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SYMPOSIUM

Masticatory Motor Programs in Australian Herbivorous Mammals: Diprotodontia

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Synopsis Movement of the jaw during molar occlusion is determined by the sequence of activity in the adductor muscles and this sequence is one way to define a masticatory motor program. Based on the similarity of molar structure, it is probable that the American opossum and the early Tertiary mammals that gave rise to all Australian marsupials probably shared a common "primitive" masticatory motor program. The distinct and various patterns of movement of the jaw in the major groups of Australian marsupial herbivores (diprotodontids) are achieved by both subtle and substantial shifts in the timing of the primitive sequence. All diprotodonts divide jaw movements during occlusion into a vertical Phase Im and horizontal Phase IIm, but the number of muscles involved and the level of activity associated with each phase varies considerably. In macropodids (potoroos and kangaroos) Phase Im dominates; in wombats Phase IIm dominates and in koalas the two phases are more evenly divided, with a more equal distribution of muscles between them. The motor program of koalas parallels that of some placental ungulates, while both macropodids and wombats have motor programs unique among mammals.

Introduction

Mammalian herbivores evolved in Australia independently of the evolution of placental herbivores on other continents during the Tertiary when the Australian continent was isolated (Long et al. 2002). It is generally accepted that the common ancestor of marsupial and placental herbivores possessed tribosphenic molars (Crompton 1971; Crompton and Kielan-Jaworowska 1978; Kielan-Jaworowska et al. 2004). The masticatory motor program (sequence and duration of activity in the adductor muscles) of animals with tribosphenic molars is relatively well known for placentals (Vinyard et al. 2006a, 2006b), but poorly documented for marsupials (Lieberman and Crompton 2000; Crompton et al. 2008b). Weijs (1994) used the term "primitive" to describe the masticatory motor patterns of a variety of animals many of which possessed tribosphenic molars. Weijs (1994) and several other authors (Hiiemae 2000; Hylander et al. 2005; Williams et al. 2007, 2008) have shown that placental mammals modified this primitive motor pattern, as well as the dentition associated with this pattern, to deal with various diets.

Weijs (1994) also established the term "transverse" to describe the motor program of ungulates. The molars of placental ungulates possess flattened (lophodont or bunodont) occlusal planes and food is broken down as the lower molars are drawn transversely in a medial direction across the corresponding uppers (Becht 1953; Fortelius 1985; Janis and Fortelius 1988; Janis 1990; Crompton et al. 2006; Williams et al. 2007, 2008). Marsupial herbivores have more varied patterns of jaw movements during molar occlusion than do placental herbivores (Ride 1959; Lanyon and Sanson 1986a, 1986b; Lentle et al. 1998, 2003; Murray 1998), but little, until recently, has been published on the activity patterns of their adductor muscles. The purpose of this article is to describe the primitive motor program of the American opossum, Didelphis, and to show how this motor program was modified in response to

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shifts in the diet of the major groups of marsupial herbivores (Diprotodontia). Descriptions of the motor programs in wombats, koalas, potoroos, and kangaroos draw from data included in a series of recent papers on mastication in Australian marsupial herbivores (Crompton et al. 2008a, 2008b, 2010).

Didelphis

The earliest known Australian marsupial, the didelphoid *Djarthia* (Godthelp et al. 1999) possessed tribosphenic molars similar to those of *Didelphis* (Crompton and Hiiemae 1970) and to the metatherian *Deltatheridium* from the late Cretaceous of Asia (Crompton and Kielan-Jaworowska 1978; Rougier et al. 1998). It appears that all animals with tribosphenic molars have shared the same pattern of jaw movement during occlusion. For this reason we regard the motor program of *Didelphis* as representative of the motor program of early Australian marsupials in the absence of EMGs of any other primitive marsupial.

Tribosphenic molars are characterized by embrasure shearing (Kielan-Jaworowska et al. 2004) and a set of shearing surfaces that successively come into contact with one another as the molars move into full occlusion, that is, when the protocone is firmly imbedded in the talonid basin (Fig. 1). The power stroke consists of a single medio-dorsally directed linear stroke (Crompton and Hiiemae 1969). During opening of the jaw the molars move ventrally out of occlusion and no further breakdown of food occurs at this time (Crompton and Hylander 1986).

It is customary to divide the jaw adductors of mammals according to their action on movements of the jaw into two groups each of which include working-side muscles and balancing-side muscles. These are often referred to either as Triplets I and II (Weijs 1994; Vinyard et al. 2006b) or diagonals (Herring 1985). In this article, we simply refer to them as Groups I and II (Crompton et al. 2010).

Acting alone, Group I muscles (working-side deep masseter and posterior temporalis and balancing-side

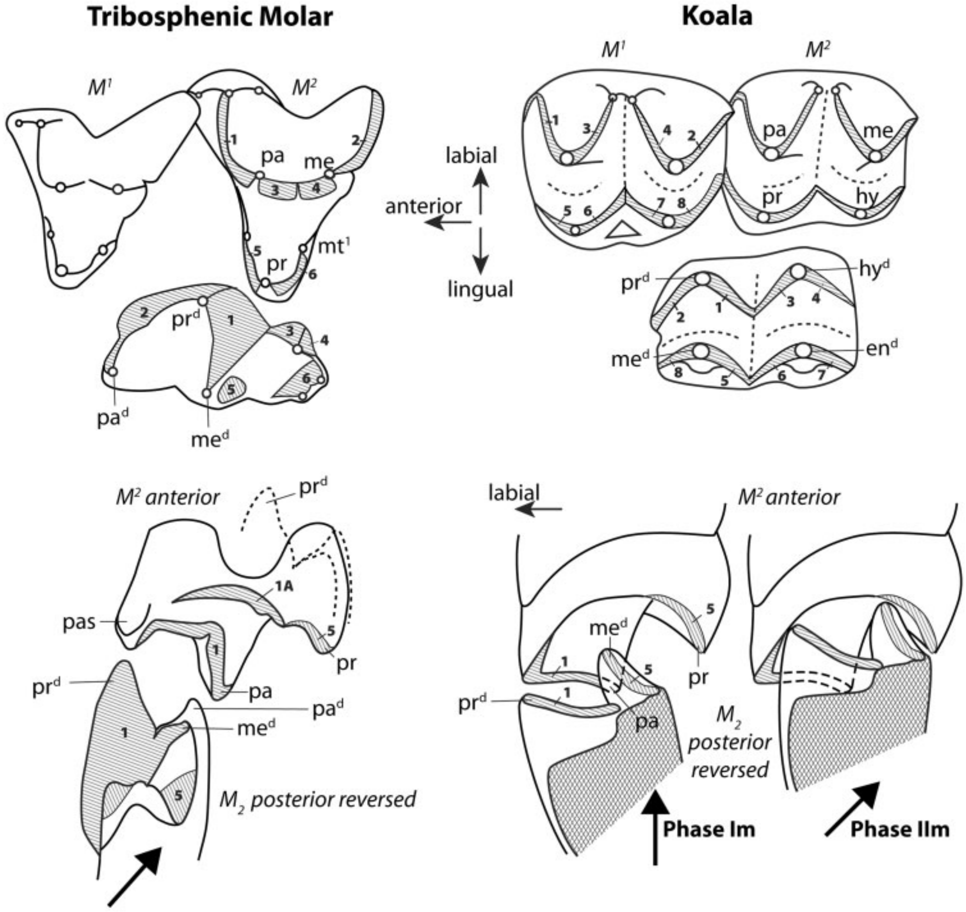

Fig. 1 Comparison of occlusal and anterior/posterior views of tribosphenic and koala molars. Based on Fig. 2 in Crompton et al. (2010). The direction of jaw movements during occlusion in animals with tribosphenic molars consists of a single dorso-medially directed linear stroke. In koalas, it is divided into a vertical Phase Im and a transverse Phase IIm.

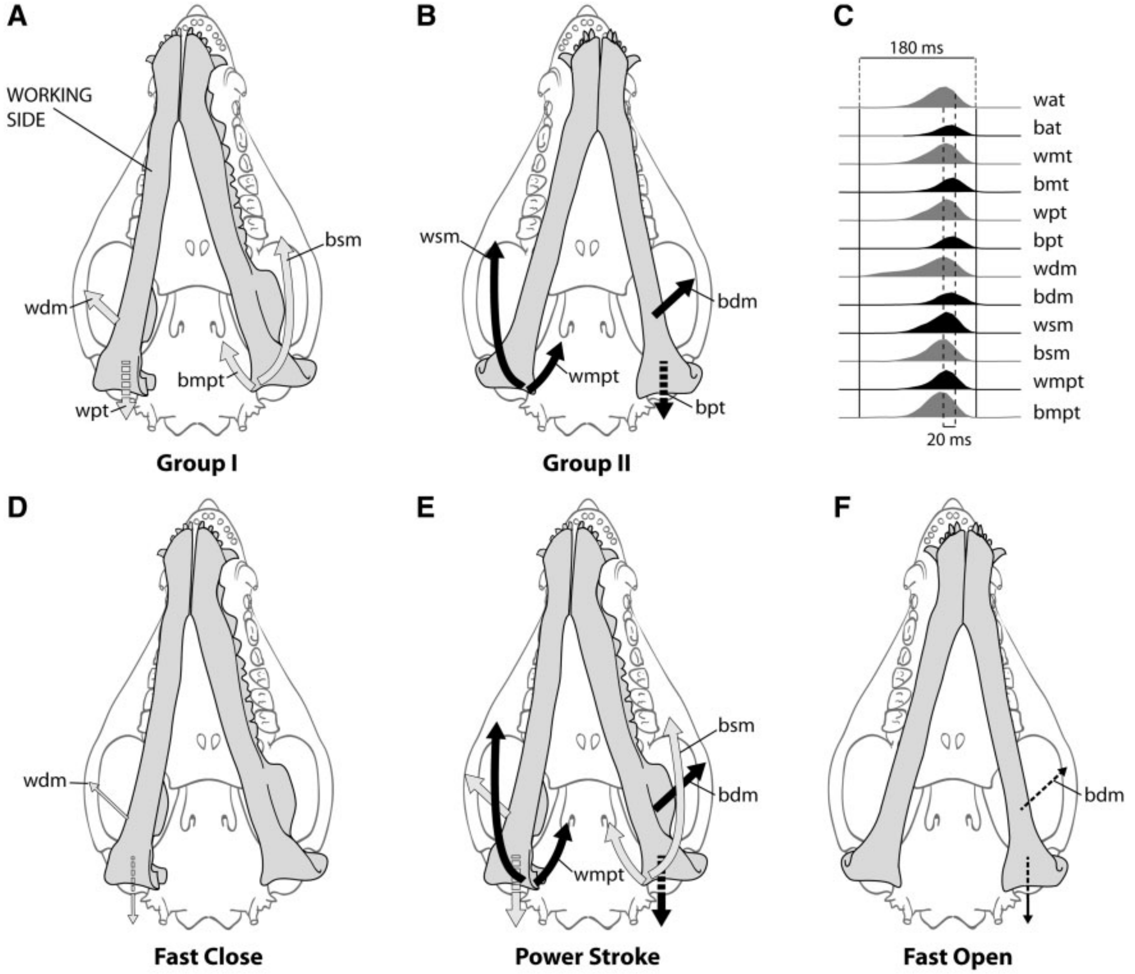

Fig. 2 *Didelphis virginianus*. Jaw movements and motor pattern. (**A**) and (**B**) Orientation and position of Groups I and II muscles. (**C**) EMGs of the principal adductor muscles during a single power stroke when the animal is chewing on tough food. (**D**–**F**) muscle activity during fast close, power stroke and fast open. Based on the data cited by Crompton and Hylander (1986) and Lieberman and Crompton (2000).

medial pterygoid and superficial masseter) would move the working-side jaw laterally (Fig. 2A). Group II muscles (working-side superficial masseter and medial pterygoid, and balancing-side deep masseter and posterior temporalis) would move the working-side jaw medially (Fig. 2B). However, the EMG pattern (Fig. 2C and E) shows a broad overlap of activity between muscle groups, with peak activity in Groups I and II muscles occurring within 10–20 ms of one another. In several recordings of four different opossums chewing rhythmically on tough food, activity levels in working-side temporalis and deep masseter (Group I) muscles tend to exceed that of their matching balancing-side muscles, which would explain the working-side hemimandible's lateral movement as the jaw begins to close during Fast Close (FC). During the power stroke the jaw moves medially because peak activity of Group II muscles occurs slightly later than that of Group I muscles. In addition, activity in Group II muscles extends beyond that of Group I (Fig. 2C). It is suggested that this pattern of activity (broad overlap and slight differential in the timing of Groups I and II muscles) results in the working side of the jaw moving linearly in a medio-dorsal direction during the power stroke.

Diprotodontia

Most Australian marsupials herbivores are diprotodonts (Fig. 3), the origin of which extended back to the Cretaceous/Tertiary boundary (Meredith et al. 2008, 2009). Extant diprotodonts are the relics of a large and varied fauna that flourished during the Miocene and Pliocene (Long et al. 2002). All diprotodonts modified the ancestral tribosphenic molars by adding a hypocone (Fig. 1); in addition, in all the extant forms jaw movements during the power

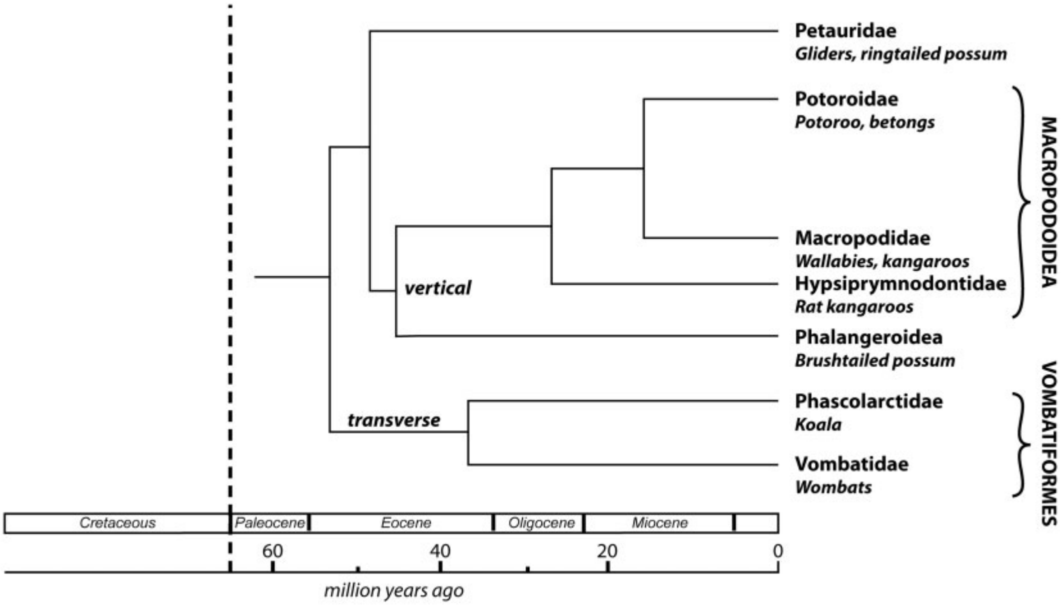

Fig. 3 Timeline in millions of years ago to illustrate the origin and relationship of diprotodont lineages. Based on Fig. 3 in Meredith et al. (2009).

stroke divide into a vertical Phase I and transverse Phase II. These are not homologous with the Phases I and II of placental herbivores (Crompton et al. 2008a, 2010) and for this reason the terms Phase Im and Phase IIm are used for marsupials. Within the Macropodoidea, in terms of total muscle activity, Phase Im dominates. Among Vombatiformes, koalas have roughly equal phases, while Phase IIm dominates in wombats. These differences are reflected in their motor programs.

The Musky rat-kangaroos (Hypsiprymnodontidae), potoroos (Potoroidae) and wallabies and kangaroos (Macropodidae) all possess a large deep masseter, the insertion of which extends forward in a large mandibular canal (Abbie 1939; Ride 1959; Sanson 1989) as far forward as the first molar (Fig. 4A, mc). The first two of these groups possess large shearing third premolars (Fig. 4A), also present but reduced in browsing wallabies and kangaroos, and lost in grazing kangaroos (Sanson 1989). This reduction or loss of the third premolar is associated with the development of a continuous shearing surface on the lingual aspect of the three upper incisors (Lentle et al. 1998, 2003).

The terms Triplets I and II and Groups I and II are not always synonymous. Animals with a primitive masticatory motor program, as in this article, have the same muscles traditionally assigned to Triplets I and II and to Groups I and II. However, in animals with derived motor programs, the muscles that activate when the working side of the jaw moves either laterally or medially may differ from those of the primitive program. In this article, the assignment of individual muscles to either Group I or II is based upon the relationship between the direction of movement of the working side of the jaw and activity in individual adductors. When the terms Triplets I and II are correctly used, as in Williams et al. 2011, it implies that a consistent set of muscles are included in each Triplet.

Potoroidea

Potoroos (Fig. 4) preferentially use their premolars for the initial break down of ingested food items (invertebrates, fruits, seeds). For shearing premolars effectively to break down food items, the lower premolar must be forced laterally against its matching upper during occlusion to prevent food forcing the blades apart. The third premolars act like conventional scissors that rely on the way they are held to automatically force the blades together as they close—hence the different design of right-handed and left-handed scissors. During the vertical Phase Im of mastication in potoroos, the apical edges of the lower premolars meet and shear past the uppers before the molars come into contact. The molars possess low bunodont cusps and have lost the well-defined shearing crests of tribosphenic molars. The lower molars lie slightly medial to their corresponding uppers at the beginning of molar occlusion [Fig. 4B(i)]. Wear reduces their occlusal surfaces to flat planes with a lingual ridge on the lower and labial ridge on the upper molars [Fig. 4B(ii)].

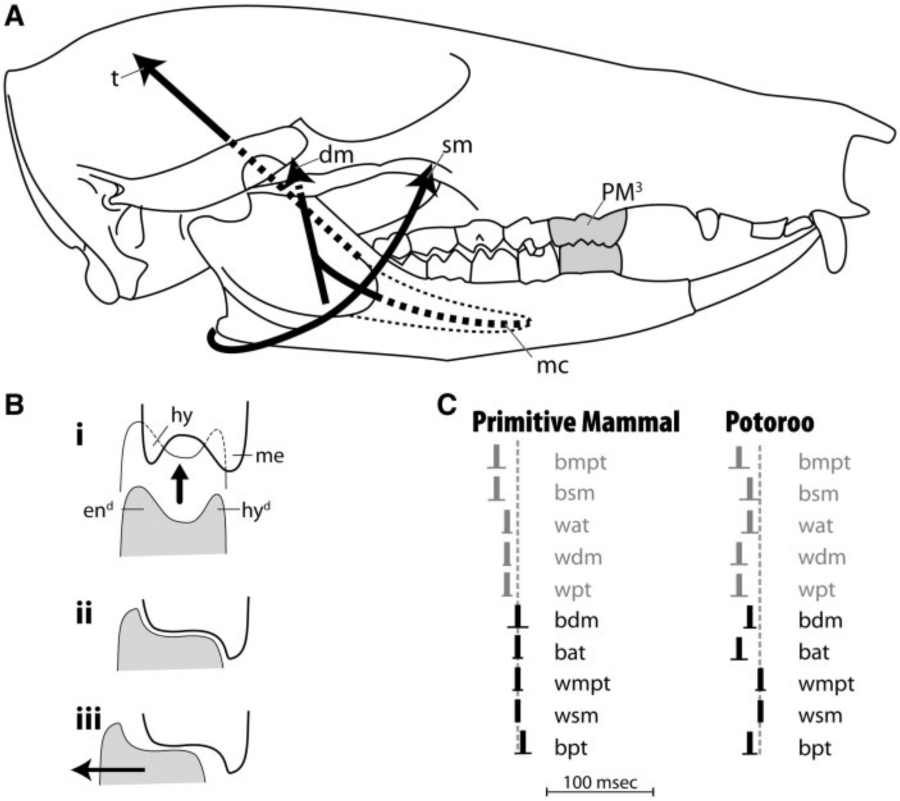

Fig. 4 *Potorous tridactylus*. (**A**) Lateral view of the skull. [**B**(i)] Posterior view and movement of the lower molar during a power stroke; [**B**(ii)] outline of a worn molar; [**B**(iii)] movement of the jaw during Phase IIm. (**C**) Comparison of the median sequence of activity of adductor muscles in a primitive mammal and in a potoroo (Group I muscles: gray; Group II muscles: black). Based on A. W. Crompton, T. Owerkowicz, and J. Skinner (submitted for publication).

The vertical Phase Im is followed by medial movement of the jaw [Fig. 4B(iii)], the extent of which is limited by the distance between the lower premolars, only slightly less than the distance between the upper premolars.

The motor pattern of potoroos (Fig. 4C, A. W. Crompton, T. Owerkowicz, and J. Skinner, submitted for publication) represents, in terms of duration and the degree of overlap of Groups I and II muscles, only a slight modification of the primitive pattern. The difference is best illustrated by superimposing the activity profiles of working-side and balancing-side muscles (Fig. 8). Figure 8 also shows the relationship between muscle activity and the two phases of occlusion. Early activity in the balancing-side medial pterygoid and working-side deep masseter and posterior temporalis draw the working-side laterally. Peak activity in both sides of the temporalis and deep masseter occurs at the end of Phase Im and that of the working-side medial pterygoid and superficial masseter a few milliseconds later. The extended activity in the working-side medial pterygoid and superficial masseter corresponds with transverse movement during Phase IIm. This activity profile shows major adductor force generated at the end of Phase Im. During Phase IIm activity in the working-side medial pterygoid and superficial masseter declines rapidly suggesting that potoroos generate little vertical force during Phase IIm and that their molars are selected for crushing rather than for grinding.

The nearly equal levels of activity in Groups I and II muscles during Phase Im ensures that the direction of movement of the working-side of the jaw remains vertical so that food does not force the sectorial premolars apart. It is suggested that the reason the Potoroidea have such large deep masseters is that this muscle plays a primary role in maintaining contact between the occluding premolars during occlusion.

Macropodidae

Red kangaroos and tamar wallabies have modified their molars and incisors to crop and break down tough plant material (Sanson 1989). To this end, they have evolved conjoined shearing surfaces on the lingual aspect of the upper incisor arcade. The tall transverse lophs (Sanson 1980) on the molars

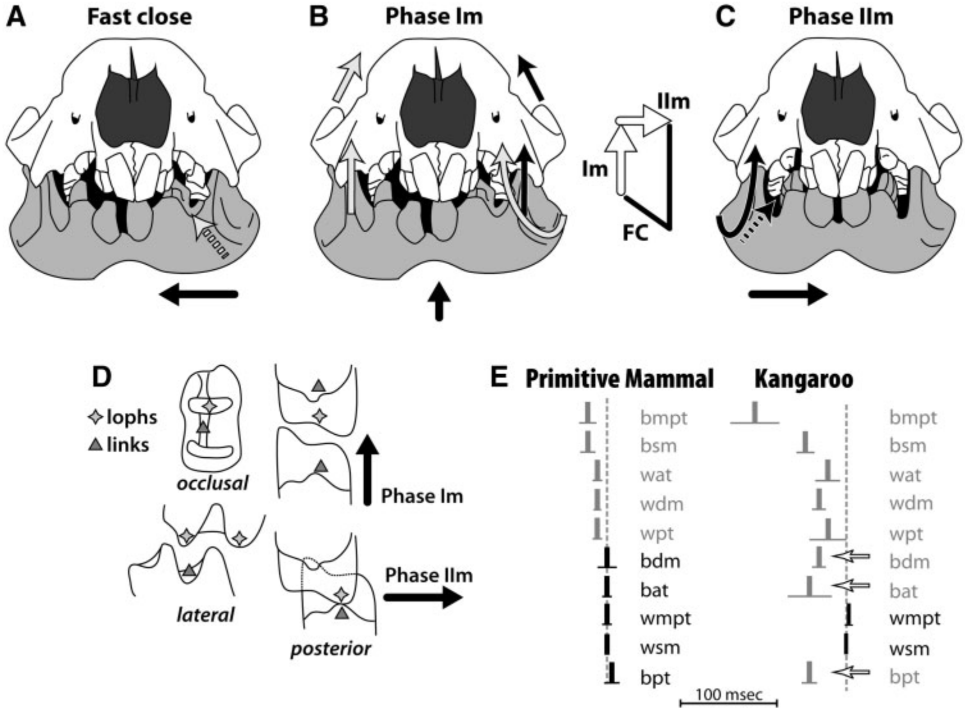

Fig. 5 *Macropus rufus*. (**A**–**C**) Muscle activity during fast close and two phases of the power stroke. (**D**) Occlusal, lateral and posterior views of molars. Lophs shear past one another during the vertical Phase Im (vertical arrow) and lophs and links are drawn past one another during the transverse Phase IIm (transverse arrow). Based on Sanson (1989). (**E**) Comparison of the median sequence of activity of the principal adductors in a primitive mammal and in a kangaroo (based on Crompton et al. 2008a).

shown in occlusal, lateral, and posterior views (Fig. 5D) are adapted to shear food as the jaw moves vertically during Phase Im (Fig. 5D, vertical arrow) and to crush food between the lophs and the links at the end of Phase Im (Fig. 5D, horizontal arrow). During Phase IIm, the working-side hemimandible rotates around its longitudinal axis (Crompton et al. 2008a). As a result the labial edge of the procumbent lower incisor moves in a superomedial direction across the upper incisal arcade (Lentle et al. 2003) and the lower molars move across the uppers simultaneously with medial movement of the body of the hemimandible. During Phase IIm, food can potentially be cut by the incisors or ground between the lophs and links. The amount of transverse movement of the jaw is limited by the narrow upper incisal arcade (Janis and Fortelius 1988). These essential features of the macropod dentition are reflected in their masticatory motor pattern which Fig. 5E shows alongside the primitive pattern for comparison. The working-side hemimandible is drawn laterally by early activity in the balancing-side medial pterygoid during fast close (Fig. 5A). Three Group II muscles (balancing-side deep masseter, anterior temporalis and posterior temporalis, and the balancing-side deep masseter) shift the time of their peak activity to overlap with Group I muscles (Fig. 5E). Consequently, only two muscles are active during Phase IIm (Fig. 5C).

Vombatiformes

Koalas

The origin of Vombatiformes (which includes koalas and wombats) dates back to the beginning of the diprotodont radiation, and the split between wombats and koalas dates back to the late Eocene (Fig. 3). Their common ancestor was probably arboreal (Meredith et al. 2008, 2009). Koalas retained the arboreal life style whereas wombats adopted a terrestrial and burrowing life style.

Koalas' molars retain the six shearing crests of tribosphenic molars and have added additional shearing surfaces on the hypocone and endoconid (Fig. 1). The power stroke is also divided into a vertical Phase Im and a transverse Phase IIm. One set of shearing surfaces comes into occlusion as the jaw moves vertically and a second set as movement of the jaw shifts from vertical to transverse. Neither incisors nor premolars restrict transverse movement (Fig. 6) in the koala as they do in the macropodids. There is a clear distinction between the periods of

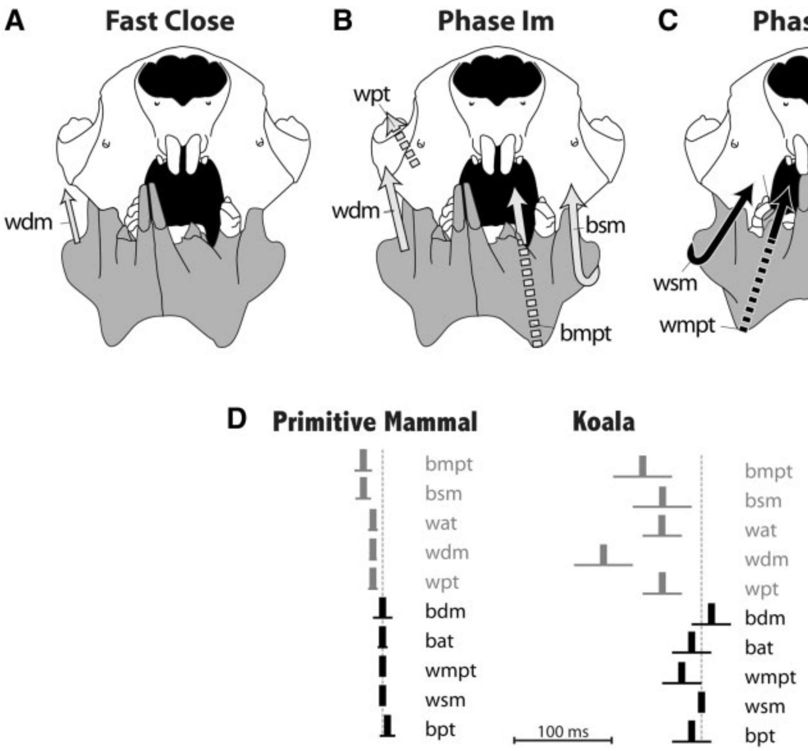

Fig. 6 *Phascolarctos cinereus.* (**A**–**C**) Muscle activity during fast close and the two phases of the power stroke. (**D**) Comparison of the median sequence of activity of the principal adductors in a primitive mammal and in the koala. Based upon Crompton et al. (2010).

activity in both Groups I and II muscles (Fig. 6D). Compared to the primitive program, the koala has a longer duration of activity during the power stroke and a greater temporal distance between peaks of activity in the individual muscles (Crompton et al. 2010). Early activity in the working-side deep masseter draws the working-side jaw laterally (Fig. 6A and D). There is considerable overlap in activity between Groups I and II muscles, but earlier firing of Group I muscles moves the working-side jaw vertically during Phase Im (Fig. 6B) and as activity fades in Group I muscles and builds up in Group II, movement of the jaw shifts from vertical to transverse (Fig. 6C). The mandibular symphysis is fused in koalas and this appears to be an adaptation that prevents wish-boning of the symphysis as a result of late activity in the balancing-side deep masseter (Hylander and Johnson 1994). Macropodids have a mobile symphysis and their balancing-side deep masseter fires well before the working-side superficial masseter (Fig. 5E) rather than afterward as it does in koalas. When the molar cusps are worn down in the koala the enamel crests can crush but not shear food during Phase Im. However, the remaining low enamel crests can still grind food during Phase IIm (Lanyon and Sanson 1986b).

Wombats

Wombats evolved ever-growing molars (Murray 1998; Crompton et al. 2008b) that allow them to ingest plant material that contains a fair amount of grit (Finlayson et al. 2005). Their power stroke is restricted to a single linear transverse phase (Fig. 7B), in sharp contrast to the vertical and transverse phases in that of kangaroos and koalas. At the beginning of the power stroke, the working-side lower molars are positioned laterally to the uppers (Fig. 7A and C) and are drawn across the uppers during the power stroke. This, too, contrasts with koalas, kangaroos, and potoroos in which the lower molars are positioned directly below the matching uppers at the beginning of the power stroke. The molar rows are isognathus, but occlusion is nevertheless unilateral. The skulls of wombats are wide and low (Fig. 7B) and consequently much of the adductor mass lies well-lateral to the molar dentition. Any activity in the balancing-side adductors during the power stroke would tend to rotate the mandible around the working-side dentition, bring the balancing-side molars into occlusion and preventing transverse movement of the jaw. This may account for the unique motor program of wombats whereby only working-side muscles are active during

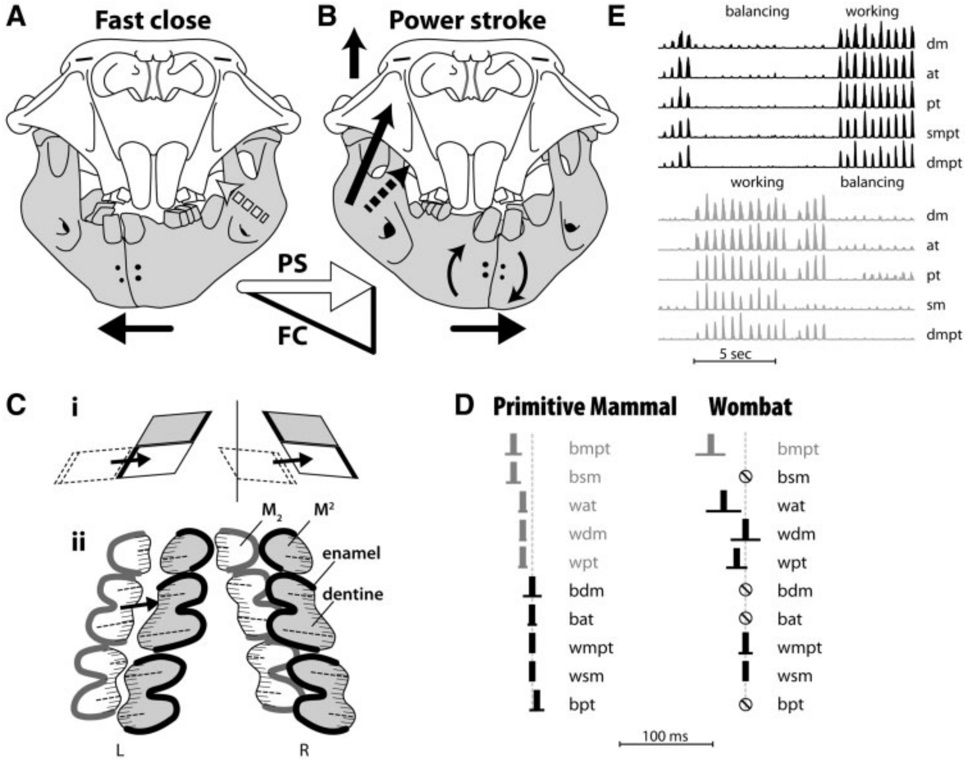

Fig. 7 *Lasiorhinus latifrons*. (**A** and **B**) Muscle activity during fast close and the power stroke. [(**C**(i)] Schematic transverse section through the upper molars (upper: gray; lower: clear) at the beginning (dotted outline) and end (solid outline) of the power stroke. [(**C**(ii)] Occlusal view of the molars at the beginning of the power stroke. (**D**) Comparison of the median sequence of activity of the principal adductor muscles. Note that only the balancing-side medial pterygoid is active during fast close and no balancing-side muscles are active during the power stroke (ø). (**E**) EMGs of a chewing sequence during which there are two shifts in the chewing sides. Based on Crompton et al. (2008b).

the power stroke (Fig. 7D) and activity in the balancing-side muscles decreases to almost zero (Fig. 7E). Only a single muscle, the balancing-side medial pterygoid, draws the working side of the jaw laterally during fast close (Fig. 7A). When wombats chew or bite with their incisors both balancing-side and working-side muscles are active. The closest parallel to the masticatory motor program of wombats is that of some hystricomorph rodents where only Group II muscles (that is Triplet II in Weijs 1994) are active during the transversely directed power stroke. However, as Triplet II includes a balancing side muscle, wombats and hystricomorph rodents are not completely comparable.

Summary

The motor programs of the four marsupial herbivores discussed in this article can be viewed as independent modifications of a primitive program. The differences involve both subtle and substantive shifts in the amplitude of activity levels as well as changes in timing and duration of activity in individual adductor muscles (Fig. 8).

Potoroos retain the powerful linear vertical closing stroke of primitive mammals as a result of the near synchronous timing of peak activity in all the adductors. The only significant change from the primitive program is that declining activity in their working-side superficial masseter and medial pterygoid extends beyond that of the other muscles and draws the working-side hemimandible medially. Potoroos have a powerful Phase Im during which food is sheared by their large third premolars and crushed between bunodont molars. Their Phase IIm is weak by contrast.

In kangaroos, synchronous activity occurs in all but two Group II muscles, resulting in a powerful Phase Im when food is sheared between the upper and lower molar lophs and crushed between the lophs and links. In comparison with potoroos, kangaroos peak activity in the working-side superficial masseter and medial pterygoid occurs later in the chewing cycle, making for a well-defined transverse Phase IIm. Transverse movements of the jaw came late in the evolution of the macropodids and accompanied a shift to a more resistant diet.

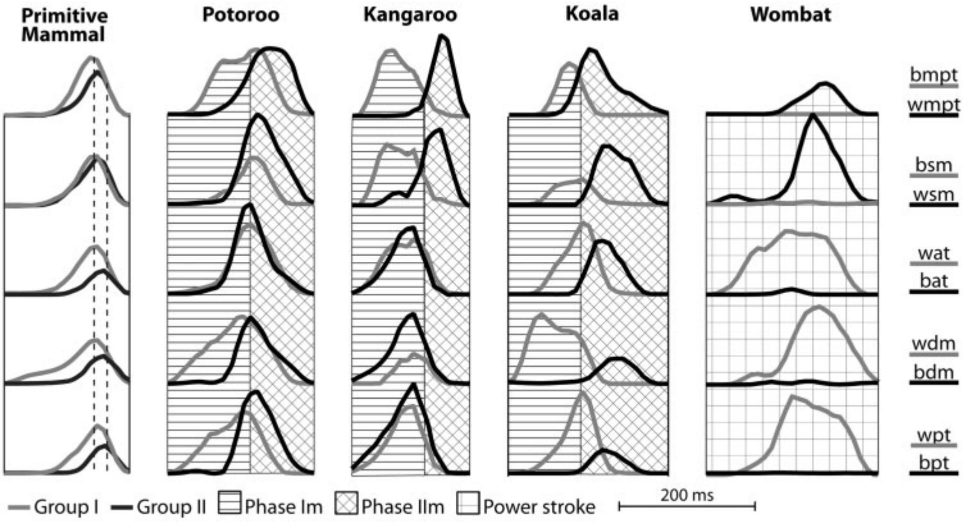

Fig. 8 Comparison of the motor programs of a primitive mammal, potoroo, kangaroo, koala, and wombat during single power strokes. The profiles of the muscle activity of working-side and balancing-side muscles are superimposed on one another (Group I muscles: gray; Group II muscles: black).

Koalas have evolved a different sequence of adductor activity to control vertical and transverse movements of the jaw during the power stroke. They have increased the spread of timing between peaks of activity in the adductors. Although muscle activity overlaps between Groups I and II, most of Group I muscle activity occurs during Phase Im and that of Group IIm during Phase IIm. In contrast to potoroos and kangaroos, the upper dentition does not restrict transverse movements. As in placental herbivores late firing of the balancing-side deep masseter in koalas is associated with a fused mandibular symphysis.

Wombats use only one muscle to draw the working-side of the mandible laterally. Working-side muscles alone draw the jaw transversely during the power stroke while balancing-side muscles remain passive. In comparison with koalas (Fig. 8), three Group I muscles, the working-side anterior and posterior temporalis and working-side deep masseter, fire later in the wombat, together with the working-side medial pterygoid and superficial masseter. The power stroke consists of a single linear transverse movement of the working side of the jaw.

While the motor program of koalas parallels that of placental ungulates, neither the motor program of macropodoids nor that of wombats has any parallel among placental herbivores.

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Supplementary Data

Supplementary data are available at *ICB* online.

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