A MORPHOMETRIC AND KINETIC ANALYSIS OF THE DEVELOPMENT OF THE
FEEDING APPARATUS OF *MONODELPHIS DOMESTICA*

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Elicia N. Thompson

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A MORPHOMETRIC AND KINETIC ANALYSIS OF THE DEVELOPMENT OF THE
FEEDING APPARATUS OF *MONODELPHIS DOMESTICA*

BY

ELICIA N. THOMPSON

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and the College of Arts and Sciences of Ohio University

Audrone R. Biknevicius
Associate Professor of Biomedical Sciences

Leslie A. Flemming
Dean, College of Arts and Sciences
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Director of Thesis: Audrone R. Biknevicius

While juvenile and adult mammals must overcome similar challenges in order to survive, these must be accomplished with very different tools and strategies. Using *Monodelphis domestica* ontogeny of masticatory mechanics was examined. Under the framework of the constrained model of jaw biomechanics, linear measurements were used to describe age-dependent changes in shape and mechanical advantage of the jaws. Additionally, bite force data were collected from both juveniles and adults. Both age categories maintained similar numbers of molariform teeth within the jaw. However, because of improved mechanical advantage, adults produced absolutely greater bite forces with these teeth. By contrast, juveniles produced relatively greater bite forces, powered by relatively larger resultant muscle forces. Therefore, ontogenetically-determined size and shape differences between juveniles and adults have large affects on the biomechanical properties of opossum jaws. Juveniles can produce relatively high bite forces for their body size, but these bite forces require greater energy expenditures.
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ONTOGENY OF FEEDING FUNCTION IN *MONODELPHIS DOMESTICA*

Elicia N. Thompson, Audrone R. Biknevicius, and Rebecca Z. German

*Department of Biological Sciences, Ohio University, Athens, OH 45701 (ENT)*
*Department of Biomedical Sciences, Ohio University College of Osteopathic Medicine, Athens, OH 45701 (ARB)*
*Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221 (RZG)*

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**ABSTRACT**

Although it has been shown that craniofacial configurations change during development, the biomechanical consequences of these changes have not been fully documented. A constrained lever model of the masticatory apparatus championed by Greaves (1978) and others specifies limitations on the size and distribution of bite and masticatory muscle resultant forces in a way that allows assessment of how craniodental configurations affect bite force production. In this study, growth series of *Monodelphis domestica* were used to assess how force production capability changes with growth;
craniodental changes were quantified using a longitudinal set of dorsoventral radiographs. While Region II (area of highest bite force potential along the jaw) always encloses three molariform teeth in the jaws of juveniles and adults alike, growth-based elongation of the masticatory muscle resultant lever arm and preferential narrowing of the palate enhances mechanical advantage of the muscle resultant in adults. Higher mechanical advantage paired with absolutely larger masticatory muscles should yield greater bite forces in adults, so that wild juvenile *M. domestica* may be at a competitive disadvantage in comparison to their adult counterparts when feeding on comparable dietary resources.

**INTRODUCTION**

While juvenile and adult mammals are commonly confronted with similar challenges, body shape and size differences (and the physiological consequences of these) between age groups may correlate with a use of different strategies to deal with these challenges. For example, ontogenetic limits on locomotion were found in jackrabbits (*Lepus californicus*; Carrier, 1995). Juvenile hares, which forage independently at a very young age, are able to accelerate more rapidly than adults, and this is accomplished in part by a greater mechanical advantage in the gastrocnemius muscle of juveniles. Conversely, the overall smaller size of juvenile hares negatively affect their locomotor stamina. Consequently, juvenile hares tend to avoid predation primarily by crypsis and, if detected, greatly accelerating to another refuge rather than attempting out-running their predators. Allometric changes in the appendicular
musculoskeletal system across postnatal ontogeny necessitate different locomotor behaviors in order to accomplish a similar outcome (avoiding predation).

Craniofacial structures also differ in juvenile and adult mammals. The juvenile masticatory apparatus consists of deciduous teeth, which are smaller and often fewer in number compared to the permanent set, and weaker masticatory musculature. There are also differences in the shape of juvenile jaws that result in gross differences in their biomechanical capabilities. For example, puma (*Felis concolor*) and spotted hyena (*Crocuta crocuta*) juveniles have short, wide jaws compared to their adult counterparts, and this shape difference contributes to the reduced bite force production of juveniles (Biknevicius, 1996; Binder and Van Valkenburgh, 2000). The competitive disadvantage that may result from any functional inadequacy of juvenile jaws is counteracted by maternal provisioning of food to the weaned offspring. This extended period of parental care allows more time for the development of the masticatory apparatus. Consequently, this ensures that weaned juveniles will have adequate masticatory tools to be able to forage and care for themselves more independently, thereby increasing the likelihood of offspring survival (Kruuk, 1972; Schaller, 1972).

An extended period of parental care is not ubiquitous among mammals. Indeed, many species provide little care so that juveniles must forage independently for food soon after weaning, as is the case for dwarf opossums, *Monodelphis domestica*. Indeed, juvenile *M. domestica* may be competing with adults for similar foods because there is no data on resource partitioning between age groups (Parker, 1977). This study explores the configuration of the upper jaw of *M. domestica* in order to assess whether or not juvenile
jaws display similar adaptations for bite force production as do adults. The method used is based on constrained lever mechanics of jaws largely developed by Greaves (1978).

**Biomechanical Model.**—In the 1970’s, the study of masticatory function was elevated from a two-dimensional (largely lateral) perspective of a single dentary to a three-dimensional model by the consideration of masticatory muscle and bite force vectors together with both right and left jaws (Bramble, 1978; Greaves, 1978; Hylander, 1979). The model describes three points of resistance ("triangle of support") created during unilateral biting: one at each temporomandibular joint (TMJ) and one at the bite point (Fig. 1a). The side of the jaw where the bite occurs is known as the working side (WS) and the contralateral side is the balancing side (BS). A line trajectory may be drawn which originates at the balancing-side TMJ, passes through a point representing a midline muscle resultant force vector (bilateral sum of all adducting masticatory muscle forces), and intersecting the working-side toothrow. This intersection designates what has come to be known as Region I anteriorly and Region II posteriorly (Spencer and Demes, 1993).

The magnitude of bite forces in Region I follow simple lever mechanics, that is, bite force is directly proportional to muscle force and muscle force leverage but inversely proportional to the leverage of the bite force. By contrast, bite forces in the Region II are, in theory, equal and maximal in magnitude (Greaves 1978). This is largely due to the need to limit distractive forces in the TMJs, because these joints are poorly designed to withstand high tensile stresses (Greaves, 1978). Proper position of the muscle resultant is
critical for maintaining TMJ stability. The anteriormost position of the muscle resultant is limited by the position of the distal-most molar. This is because tensile forces at the working-side TMJ would occur if a bite force is applied behind the muscle resultant. Hence, the maximum lever arm of the muscle resultant is assumed to be fixed as the perpendicular distance between the caudalmost molars and the TMJs.

The need to avoid TMJ distraction also determines the mediolateral position of the muscle resultant, but this is predictably variable. When biting with teeth located in Region I the adductor musculature can contract equally and maximally to obtain high bite forces, therefore, the muscle resultant is located at or near the interpalatine suture and, as indicated above, no further anterior than the caudalmost molars. By contrast, because the triangle of support becomes smaller when biting with Region II teeth, the muscle resultant must necessarily shift away from a midline position toward the working side jaw. This is accomplished by a reduction in balancing-side muscle activity. While maximum muscle resultant forces are actually lower in Region II than in Region I, high bite forces are maintained across Region II because lower muscle forces are paired with reduced muscle resultant leverage.

This study documents ontogenetic changes in the jaw of *Monodelphis domestica*. By applying principles of jaw design specified by the constrained lever model, the size and composition of Region II is evaluated ontogenetically. Furthermore, growth-based changes in the mechanical advantage of the resultant force of the masticatory muscles is determined. In this way, the affect of ontogenetic changes of craniodental anatomy on bite force potential is assessed.
MATERIALS AND METHODS

Linear measurements of the upper jaws were obtained from longitudinal sets of dorsoventral radiographs of *Monodelphis domestica*. These radiographs represented eleven individuals from three different litters (Maunz and German, 1996). The animals were weaned at 48 days of age, similar to the time of weaning in the wild (50 days of age; Parker, 1977). In order to capture shape changes in the jaws during early growth (Smith, 1994), the animals were radiographed in two-day increments starting from 50 days of age until 160 days old. After 160 days of age radiographs were taken every 10 to 20 days until the animals reached 395 days of age. Although *M. domestica* stops gaining weight at around 250 days of age (Maunz and German, 1996), periodic radiography continued through 395 days of age to ensure that skeletal growth was completed. Ancillary data (age, sex, mass) were recorded for each individual during every session.

The radiographs were imported into the computer by either downloading digital images captured with a Kodak DC265 digital camera or scanning the radiographs directly into the computer using a Hewlett Packard ScanJet HDF scanner; these techniques produced equivalent results. Nine landmarks were identified along the skull, primarily along the upper jaw (Figure 1b); all landmarks but four represent homologous structures on the juvenile and adult skull (Table 1). The exceptions are landmarks 2, 6, 8, and 9. The caudal border of the distalmost molars (landmarks 2 and 6) necessarily shift caudally with dental eruption. Consequently, the adductor muscle resultant (landmark 8), whose location is determined by landmarks 4 and 8, also shifts caudally with dental eruption. Finally, an oblique line was drawn from the right TMJ (landmark 7), through the midline muscle resultant; the
intersection of this trajectory with the contralateral tooth row determines the location of
the boundary between Region I and Region II (landmark 9) (Figure 1b).

Landmarks were digitized using the Thin Plate Spline digitizing program (TPS dig; Rohlf, 1998). Seven of the landmarks were used to define the following linear measurements (Figure 1c). Anterior palatal width (APW) was calculated as the width of the palate distal to P³. A baseline axis was drawn between the centroids of the glenoid fossae, the length of which was used as the intercondylar width (ICW). Jaw length (JL) was calculated as the perpendicular distance from the baseline axis to the I¹-I² interdental gap. The resultant adductor muscle force lever arm (LM) and the maximum Region II lever arm (LRII) were calculated as the perpendicular distances from the baseline axis between the glenoid fossae to landmarks 8 and 9, respectively.

Allometric analyses.—Two sets of reduced major axis regressions were run using the SYSTAT 9 statistics package (Wilkinson, 1998). All measurements were log₁₀-transformed for these analyses. The first set of regressions explored the relationship between width measurements (APW, ICW) and jaw length (JL). Because jaw length increases predictably with age (Maunz and German, 1996), jaw length is used as a proxy not just for body size but age as well. The second set evaluated the relationship among lever arms (LM and LRII) and jaw length. Exploratory data analysis indicated that caudal tooth eruption caused a punctuated change in the length of the muscle resultant lever arm. Because LRII is determined by LM, it, too, decreased instantaneously with dental eruption. Therefore, the data for these regressions were split into two samples, those with a fully erupted M³ (adults) and those without (juveniles and sub-adults) and separate regression coefficients were
calculated for each. Significant allometric patterns were identified by inspection of the 95% confidence intervals for each regression slope (isometry indicated by a slope of 1). Additionally, regression of mechanical advantage (ratio of LM to LRII) against \( \log_{10}\)-body mass (\( M_b \)) evaluated the changing mechanics of the masticatory muscle resultant force when biting with teeth located at the Region I-II boundary; a slope of 0 fulfill isometry expectations.

**Ontogenic trajectories.**—The ontogenetic growth patterns for JL, ICW, and APW were established by plotting raw values of each variable against age (days) and using the Gompertz non-linear curve-fitting equation (Maunz and German, 1996; Lammers et al., 2001):

\[
Y = Ae^{-be^{-kt}}
\]  
(1)

where \( Y \) represents the variable measured, \( A \) is the asymptote of \( Y \), \( b \) is the onset of rapid growth of the measured variable, \( k \) describes its rate of growth decay, and \( t \) is age. Additionally, the rate of instantaneous growth \( (I) \) was calculated by multiplying \( b \) with \( k \); \( I \) is also shown by the \( y \)-intercept of the first derivative of equation (1). The time of growth cessation \( (T_f) \) was described as the time at which growth slows to 5% of its maximum rate (modification of Lammers et al., 2001) and was calculated as:

\[
T_f = \left[ -\ln(0.05/b) \right] k^{-1}
\]  
(2)

Gompertz parameters were determined for APW, ICW, and JL for each individual \( M. \) *domestica*. Significant differences between these Gompertz parameters were quantified by running one-way ANOVAs and confirming the pattern of variation with the Tukey post-hoc
test using the NCSS statistics package (Hintze, 2000). Parameters were identified as being significantly different from each other if $p<0.05$.

**RESULTS**

The boundary between RI and RII, or the anteriormost extent of the LRII lever, in *M. domestica* occurs at dP$^3$ in juveniles (Fig. 2a), M$^1$ for sub-adults, and at either M$^1$ or M$^2$ for adults (Fig. 2c). Therefore, across all age groups, Region II always encloses the molariform teeth and always contains at least three teeth (Table 2).

*Allometric Analyses.*--Regression slopes and their 95% confidence intervals are listed in Table 3. The width measurements (APW and ICW) show a negative allometric relationship with jaw length (Fig. 3a). APW is also negatively allometric with respect to ICW (Fig. 3b). Therefore, palatal and intercondylar widths are relatively narrower in *M. domestica* adults, with palatal widths being particularly narrow relative to intercondylar widths in older animals.

The plots of the lever arm measurements show a biphasic distribution (Fig. 4a). Abrupt reductions in lever arm length are apparent with eruption of M$^3$. In order to alleviate any bias that might arise from fitting the regression lines through the entire sample, the sample was split into two groups representing juveniles versus sub-adults and adults. Both the lever arms to the resultant adductor muscle force vector (LM) and the RI/RII boundary (LRII) show positive allometric relationships with jaw length in both age groups (Fig. 4a). The regression of LM against LRII also exhibited a positive allometric relationship indicating that the growth of the Region II lever arm falls behind
that of the muscle resultant through ontogeny (Fig. 4b). As a result, mechanical advantage scales to $M_b^{0.11}$ (Table 3). Consequently, not only do *M. domestica* adults exhibit relatively longer lever arms in comparison to juveniles but the muscle resultant leverage is particularly elongated in adults. This contributes to the increase in mechanical advantage with growth. Furthermore, within both the juvenile and adult samples, older individuals had relatively longer lever arms than the younger juveniles and adults.

The relationships between the lever arm measurements (LRII and LM) and the width measurements (APW, ICW) are all positively allometric (Table 3, Fig. 5). Therefore, adults have longer lever arms with respect to the width of the skull in comparison to juveniles.

*Ontogenetic Trajectories.*--Growth curves for JL, ICW, and APW are shown in Fig. 6, and the Gompertz parameters derived from the data are listed in Table 4. The onset of rapid growth ($b$) is significantly different in all three linear measurements ($p<0.001$), with $b$ being greater for JL and ICW than APW, indicating a delay in rapid growth of JL and ICW. The instantaneous rate of growth ($I$) of JL is significantly larger than either width measurement. This is also revealed by the first derivative plot (inset plots on Fig. 6), whereby $I$ is indicated by the y-intercept of the curves. There was no significant difference between the measurements in the rate of growth decay ($K$), however, the time of growth cessation ($T_f$) was significantly earlier in APW. In summary, it appears that palatal width has an earlier onset of rapid growth but also ceases to grow at an earlier time than either intercondylar width or jaw length. In addition,
although growth of intercondylar width and jaw length is delayed, both have faster rates of growth in comparison to palatal width.

**DISCUSSION**

The constrained model of lever mechanics of the jaws (Greaves, 1978; Spencer and Demes, 1993) allows predictions for different jaw configurations that have similar functional consequences. Functional outcomes include, but are not limited to, high bite force magnitudes within Region II as well as the amount and nature of dental material constituting the Region II dental battery.

*Maximizing Bite Forces.*—Bite force magnitudes generated by teeth in Region I increase caudally due to simple lever mechanics, with maximal bite forces generated at the boundary between Regions I and II \((F_{B-max} = F_M * L_M / L_{RII})\) where \(F_{B-max}\) is the maximum bite force, \(F_M\) is the masticatory muscle resultant force). Any additional caudal shifting in bite location (i.e., more caudally within Region II) is accompanied by a reduction in overall adductor muscle force (a consequence of necessary reductions in balancing-side muscle force in order to maintain the muscle resultant vector within the triangle of support), and these reductions in muscle resultant force are compensated by reductions in the bite force lever arm. Therefore, bite force magnitudes are expected to either stay equally high (Greaves 1978) or reduce slightly caudally in Region II (Spencer, 1999; Keiser et al., 1996). If maximization of bite force (for a given resultant muscle force) is desirable then a jaw should be configured with a high mechanical advantage of the muscle resultant for biting with teeth located at the RI-II boundary. The value of
mechanical advantage be increased by elongating the lever arm of the muscle resultant force or shortening the bite force lever arm.

Mechanical advantage was found to increase with age in *M. domestica* (as indicated by the positive allometric slope in Fig. 3). Because both lever arms show significant positive allometry tendencies and because adults have particularly enhanced muscle resultant lever arms, this leads to the conclusion that mechanical advantage of adult masticatory systems is enhanced by preferential elongation of the muscle lever arm. However, this explanation is insufficient because another mechanism is clearly at work in adult skulls, namely, relative narrowing of the palate. Mathematical modeling shows that mechanical advantage also increases substantially with narrowing of the palate (particularly when palatal narrowing is accompanied by an even greater narrowing across the glenoid fossae; Appendix I; pers. com. Walter Greaves).

While it appears that juvenile skulls are poorly configured for bite force production (i.e., they lack the long muscle resultant lever arms or narrow palates that enhance mechanical advantage in the adults), there is at least one feature that helps to improve bite force in juveniles. Juveniles were found to have relatively short bite force lever arms when biting with teeth located at the RI-II boundary, and this feature helps boost the mechanical advantage of the juvenile masticatory apparatus so that resulting bite forces are not as weak as they would be if bite force leverage was longer.

*Maximizing the Length of Region II.*—Once erupted, occlusal surfaces of teeth degrade progressively due to abrasive wear. *M. domestica* are omnivorous animals, and their varied diet is reflected in the shape of their post-canine dentition. Similar to the
other didelphids, *M. domestica* possess tribosphenic molars which enable both puncture crushing and shearing modes of food processing (Crompton and Hiiemae, 1970). Teeth located in Region II of the jaw not only apply the highest bite forces, they also tend to be used preferentially for chewing, further increasing the potential for dental wear. Therefore, it may be advantageous to have an elongate Region II so that the Region II dental battery contains numerous teeth for efficient processing of food and so that any one individual tooth is not excessively worn.

The craniofacial widths have opposing effects on the length of Region II. On the one hand, relatively narrower palates should be associated with a more caudal RI-II boundary (Biknevicius, 1996; Greaves, pers.com). This is because the RI-II boundary is determined by a trajectory from the balancing-side TMJ through the midline muscle resultant: the narrower the palate, the shorter the trajectory, and, thus, the more caudal its intersection with the toothrow (Figs. 2b, 7a). By contrast, a relatively narrow intercondylar breadth would tend to situate the RI-II boundary more anteriorly as the angular trajectory from the balancing-side TMJ is less acute when glenoid fossae are closer together (Fig. 7b). In *M. domestica*, both palatal and intercondylar widths demonstrate negative allometry with jaw size, consequently, adults have relatively narrower craniofacial widths than do juveniles. Furthermore, palatal width scales positively with intercondylar width, so that the palates of adults are particularly narrow. This might lead to the conclusion that Region II of adult skulls should be relatively shorter than those of juveniles. Surprisingly, when the length of Region II is estimated as the subtraction of the RI-II lever arm from the muscle resultant lever arm, a positive
allometry is found for the regression of Region II length on skull length. In other words, contrary to expectations, Region II is actually relatively longer in adult skulls.

How then can the elongation of Region II in *M. domestica* adults be explained? Simply erupting more molars and elongating Region II caudally is not a particularly productive method because this would coincidently shifts caudally the midline muscle resultant (which is restricted anteriorly to a transverse axis passing along the distal edge of the caudalmost molar). This has the circular effect of also shifting the RI-II boundary caudally because the trajectory from the balancing-side TMJ becomes more acute. But dental eruption is not a solitary event in *M. domestica* as it paired with differential skull growth in the region of the skull between the molars and the glenoid fossae. As a consequence, the caudalmost molars are located further from the TMJ’s as reflected by the significantly longer muscle resultant lever arms in *M. domestica* adults (Fig. 7c). A more rostral muscle resultant shifts the RI-II boundary anteriorly and thereby elongates Region II in *M. domestica* adults (Appendix II).

Whereas most allometric patterns favor a longer Region II in adult skulls, juveniles do have relatively wider palates. Wider palates allow a longer trajectory from the balancing-side TMJ which translates to some anterior elongation of Region II in juveniles (Fig. 7a).

In spite of scaling differences in Region II lengths in juveniles and adults, both age groups maintain a similar number and morphology of teeth in Region II (Table 2). Specifically, the occlusal surfaces of three teeth are located in Region II regardless of age. Furthermore, although the RI-II boundary coincides with the caudal premolar (dP$^3$)
in juveniles, this tooth is molariform so that *M. domestica* juveniles are equipped with similar, albeit somewhat smaller, grinding surfaces for Region II as adults.

**Ontogeny of Feeding.**—Body size and shape differences of juvenile and adult mammals often affect the function of their musculoskeletal units and, therefore, dictate the use of different strategies to deal with locomotor challenges (e.g., Carrier, 1995a, 1995b; Miles et al., 1995). The feeding apparatus is not immune to ontogenetic constraints. *Monodelphis domestica* juveniles must forage independently soon after weaning. If diets of juveniles and adults are not qualitatively different then one might expect to find evidence of biomechanical strategies in the masticatory apparatus of juveniles that would allow them to successfully compete with adults for food. And, indeed, the relatively wider palates of juveniles helps to configure their jaws with a moderately long Region II thereby enabling the inclusion of the molariform dP3 into the region of high bite force potential. But in all other parameters noted the masticatory apparatus of *M. domestica* juveniles appear to be at a mechanical disadvantage relative to adults. Therefore, juvenile jaws are unlikely to produce bite forces of equivalent magnitudes as the adults (Chapter 2/ Thompson and Biknevicius).

Indeed, the lower bite force potential of juveniles may place younger animals at competitive disadvantage relative to adults when feeding on similar foods. It is worthwhile noting that bite force magnitudes alone are unlikely to adequately reflect the ability of animals to comminute food. Unworn deciduous teeth and new erupted permanent teeth often display very sharp cusps. The ability of teeth to develop cracks in foods is, in part, a function of the stress applied to the surface of the food (Lucas et al.,
Because stress is determined by the quotient of bite force and area of force application (F_B / A), the sharper cusps (low area) of the dental battery of juveniles may partially compensate for their lower absolute bite forces.

Our findings are a reminder of the lack of field data regarding the feeding behavior of *M. domestica* in the wild. It is possible that age groups partition foods by choosing items of different sizes or toughness (e.g. maturity of leaves or fruit) even if they choose similar types of foods (Dumont, 1999; Strait, 1993).

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Elicia N. Thompson and Audrone R. Biknevicius

Department of Biological Sciences, Ohio University, Athens, OH 45701 (ENT)

Department of Biomedical Sciences, Ohio University College of Osteopathic Medicine, Athens, OH 45701 (ARB)

Keywords: *Monodelphis domestica*, Bite force, Biomechanics, Ontogeny, Feeding

**Abstract**

The force with which bites are generated plays a key role in food acquisition. Simple lever models were historically used to describe jaw mechanics, but appreciation of the more complex role of masticatory muscles in producing bite forces at the molars has inspired the use of a constrained lever model. This model specifies that bite force magnitudes are maximal at the Region I-II boundary, which in *Monodelphis domestica* lies at dP3 in juveniles and M1 in adult. In an attempt to test the predictions of the constrained lever model, we used dwarf-oppossums (*Monodelphis domestica*) to evaluate bite force magnitudes along the jaw. In addition, we compared bite forces from juveniles and adults to determine ontogenetic variation in bite force production. Data on adults supported the constrained model in that bite forces tended to increase caudally within Region I and did not increase in magnitude within Region II. Adherence to the constrained model was also generally maintained in the juveniles. Finally, adults were
able to produce absolutely greater bite forces as expected by their larger body size and improved mechanical advantage of their masticatory muscles.

INTRODUCTION

Several models have been proposed for simplifying the mechanics of the masticatory apparatus in mammals (see Spencer, 1999). The historically older models are based on simplified lever mechanics of a single dentary (e.g. Biknevicius and Ruff, 1992). According to these models, bite force ($F_B$) can be estimated using the following equation: $F_Bb = F_Mm$, where $F_M$ is the masticatory muscle force and $b$ and $m$ are the lever arms for the bite and masticatory muscle forces, respectively. The simplified lever model specifies that maximum bite force magnitudes should increase linearly with muscle force and its mechanical advantage ($MA = m/b$) and that mechanical advantage increases when the masticatory muscle lever arm shortens or the bite point shifts closer to the temporomandibular joint (TMJ).

In the 1970’s, the inadequacies of the simplified lever (or unconstrained) model became apparent and a new model was developed that evaluated masticatory mechanics using a more accurate bilateral perspective (Bramble, 1978; Greaves, 1978). The foundation of the constrained model of the masticatory apparatus is the need to avoid TMJ distraction during biting or chewing. Indeed, the articular ligaments surrounding the TMJ do indeed appear poorly suited for high tensile loads (Greaves, 1978, 1982, 1983, 1985, 1988; Spencer and Demes, 1993, 1999; Werdelin, 1987) and experimental studies of masticatory mechanics appear to verify that TMJ distractions rarely occur (Dessem
and Druzinsky, 1992; Lane, 1982; Stewart et al., 1975). This three-dimensional model describes three points of resistance along the jaw during unilateral biting (Fig. 1A): one each at the balancing-side and working-side TMJs and one at the bite point itself. These three points make up the vertices of what is commonly recognized as the triangle of support. In order for an animal to avoid jaw distraction while chewing the resultant muscle force vector must lie within the triangle of support. The muscle resultant vector lies at a midline position along the jaw when masticatory muscles are contracting with equal force bilaterally and can be positioned no further anterior than the distal-most tooth.

According to the constrained model, the dental array is divided into two regions (Spencer and Demes, 1993). The anterior region of the jaws is known as Region I, and it contains incisors, canines, and most, if not all, premolars. Because working- and balancing-side masticatory muscles can contract maximally and their muscle resultant can be maintained within the large triangle of support, Region I teeth generate bite forces following simple lever mechanics. In other words, maximum bite force magnitudes in Region I are expected to increased as the animal bites with more posteriorly positioned teeth simply as a function of the shortening of the effort lever.

The caudal dentition are contained within Region II. The boundary between Region I and II is determines by a line trajectory which initiates at the balancing-side TMJ, passes through a point representing the midline resultant muscle force vector, and then intersects the working-side tooth row. Consequently, Region II typically contains the molars as well as, in some animals (e.g., Crocuta; Biknevicius, 1996), one or more of
the premolars. As the triangle of support becomes smaller when an animal bites using more posteriorly positioned teeth in Region II, resultant muscle force vector must shift toward the working-side in order to stay within the triangle of support (Fig. 1b). This lateral shift can only be accomplished by a decrease in the balancing-side masticatory muscle force (because the working-side musculature is already contracting maximally), thereby reducing the overall magnitude of the muscle resultant force (Dessem, 1989; Hylander et al., 1992; Spencer, 1998). The diminished muscle force is largely compensated by the improved leverage of the bite point, so that bite forces produced within Region II will be of equal or of slightly decreasing magnitude (Keiser et al., 1996; Spencer, 1998).

Therefore, the constrained model of jaw mechanics maintains that maximum bite force magnitudes should increase caudally within Region I, reach their highest values at the Region I-II boundary, and then stay fairly high throughout Region II. A variety of studies have directly or indirectly evaluated the model using morphometrics (Greaves, 1983, 1988; Werdelin, 1987; Biknevicius, 1996), electromyography (Lagenbach et al., 1991; Spencer, 1998), and bone strain analysis (Hylander, 1979). While the function of the masticatory apparatus as a semi-constrained lever system has become axiomatic, empirical data on bite force magnitudes are extremely limited (Dessem and Druzinsky, 1992).

The present study evaluates bite force magnitudes across the jaws of *Monodelphis domestica*, the dwarf opossum. Data from Region I and Region II are used to evaluate
the constrained model of lever mechanics. Additionally, data from juveniles and adults are compared to assess ontogenetic differences in the ability to generate large bite forces.

**MATERIALS AND METHODS**

Bite force data were collected from eight juvenile (all female) and eight adult (four females, and four males) dwarf opossums, *Monodelphis domestica*. The juveniles were between 70 and 80 days of age during the data collection period, thus the animals may be considered both reproductively and anatomically immature (Parker, 1977; Maunz and German, 1996). The adults were fully grown, being well over on 100 days old. Body mass ranged from 0.030 to 0.040 kg (mean of 0.0355 kg) in the juveniles and from 0.061 to 0.125 kg (mean of 0.09 kg) in the adults.

*Bite force measurements*

Two bite force transducers were built sized specifically to be used with the juvenile and adult opossums (designed after the model in Binder and Van Valkenburgh, 2000; Lance McBrayer, pers. com.). The transducers were composed of two parallel steel plates that were cantilevered to a brass handle. Four foil strain gauges were firmly bonded on each surface of each tine at the cantilevered end, and these were configured into a full Wheatstone bridge. The tips of the tines were tapered so to allow specificity of tooth use. The distal end of each tine was also covered with a rubber coating to protect the teeth of the opossums during forceful biting (Rubberize-It!, dist. by Rhodes American). The distal end of the smaller transducer (including the rubber coating) was 3.2 mm in width whereas the larger transducer was 4.8 mm wide.
Biting on the force transducer caused the tines to bend toward one another and thus altered the voltage output of the Wheatstone bridge. Voltage changes were recorded with a LabView virtual instrument data acquisition program (National Instrument). The transducers were calibrated each day by simultaneously loading the tines with known weights (50-500 grams); the resulting voltage outputs were then regressed against weight (in Newtons) to determine the scaling relationship between the variables.

Adults and juveniles either readily bit on the bite force transducers or were induced to bite by pinching the nape of their necks (which caused them to open their jaws). The position of the transducer along the jaw was determined videographically. Unilateral bite locations were categorized as: incisor/canine (I/C), premolar (excluding the distalmost premolars in juveniles) and Region II, which included the molars plus, in the juveniles, dP³ or P³ (Fig. 2).

Bite force data were captured during multiple trials over several days, but because the constrained model predictions are based on maximum force production, only the maximum voluntary bite force record from each individual was used in the analysis. Bite force data were analyzed raw as well as weight-adjusted data. Due to the problem of interdependence that is inherent in collecting multiple measurements from a given animal, repeated-measures ANOVA was used to determine position and age-related variation in maximum bite force using SYSTAT 9 (Wilkinson, 1998). This was followed by a Bonferroni pairwise comparison where significant variation was determined.

The *Monodelphis* adults were additionally evaluated for bite force differences within Region II. The tines of the smaller bite force transducer were sufficiently narrow
(3.2 mm) to allow collection of force data from individual molars within Region II. Force data were collected from M$^1$-M$^3$ (the caudalmost molar was difficult to visualize); the smaller mouths of juveniles provided limited visibility for discriminating Region II teeth, therefore juvenile data were not included in this aspect of the study.

Estimation of masticatory muscle force

The heads of *Monodelphis* juveniles and adults were radiographed in dorsoventral projection in order to measure the lever arms to the tooth located at the boundary between Regions I and II (LRII) and to the muscle resultant (LM; Fig. 2B). First, a baseline axis was drawn between the glenoid fossae. Then, the Region I-II lever arm was measured as the perpendicular distance between the baseline axis and the boundary between Regions I and II. Similarly, the muscle resultant lever arm was measured as the perpendicular distances between the baseline axis and an axis drawn immediately behind the caudalmost molar.

Mechanical advantage (MA) of the masticatory muscle resultant for biting with the tooth located Region I-II boundary was computed as:

\[
MA = \frac{LM}{LRII}
\]

Both raw and weight-adjusted bite forces were used to estimate the raw and weight-adjusted masticatory muscle forces for biting maximally with teeth located at the Region I-II boundary:

\[
F_M = F_{B-max} \times \frac{LRII}{LM}
\]

Differences between adults and juveniles in mechanical advantage and estimated masticatory muscle force were assessed using ANOVA (Wilkinson, 1998). Finally,
scaling coefficients of bite force, estimated muscle force, and mechanical advantage against body mass was assessed by reduced major axis regression, with an isometry expectations for slopes of 1 for the forces and 0 for mechanical advantage.

**RESULTS**

*Variation of bite force along the jaw*

Within adults, maximum voluntary bite forces varied significantly with respect to tooth position in *Mondelphis domestica* (P<0.001, Fig. 3a). Bite force magnitudes of Region II teeth were significantly greater than those of Region I (P<0.002). Furthermore, bites with the premolars were stronger than those with the incisors or canines (P<0.02). By contrast, maximum bite forces did not vary significantly within Region II, so that bites with M1, M2 or M3 were equivalently strong (P>0.17).

Juvenile data largely followed that of the adults in that bite force magnitudes of Region II teeth were significantly greater than those of Region I (P<0.002). However, while bites at the premolar region also tended to be greater than those with the incisors or canines, this difference did not attain statistical significance in juveniles.

*Age-based differences in bite forces*

Maximum voluntary bite force and estimated masticatory muscle resultant forces also varied significantly with respect to age in *M. domestica*. (Fig. 3a). Absolute bite force magnitudes of adults exceeded those of juveniles when comparable teeth were examined (P<0.001). Although differences between age groups dissolved when bite forces were divided by subject body weight (P>0.05, Fig. 3b), a significant size-
dependency was demonstrated as bite force at the Region I-II boundary was found
to scale to $M_b^{0.77}$ so that there is a tendency for younger animals to generate relatively
stronger bites for their body size.

Similarly, muscle resultant forces for biting at the Region I-II boundary were
significantly greater in adults than in juveniles as demonstrated by their means of 33.61N
(SE = 2.30N) in adults versus 21.77N (SE = 2.10N) in juveniles (P<0.004). By contrast,
weight-adjusted forces were equivalent across age groups (P>0.2; Fig. 3b). Again, a
significant size-dependent decrease in masticatory muscle force was found as the muscle
resultant force is proportional to $M_b^{0.70}$.

**Mechanical advantage**

Mechanical advantage of the masticatory muscle resultant was computed for
biting with teeth located at the Region I-II boundary. Significantly greater mechanical
advantage was found for adults (0.91, SE = 0.03) than juveniles (0.82, SE = 0.03;
P<0.04). Furthermore, a significant size-dependent increase in mechanical advantage
was demonstrated because mechanical advantage was found to scale to $M_b^{0.34}$ (P<0.02).

**DISCUSSION**

**Constrained lever model of the masticatory system**

Predictions of both unconstrained and constrained lever models of jaw mechanics
were upheld with bite force data obtained when *Monodelphis* adults bit with teeth at and
anterior to the Region I-II boundary (i.e., incisors/canines, premolars, and the molar at the
Region I-II boundary; Fig. 3A). Specifically, maximum voluntary bite forces increased
significantly as the animals bit with more caudal teeth. Assuming that the masticatory muscles were recruited bilaterally and close to their voluntary maximum contraction, bite forces in Region I appear to be primarily a function of improved mechanical advantage as caudal teeth have shorter out-lever lengths.

By contrast, bite force data from Region II provide support for the constrained lever model and unequivocal refutation of the unconstrained (simple) lever model. This study did not find caudal enhancement of bite force production within Region II teeth as was expected by the unconstrained model. Indeed, forces produced by M₁ through M₃ were of equivalent strength. This is precisely what was predicted by the original conception of the constrained lever model (Greaves, 1978). Because the leverage to the bite point decreases caudally within Region II, the most likely explanation for the equivalence of bite force is a reduction in masticatory muscle activity. This is supported by masticatory muscle data in human whereby biting on more caudal molars was associated with reductions in the balancing/working electromyography (EMG) ratios (Spencer, 1998).

Indirect evidence obtained using EMG (Spencer, 1998) and jaw geometry (Keiser et al., 1996) has suggested that bite force magnitudes might actually fall somewhat as the bite point moves caudal from the Region I-II boundary. This may be caused by reduced activity of working-side as well as balancing-side masticatory muscles during Region II biting. This is precisely what was demonstrated by EMG data in humans (Spencer, 1998), although the degree with which activity of the working-side muscles was reduced is far less than that of the balancing-side. Spencer (1998) suggested that caudally-
reduced muscle activity patterns in humans may be an effect of the differential ability of the teeth with withstand occlusal loads because root size and structure is related to a tooth’s ability to resist loads. In humans, both tooth root surface area and complexity declines from M1 to M3. Conceivably, opossums circumvent the constraints found in humans by retaining large teeth and roots across Region II so that *M. domestica* adults are able to maintain a fairly high and constant activity levels of the working-side musculature and therefore avoid the caudal decline in bite forces across Region II found in humans.

**Ontogeny of masticatory function**

Locomotor and masticatory function must be well developed early in life so that juvenile mammals can successfully avoid predation and adequately obtain nourishment after weaning. But early function does not necessarily reach adult capability. Locomotor biodynamics are quantitatively different in juvenile than adults because of ontogenetic limits on locomotor performance (see Carrier, 1996). For example, the small mass of juvenile jackrabbits (*Lepus californicus*) negatively affects their locomotor stamina but young hares are able to accelerate more rapidly than adults, accomplished in part by the greater mechanical advantage in the gastrocnemius muscle of juveniles (Carrier, 1995). Therefore, whereas adult hares will attempt to out-run their predators, juvenile hares tend to avoid predation primarily by crypsis and, if detected, greatly accelerating to a refuge. The data presented here on the ontogeny of bite force production may be used to explore whether ontogenetic limits exist on masticatory function.
Comparisons between animals of different size (and age) offer suffer because of difficulties in determining what constitutes equivalent functional conditions. For feeding function, bites generated with teeth located at the Region I-II boundary may be compared between age groups because, according to the constrained lever model, this is where bite forces are expected to be greatest in all jaws. Thus, biting with these teeth can be considered functionally equivalent events for juveniles and adults even though the teeth themselves are different (typically dP³ in juveniles and M¹ in adults). *M. domestica* adults are substantially superior in developing high bite forces as values of voluntary maximum forces of adults were, on average, 181% that of the juveniles (Fig. 3A). That older, and thus larger, animals generate larger forces compared with the juveniles was not unanticipated. More intriguing is the relationship between bite force and body mass, because maximum voluntary bite forces at the Region I-II boundary scaled with negative allometry ($M_b^{0.77}$). In other words, bite force capability in *M. domestica* lags behind body mass increases across ontogeny, so that smaller (and younger) animals tend to generate relatively larger bite forces than larger (older) animals (Fig. 3B). What is the root of the size-dependent decrease in maximum bite force? Because the Region I-II boundary is the caudalmost location for which the simple lever mechanics are applicable, this question can be explored by assessing how mechanical advantage and magnitude of the muscle resultant force changes with size (and therefore age).

Mechanical advantage of the masticatory muscle resultant in *M. domestica* displays an ontogenetic increase, scaling with $M_b^{0.34}$ in this study and $M_b^{0.11}$ in a much larger and more complete ontogenetic series (Thompson et al., chapter 1; Table 1). These
scaling results support previous findings of ontogenetic increases in the mechanical advantage for some individual masticatory muscles in *Rattus norvegicus* (superficial masseter and internal pterygoid, although the mechanical advantage of most other craniomandibular muscles in rats were not found to change significantly with growth; Hurov et al., 1988).

Although changes in mechanical advantage of muscles with size have also been reported in the locomotor system, there is some evidence that ontogenetic (intraspecific) shifts in mechanical advantage may be quite different than those found among adults in interspecific allometry studies. For example, while the mechanical advantage of appendicular muscles generally scales with positive allometry ($M_b^{0.25}$) in adult mammals (Biewener, 1989), ontogenetic decreases in mechanical advantage have been found for some limb muscles (Carrier, 1995). Therefore, skeletal geometry does not appear to provide a mechanical advantage for the masticatory muscles of juveniles as it can for their locomotor muscles.

*M. domestica* juveniles apparently compensate for their poorer mechanical advantage by generating relatively higher masticatory muscle resultant forces since these forces scale to $M_b^{0.70}$ (Table 1); this scaling coefficient is remarkably close to that found for locomotor muscle force among adult mammals ($M_b^{0.75}$; Biewener, 1989).

In conclusion, enhanced absolute bite force may translate to a competitive advantage for food among *M. domestica* adults if desirable food items of both juveniles and adults require high occlusal forces to fracture. Although smaller animals generate
relatively greater bite force, it is at a price because bite forces are not enhanced by lever mechanics but rather by relatively greater muscular effort.

ACKNOWLEDGMENTS

I gratefully acknowledge the Ohio University Tunnel Maintenance Department and Physics shop for assistance milling the metal component of the bite force transducers. Rachel Coe, Tonya Rogers, Andy Parchman, Andy Lammers and Jeff Willey assisted data collection; the staff of Department of Lab Animal Resources at Ohio University were key in maintaining a healthy colony of Monodelphis. Steve Reilly modified a data acquisition program for use with the force transducers. The Evolutionary Morphology group at Ohio University provided input and guidance throughout this study. Finally, financial support was provided by National Science Foundation (IBN-9723768 and 0080158) to ARB, the Department of Biological Sciences at Ohio University, and a direct grant from the Ohio University College of Osteopathic Medicine.


Table 1. Description of landmarks and their use in each analysis.

<table>
<thead>
<tr>
<th>Landmarks</th>
<th>RMA</th>
<th>Gompertz</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Geometric center of the left TMJ</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>2 Bucco-distal corner of left distalmost molar</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>3 Left P³-M¹ interdental gap</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>4 I¹-I² interdental gap</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>5 Right P³-M¹ interdental gap</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>6 Bucco-distal corner of right distalmost molar</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>7 Geometric center of the right TMJ</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>8 Midline adductor muscle resultant vector, located immediately posterior to distalmost molar</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>9 Region I/Region II border on the left jaw</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Identification of the tooth marking the RI-RII boundary (the anteriormost extent of Region II) and description of the teeth enclosed within Region II for each age group.

<table>
<thead>
<tr>
<th>Age Group</th>
<th>RI-RII boundary</th>
<th>Teeth within RII</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juveniles</td>
<td>Distal P³</td>
<td>P³-M²</td>
</tr>
<tr>
<td>Adults and Sub-adults</td>
<td>Distal M¹ or Mesial M²</td>
<td>M¹(2)-M⁴</td>
</tr>
</tbody>
</table>
Table 3. Allometric relationships for the reduced major axis regressions as indicated by slope calculations and 95% confidence intervals. N = negative allometry; P = positive allometry.

<table>
<thead>
<tr>
<th>X variable</th>
<th>Y variable*</th>
<th>Slope</th>
<th>95%CI</th>
<th>Allometric Association</th>
</tr>
</thead>
<tbody>
<tr>
<td>JL</td>
<td>APW</td>
<td>0.518</td>
<td>0.501 – 0.535</td>
<td>N</td>
</tr>
<tr>
<td>ICW</td>
<td>0.832</td>
<td>0.813 – 0.852</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>L2_j</td>
<td>1.750</td>
<td>1.603 – 1.897</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>L2_a</td>
<td>1.391</td>
<td>1.335 – 1.447</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_j</td>
<td>1.853</td>
<td>1.710 – 1.995</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_a</td>
<td>1.487</td>
<td>1.427 – 1.547</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>ICW</td>
<td>APW</td>
<td>0.622</td>
<td>0.603 – 0.642</td>
<td>N</td>
</tr>
<tr>
<td>L2_j</td>
<td>2.259</td>
<td>1.944 – 2.574</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>L2_a</td>
<td>1.575</td>
<td>1.489 – 1.661</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_j</td>
<td>2.392</td>
<td>2.091 – 2.692</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_a</td>
<td>1.684</td>
<td>1.598 – 1.710</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>APW</td>
<td>L2_j</td>
<td>2.997</td>
<td>2.549 – 3.444</td>
<td>P</td>
</tr>
<tr>
<td>L2_a</td>
<td>2.522</td>
<td>2.351 – 2.694</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_j</td>
<td>3.173</td>
<td>2.707 – 3.638</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>LM_a</td>
<td>2.697</td>
<td>2.516 – 2.878</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>Mb</td>
<td>MA</td>
<td>0.11</td>
<td>0.09 – 0.12</td>
<td>P</td>
</tr>
<tr>
<td>L2</td>
<td>LM</td>
<td>1.047</td>
<td>1.022 – 1.071</td>
<td>P</td>
</tr>
</tbody>
</table>

* j = juvenile sample; a = adult sample
Table 4. Average Gompertz parameters: onset of rapid growth (b), instantaneous growth rate (I), rate of growth decay (K), time of growth cessation (T_f). Significant differences based on ANOVA and Tukey post-hoc test are indicated by the asterisks.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Measurement</th>
<th>b</th>
<th>I</th>
<th>K</th>
<th>T_f</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ICW</td>
<td>0.798*</td>
<td>0.012</td>
<td>0.013</td>
<td>211.73</td>
</tr>
<tr>
<td></td>
<td>APW</td>
<td>0.571*</td>
<td>0.008</td>
<td>0.015</td>
<td>164.13*</td>
</tr>
<tr>
<td></td>
<td>JL</td>
<td>0.999*</td>
<td>0.016*</td>
<td>0.014</td>
<td>214.68</td>
</tr>
</tbody>
</table>

*P<0.001
<table>
<thead>
<tr>
<th></th>
<th>Adults</th>
<th>Juveniles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mechanical advantage</td>
<td>0.910 (0.027)**</td>
<td>0.822 (0.025)**</td>
</tr>
<tr>
<td>Muscle resultant force (N)</td>
<td>33.614 (2.304)*</td>
<td>21.769 (2.104)*</td>
</tr>
<tr>
<td>Weight-adjusted muscle</td>
<td>45.731 (4.796)</td>
<td>53.745 (3.601)</td>
</tr>
<tr>
<td>resultant force (BWU)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.004

**P < 0.02
Fig. 1. Ventral view of Monodelphis domestica skull. a) Triangle of Support indicating: Balancing side TMJ (BS), Working side TMJ (WS), line trajectory dividing Region I (RI) from Region II (RII). b) Landmarks digitized on radiographs. c) Linear measurements produced for the reduced major axis and Gompertz regressions.
Fig. 2. Ventral views of the dental arcade, glenoid fossae (paired ovals), midline muscle resultant force (circle) and Region II teeth: a) juvenile condition; b) presumed juvenile condition if the juvenile jaw was a miniaturized version of the adult orodental configuration; c) adult condition.
Fig. 3. Log-log plots of: a) intercondylar width (ICW) and anterior palatal width (APW) against jaw length (JL). b) anterior palatal width against intercondylar width. Scaling coefficients listed in Table 3.
Fig. 4. Log-log plots of: a) Region II lever (LRII) and resultant adductor muscle force lever arm (LM) against jaw length (JL). b) Resultant adductor muscle force lever against
Region II lever. A, adult and sub-adult data; J, juvenile data.

Fig. 5. Log-log plots of Region II lever arm (LRII) against intercondylar width (ICW). A, adult and sub-adult data; J, juvenile data. Regression coefficients listed in Table 3.
Fig. 6. Length and width measurements of the Monodelphis jaw with best-line fit by the Gompertz model. a) intercondylar width (ICW), b) anterior palatal width (APW), and c) jaw length (JL).
Fig. 7. Effect of changing craniofacial configurations on the location of the Region I-II boundary: (a) palatal width; (b) intercondylar width; and (c) length of the masticatory muscle resultant lever arm. The rectangular shape represents the palate, and the paired ovals are the glenoid fossae. The Region I-II is determined by the intersection with the toothrow of the oblique line that originates at the glenoid fossa and passes through the midline muscle resultant. The juvenile (J) and adult (A) conditions are represented by the solid and dashed lines, respectively.
Fig. 1. The constrained lever model of the masticatory apparatus illustrated on the ventral skull of Monodelphis domestica. (A) The triangle of support is defined by the working- and balancing-side temporomandibular joints (TMJ) and the bite point. The Region I-II boundary is located where the trajectory from the balancing-side TMJ intersects the working-side jaw after passing through the midline muscle resultant. That part of the dental array anterior to the Region I-II boundary is located in Region I where maximum bite force are expected to follow simple lever mechanics. (B) The triangle shrinks necessarily as bites are produced with teeth located posterior to the Region I-II boundary (molars and, in juveniles, the deciduous premolar). The muscle resultant vector must shift laterally toward the working side tooththrow in order to remain within the triangle of support; this shift accomplished via a reduction in the contractile force of the balancing-side musculature.
Fig. 2. Data capture (A) Maximum bite forces were measured from three locations along the jaw: incisors/canines (I/C) or premolars (P) within Region I and teeth located in Region II (RII, molars and deciduous premolar). (B) Lever arm measurements used to calculate mechanical advantage: lever arm to the resultant muscle force vector (LM) and lever arm to Region I-II boundary or the anteriormost aspect of Region II (LRII).
Fig. 3. Box plots of bite forces collected from Monodelphis domestica juveniles and adults at three locations along the dental arcade: Region II (RII), premolar (P), and incisors or canines (I/C). (A) Raw forces (in Newtons); (B) Weight adjusted force (in body weight units, BWU). For the raw force data, there was significant variation between tooth positions within an age group (P < 0.001), and between age groups within a single dentary region (P < 0.02).
Appendix I: Effect of craniofacial widths on mechanical advantage

The accompanying figure diagrammatically summarizes how differences in palatal width affects mechanical advantage. The rectangular shape represents the palate in *M. domestica*, with juveniles (solid line) having relatively wider palates than adults (dashed line). The lever arm to the muscle resultant is assumed constant but cranial widths and trajectories to the RI-II boundary differ between the age groups (shown in solid lines and arrow in juveniles, dashed in adults).
The lever arms to the muscle resultant (LM) and the Region I-II boundary (LRII) are computed as:

\[ LM = \left( \frac{1}{2} ICW \right) \tan \theta \]
\[ LRII = \left( \frac{1}{2} ICW + \frac{1}{2} APW \right) \tan \theta \]

where ICW is intercondylar width and APW is anterior palatal width. Mechanical advantage (MA) of the masticatory muscle resultant when biting at the Region I-II boundary can be computed as:

\[ MA = \frac{LM}{LRII} = \frac{\frac{1}{2} ICW}{\left( \frac{1}{2} ICW + \frac{1}{2} APW \right)} \]
\[ MA = \frac{ICW}{ICW + APW} = \frac{1}{1 + \left( \frac{APW}{ICW} \right)} \]

It then follows that mechanical advantage should increase as palatal width becomes relatively narrower compared with intercondylar width.
Appendix II: Effect of muscle resultant lever arm length on Region II length

The accompanying figure diagrammatically summarizes how differences in the lever arm of the masticatory muscle resultant force. The rectangular shape represents the palate in *M. domestica*, with the caudalmost molar in adults (dashed line) being more anterior relative to juveniles (solid line) so that adults have relatively longer muscle lever arms. In this simplification, palatal width is assumed constant but trajectories to the RI-II boundary as well as lever arms to the muscle resultant and Region I-II boundary differ between the age groups (shown in solid lines and arrow in juveniles, dashed in adults).
The consequences of elongating the muscle resultant lever arm on the length of Region II (RIIL, j = juveniles, a = adults) is complicated because a more anterior muscle resultant has the effect of simultaneously shifting anteriorly both the Region I/II boundary and the caudal end of Region II.

In juveniles, the inclination of the trajectory to the Region I-II boundary is:

$$\tan \theta = \frac{RIIL_j}{\frac{1}{2} APW}$$

whereas the trajectory in adults is defined by:

$$\tan (\theta + k) = \frac{RIIL_a}{\frac{1}{2} APW}$$

Therefore Region II of juveniles will be smaller than that of adults if:

$$RIIL_j = \frac{\tan \theta}{\frac{1}{2} APW} < \frac{\tan (\theta + k)}{\frac{1}{2} APW}$$

$$\tan \theta < \tan (\theta + k)$$

This last expression is always true, thereby showing that an elongation of the muscle resultant lever arm simultaneously lengths Region II.