. J., Ravosa, M. J., Ross, C. F., Wall, C. E., Johnson, K. R. (2004) Jaw adductor force and symphyseal fusion. In: Anapol, F., German, R., Jablonski, N. (eds.) *Shaping primate evolution: Papers in honor of charles oxnard*. Cambridge University Press, Cambridge pp 229–257.

Hylander, W. L., Vinyard, C. J., Wall, C. E., Williams, S. H., Johnson, K. R. (2003) Convergence of the "wishboning" jaw-muscle activity pattern in anthropoids and strepsirrhines: The recruitment and firing of jaw muscles in propithecus verreauxi. *Am J Phys Anthropol Suppl* 36: 120.

Hylander, W. L., Wall, C. E., Vinyard, C. J., Ross, C., Ravosa, M. R., Williams, S. H., Johnson, K. R. (2005) Temporalis function in anthropoids and strepsirrhines: An emg study. *Am J Phys Anthropol* 128: 35–56.

Kalvas, J. (1999) The masticatory musculature and temporomandibular joint of a grazing macropodid (macropus giganteus); its morphology and function as compared with that of a grazing bovid (ovis aries). Department of Anatomical Sciences. University of Adelaide, Adelaide p 52.

Langenbach, G. E., van Eijden, T. M. G. J. (2001) Mammalian feeding motor patterns. *Am Zool* 41: 1338–1351.

Lentle, R., Hume, I., Stafford, K., Kennedy, M., Haslett, S., Springett, B. (2003) Comparison of tooth morphology and wear patterns in four species of wallabies. *Aust J Zool* 51.

Lentle, R., Stafford, K., Potter, M., Springett, B., Haslett, S. (1998) Incisor and molar wear in the tammar wallaby. *Aust J Zool* 46: 509–527.

Lieberman, D., Crompton, A. (2000) Why fuse the mandibular symphysis? A comparative analysis. *Am J Phys Anthropol* 112: 517–540.

Murray, P. F. (1998) Palaeontology and palaeobiology of wombats. In: Wells, R. T., Pridmore, P. A. (eds.) *Wombats*. Surrey Beatty and Sons Pty Ltd., Adelaide pp 1–33.

Nickel, R., Schummer, A., Seiferle, E., Frewein, J., Wilkens, H., Wille, K.-H. (1986) *The locomotor system of the domestic animals*. Springer-Verlag, New York

Oron, U., Crompton, A. (1985) A cineradiographic and electromyographic study of mastication in *Tenrec ecaudatus*. *J Morphol* 185:155–182.

Ravosa, M. J., Hylander, W. L. (1994) Function and fusion of the mandibular symphysis in primates: Stiffness or strength? In: Fleagle, J. G., Kay, R. (eds.) *Advances in primatology; Anthropoid origins*. Plenum, New York pp 447–468.

Ravosa, M. J., Vinyard, C. J., Gagnon, M., Islam, S. A. (2000) Evolution of anthropoid jaw loading and kinematic patterns. *Am J Phys Anthropol* 112: 493–516.

Ride, W. (1959) Mastication and taxonomy in the macropodine skull. In: Cain, A. (ed.) *Function and taxonomic importance*. Oxford University Press, Oxford Systematics association publication, Vol 3, pp 33–59.

Sánchez-Villagra, M. R., Smith, K. (1997) Diversity and evolution of the marsupial mandibular angular process. *J Mammal Evol* 4: 119–144.

Sanson, G. (1980) The morphology and occlusion of the molariform cheek teeth in some macropodinae (marsupialia: Macropodidae). *Aust J Zool* 28: 341–365.

Sanson, G. (1989) Morphological adaptations of teeth to diets and feeding in the macropodoidea. In: Grigg, G., Jarman, P., Hume, I. (eds.) *Kangaroos, wallabies and rat-kangaroos*. Surrey Beatty & Sons Pty Limited, New South Wales pp 151–168.

Scott, G., Richardson, K. (1987) Osteological differences of the axial skeleton between lasiorhinus latifrons (owen, 1845) and vombatus ursinus (shaw, 1800) (marsupialia: Vombatidae). *Rec S Afr Mus* 22: 29–39.

Shimmin, G., Skinner, J., Baudinette, R. (2001) Life in a wombat burrow. *Nature Aust* 27:62–69.

Thexton, A. (1966) A randomisation method for discriminating between signal and noise recordings of rhythmic electromyographic activity. *J Neurosci Methods*. 66:93–98.

Turnbull, W. (1970) Mammalian masticatory apparatus. *Fieldiana: Geol* 18: 153–356.

Vinyard, C. J., Wall, C. E., Williams, S. H., Johnson, K. R., Hylander, W. L. (2006) Masseter electomyography during chewing in ring-tailed lemurs (lemur catta). *Am J Phys Anthropol* 130:85–95.

Vinyard, C. J., Williams, S. H., Wall, C. D., Johnson, K. R., Hylander, W. L. (2005) Jaw-muscle electromyography during chewing in belanger's treeshrews (tupaia belangeri). *J Am Phys Anthropol* 127:26–45.

Weijs, W. (1994) Evolutionary approach of masticatory motor patterns. In: Bels, V. L., Chardon, M., Vandewalle, P. (eds.) *Biomechanics of feeding in vertebrates*. Springer-Verlag, Belgium Advances in comparative and environmental physiology, Vol 18, pp 281–320.

Weijs, W., Dantuma, R. (1981) Functional anatomy of the masticatory apparatus in the rabbit *(orytolagus cuniculus l.). Netherlands J Zool* 31: 99–147.

Williams S. H., Vinyard, C. J., Wall, C. E., Hylander, W. L. (2004) Masticatory strains in the mandibular corpus of selenodont artiodactyls. *Int Comp Biol* 282A

Williams, S. H., Wall, C. E., Vinyard, C. J., Hylander, W. L. (2003a) Strain in the mandibular symphysis of alpacas and the evolution of symphyseal fusion in camelids. *J Vert Paleo* Sup 23: 110A.

Williams, S. H., Wall, C. E., Vinyard, C. J., Hylander, W. L. (2003b) Jaw-muscle motor patterns in ungulates: Is there a transverse pattern?*SICB Annual Meeting & Exhibition Final Program & Abstracts*: 342.

Williams, S. H., Vinyard, C. J., Wall, C. E., Hylander, W. L. (2003c) Symphyseal fusion in anthropoids and ungulates: A case of functional convergence?*Am J Phys Anthropol Suppl* 36: 226.

Williams, S. H., Wall, C. E., Vinyard, C. J., Hylander, W. L. (2008) Symphyseal fusion in selenodont artiodactyls: New insights from *in vivo* and comparative data. In: Vinyard, C. J., Ravosa, M. J., Wall, C. E. (eds.) *Primate Craniofacial Function and Biology*. Springer. New York. pp 39–62.