Are We Looking for Loads in All the Right Places? New Research Directions for Studying the Masticatory Apparatus of New World Monkeys

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ABSTRACT

New World monkeys display a wide range of masticatory apparatus morphologies related to their diverse diets and feeding strategies. While primatologists have completed many studies of the platyrrhine masticatory apparatus, particularly morphometric analyses, we collectively acknowledge key shortcomings in our understanding of the function and evolution of the platyrrhine feeding apparatus. Our goal in this contribution is to review several recent, and in most cases ongoing, efforts to address some of the deficits in our knowledge of how the platyrrhine skull is loaded during feeding. We specifically consider three broad research areas: (1) *in vivo* physiological studies documenting mandibular bone strains during feeding, (2) metric analyses assessing musculoskeletal functional morphology and performance, as well as (3) the initiation of a physiological ecology of feeding that measures *in vivo* masticatory mechanics in a natural environment. We draw several conclusions from these brief reviews. First, we need better documentation of *in vivo* strain patterns in the platyrrhine skull during feeding given their empirical role in developing adaptive hypotheses explaining masticatory apparatus form. Second, the greater accuracy of new technologies, such as CT scanning, will allow us to better describe the functional consequences of jaw

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form. Third, performance studies are generally lacking for platyrrhine jaws, muscles, and teeth and offer exciting avenues for linking form to feeding behavior and diet. Finally, attempts to bridge distinct research agendas, such as collecting *in vivo* physiological data during feeding in natural environments, present some of the greatest opportunities for novel insights into platyrrhine feeding biology. Anat Rec, 294:2140–2157, 2011. © 2011 Wiley Periodicals, Inc.

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Diet and feeding behaviors are widely recognized as key components of primate natural history and evolution (e.g., Richard, 1985; Conroy, 1990; Martin, 1990; Fleagle, 1998; Campbell et al., 2007). Not surprisingly then, primatologists have put forth significant effort in trying to understand how the morphology and function of the primate feeding apparatus relate to diet and feeding behaviors. We have learned a great deal about masticatory functional morphology in primates from research on the physiology of feeding, comparative morphometrics of skulls, jaw muscles, and teeth as well as studies of feeding ecology. As often occurs in research, some clades come to be better studied because early work sets the stage for future advancement—a form of “research inertia.” Among primates, the *in vivo* data describing the mechanics of mastication in Old World monkeys have made this group the model for studying the functional morphology of the masticatory apparatus. Moreover, the phylogenetic proximity of Old World monkeys to humans and the benefits this relationship confers for studying fossil hominins (e.g., Hylander, 1988; Daegling and Grine, 1991) likely adds to the differential focus on this group. By comparison, we know less about the functional morphology of the platyrrhine masticatory apparatus, although recent efforts point to a renewed interest in this group. Our goal in this contribution is to consider several of our recent and ongoing efforts in physiological, morphometric, and ecological research of New World monkeys that may help to better understand how loads are generated and dissipated in the platyrrhine skull during feeding. We hope that some of these ideas will initiate further advances in the understanding of the platyrrhine masticatory apparatus.

IN VIVO RESEARCH ON PLATYRRHINE FEEDING MECHANICS

The majority of *in vivo* data describing how the primate skull is loaded during feeding is based on research involving Old World monkeys (e.g., Hylander, 1979a,b,c, 1984, 1985; Hylander et al., 1987, 1991; Hylander and Johnson, 1992). These studies of catarrhine monkeys provide most of the empirical basis for identifying which parts of the skull we think experience significant loads during feeding and what types of loads occur in these regions. We routinely translate these *in vivo* data into morphological predictions as a physiological criterion for interpreting variation in skull form across anthropoids (e.g., Hylander 1979b, 1985, 1988; Bouvier, 1986a; Ravosa, 1991a; Daegling, 1992; Anapol and Lee, 1994; Ravosa et al., 2000a; Taylor, 2002; Vinyard et al., 2003). This extrapolation is essential given the impossibility of

collecting *in vivo* data for every primate species. We know, however, that our functional interpretations based on these predictions can be flawed as new *in vivo* data can reveal novel loading regimes or muscle activity patterns invalidating previous extrapolations (e.g., Hylander and Bays, 1979; Hylander and Johnson, 1997; Larson and Stern, 2007; Williams et al., 2009).

Compared to Old World monkeys, we know much less about how the skull is loaded during feeding in platyrrhines. Most of the platyrrhine *in vivo* strain data are from the circumorbital region of owl monkeys (*Aotus* sp.) and address functional questions related to the evolution of the anthropoid postorbital septum (Ross and Hylander, 1996; Ross, 2001). These data suggest a complicated loading pattern including bending and twisting regimes, relatively low magnitude strains compared to the mandible and a general similarity to loading patterns in Old World monkeys and strepsirrhines (Ross and Hylander, 1996; Ravosa et al., 2000b; Ross, 2001, 2008). Published data on mandibular corpus strains indicate that owl monkeys are more similar to macaques in their working- to balancing-side strain ratios during mastication than either is to galagos suggesting that symphyseal fusion in anthropoids facilitates increased balancing-side muscle force recruitment (Hylander et al., 1998). Additionally, owl monkeys conform to a primate-wide, and potentially tetrapod-wide, pattern where strain magnitudes across cranial bones decrease in relation to their distance from the masticatory apparatus (Ross and Metzger, 2004).

While these data suggest some basic similarities in craniofacial loading between New and Old World monkeys, we simply do not know very much about the specific loads that platyrrhine jaws experience during feeding. For example, Ross et al. (2010) provide the only data describing loading regimes in the mandibular corpus. Their results indicate that the capuchin corpus is bent, twisted, and sheared during premolar biting of hard objects. Beyond this initial report, we lack detailed data on loading of the platyrrhine mandibular symphysis or other regions of the face.

If New World monkeys load their jaws similarly to their Old World counterparts, then the lack of *in vivo* data for platyrrhines may have limited consequence as we can reasonably assume correspondence between the anthropoid infraorders. Strain patterns, however, are at least partly influenced by jaw geometry. Unfortunately, sufficient differences exist in the details of skull morphology and jaw-muscle activity patterns between the infraorders to suggest a potential divergence in feeding mechanics. These differences may challenge using macaques as an *in vivo* model for understanding the functional significance of platyrrhine jaw form.

Bouvier (1986b) demonstrated that New World monkeys possess relatively long mandibles, with deep and mediolaterally thin corpora, and relatively narrow condyles compared to Old World monkeys. Bouvier interpreted these differences to indicate reduced corporal twisting and reduced condylar loading. More reasonably, these differences only point to a reduced ability to resist these potential loads as assessment of jaw morphology cannot demonstrate loading regimes. Eaglen (1984) found that platyrrhines possess relatively smaller incisors than catarrhines and attributed some of these differences to size-related variation in diet. Comparisons of jaw-muscle recruitment patterns during chewing indicate that New World monkeys differ from other primates in the timing of masseter recruitment during the power stroke (Hylander et al., 2000; Vinyard et al., 2007). The divergent recruitment pattern may correlate with both the previously described morphological variation and suggests possible differences in jaw loading regimes. Similarly, Vinyard and Taylor (2010) compared electromyography (EMG) activity levels to jaw-muscle architecture and singled out platyrrhines as potentially different from other primates in their relationship between architecture and muscle activation. Outside of the masticatory apparatus, comparative studies have identified differences in platyrrhine and catarrhine skulls suggesting the possibility of distinct evolutionary pressures in these clades since their split from a common ancestor (Delson and Rosenberger, 1984; Rosenberger, 1986; Ravosa 1991b; Ross and Ravosa, 1993; Armfield and Vinyard, 2010). Collectively, these comparative data suggest that further investigation of *in vivo* strain patterns in platyrrhines would be useful for understanding the functional morphology of their masticatory apparatus.

We present a preliminary look at strain patterns in the mandibular corpus and symphysis of a tufted capuchin (*C. apella*) to stimulate discussions of *in vivo* loading patterns between the anthropoid infraorders during mastication. Rosette strain gages were bonded to the inferior border of the right mandibular corpus below the P_4 and the infero-labial aspect of the symphysis at the midline in an adult female (Fig. 1). Strain patterns in the mandibular corpus during almond chewing differ between working and balancing sides (Fig. 2). On the working (i.e., right) side, shear strains are fairly low ($\bar{x} = 230 \mu\epsilon$, $SD = \pm 89 \mu\epsilon$), which is not surprising given the lack of significant mechanical challenges posed by almonds (Williams et al., 2005). The orientation of principal tensile strain (ϵ_1) on the working-side corpus (Fig. 1) along with a ratio of ϵ_1 to principal compressive (ϵ_2) strains near 1.0 ($\bar{x} = 0.9$) suggests a predominance of corporal twisting with one or more additional loading regimes superposed on it. Balancing-side shear strains ($\bar{x} = 241 \mu\epsilon$, $\pm 89 \mu\epsilon$) are similar to working-side levels suggesting that capuchins follow the anthropoid pattern of maintaining relatively low ratios of working- to balancing-side shear strains in their mandibular corpora (Hylander, 1979a; Hylander et al., 1998). The orientation of principal tensile strain on the balancing-side corpus is more readily interpreted as a combination of parasagittal bending and twisting during the power stroke of mastication (Fig. 1). Although twisting may be more significant in the capuchin corpus, these preliminary data suggest a general similarity with loading regimes in the macaque mandibular corpus (Hylander, 1979a).

Fig. 1. Drawings of a *Cebus apella* mandible in (a) lateral and (b) frontal views demonstrating rosette strain gage locations on the corpus and symphysis, respectively. For the corpus gage, the solid arrow demonstrates the average orientation of principal tensile strain (ϵ_1) during chewing almonds on the working-side (WS), while the dashed arrow indicates the average orientation of principle tension when the corpus is acting as the balancing side (BS) ($N = 23$ cycles). For the midline symphysis gage, the orientation of principle tension is relatively similar during left- and right-sided chews and is averaged. Principle compressive strains (ϵ_2) are oriented at 90 degree to principle tensile strains (not shown). For both gages, the black line demonstrates the axis for determining the angle of principle strain directions. Strain gage implantation, recording, and analysis were completed following previously described protocols (e.g., Hylander, 1979a, 1984).

Symphyseal shear strains along the infero-labial aspect of the symphysis averaged $300 \mu\epsilon$ ($\pm 112 \mu\epsilon$) during almond chewing (Fig. 2). The orientation of principle tensile strains varied slightly between left- ($88 \text{ degree} \pm 3 \text{ degree}$) and right-sided ($102 \text{ degree} \pm 16 \text{ degree}$) chews ($N = 23$). The average of $94 \text{ degree} (\pm 13 \text{ degree})$ is directed nearly perpendicular to the symphyseal midline (Fig. 1). This orientation of ϵ_1 suggests either frontal bending of the symphysis associated with twisting of the mandibular corpora about their long axes or medial transverse bending of the symphysis. While a hypothesis of frontal bending (where the inferior symphysis is tensed and the alveolar border compressed) fits better with the observed strains from the corpus gage, the ratio of ϵ_1/ϵ_2 is not consistently above 1.0 as predicted for this loading regime (ϵ_1/ϵ_2 range, $=0.51\text{--}1.6$; $\bar{x} = 0.95$), suggesting the potential for additional superposed loading

Fig. 2. Plots of corpus and symphysis strains in a *C. apella* female chewing almonds during a sequence of (a) three right-sided and (b) three left-sided cycles. For both gages, shear (γ) strains are depicted as black lines, while tensile (ϵ_1) (positive) and compressive (ϵ_2) (negative) strains are shown in gray. The lower panel illustrates root mean

square (RMS) jaw-muscle electromyography recordings for the right anterior temporalis (RAT) (solid black), left anterior temporalis (LAT) (solid gray), and left superficial masseter (LSM) (dotted gray). (The right superficial masseter electrode failed in the experiment).

patterns at the symphysis. In a second capuchin with a similarly placed rosette gage on the symphysis, shear strains associated with cracking cherry pits were slightly higher (373 $\mu\epsilon$) and the orientation of ϵ_1 was comparable (110 degree) relative to the symphyseal midline. The ratio of ϵ_1/ϵ_2 at 1.4, however, is more consistent with frontal bending due to twisting of the mandibular corpora. While still very preliminary, the symphyseal loading regimes hypothesized here are sufficiently different from those observed in the macaque symphysis (Hylander, 1984) to justify additional *in vivo* research into platyrrhine symphyseal loading patterns during mastication. Moreover, Hylander (1984) points out that an inferior transverse torus (i.e., simian shelf) is an effective morphology for resisting frontal bending. Tufted capuchin symphises possess an obvious simian shelf (Herskovitz, 1977).

Jaw-muscle electromyography from platyrrhines, including capuchins, suggests a tendency for New World monkeys to contract their working- and balancing-side superficial masseters near simultaneously during the chewing cycle. This recruitment pattern differs from Old World monkeys (Hylander et al., 2000; Vinyard et al., 2007). In conjunction with temporalis activity, this derived recruitment pattern could contribute to both the twisting of the mandibular corpora as well as the frontal bending of their mandibular symphises as the difference between peak corporal and symphyseal shear strains average 12 msec in this preliminary sample (Fig. 2). We

hypothesize that this shift in jaw-muscle recruitment pattern during mastication may explain the potential difference in symphyseal loading between New and Old world monkeys.

MORPHOMETRICS OF PLATYRRHINE SKULLS, TEETH, AND JAW MUSCLES

Mandibular Morphometrics

Metric comparisons of platyrrhine skulls and teeth have drastically outpaced *in vivo* studies of chewing mechanics. The majority of morphometric comparisons focus on interpreting the functional consequences of jaw form relative to load resistance and bite force production (Bouvier, 1986b; Cole, 1992; Daegling, 1992; Kinzey, 1992; Anapol and Lee, 1994; Wright 2005; Norconk et al., 2009). Norconk et al. (2009) provide the most recent review of platyrrhine jaw metrics finding that hard-object feeding taxa such as capuchins (*Cebus*) and pitheciines (*Cacajao*, *Chiropotes*, and *Pithecia*) possess the most robust jaws and relatively improved biting leverage. Alternatively, more folivorous taxa such as howlers (*Alouatta*) and woolly spider monkeys (*Brachyteles*) exhibit jaws that are intermediate in robustness and lack mechanical advantage for biting at M_1 compared to other platyrrhines. The remaining primarily frugivorous, insectivorous, and gummivorous platyrrhines tend to possess less robust jaws compared to

these other platyrrhines (Anapol and Lee, 1994; Vinyard et al., 2003; Norconk et al., 2009).

A long-standing prediction in functional studies of jaw shapes contends that species with relatively hard and/or tough diets should have relatively robust jaws due to the magnitude and/or number of repetitive loads experienced during feeding (e.g., Hylander 1979c; Bouvier, 1986b; Ravosa, 1991a, 1996; Daegling 1992; Taylor, 2002; Vinyard et al., 2003). Following on the comparisons in Norconk et al. (2009), more folivorous platyrrhines, such as howlers, do not follow this prediction as they possess jaw shapes that would provide intermediate load resistance despite their relatively high degrees of folivory. Similar questions have been raised about the specific relationships between diet and jaw morphology in Old World monkey clades (Daegling and McGraw, 2001, 2007). While experimental manipulation of diet clearly affects both jaw mechanics (Ahlgren, 1966; Møller, 1966; Hiiemae and Kay, 1973; Hylander et al., 1987, 2000; Hylander and Johnson, 1994; Ottenhoff et al., 1996; Agrawal et al., 1998, 2000; Foster et al., 2006; Woda et al., 2006) and jaw robustness throughout the lifetime (Bouvier and Hylander, 1982; Corruccini and Beecher, 1982, 1984; Ravosa et al., 2007; Menegaz et al., 2009), we have to admit the difficulties in teasing apart the multiple competing influences that impact jaw morphology on the time scale involved in comparisons among primate species (Daegling and McGraw, 2001, 2007; Daegling, 2002; Vinyard and Ryan, 2006; Vinyard, 2008). Some of the biggest challenges we face are determining *in vivo* loading regimes and linking these loads to mechanical aspects of species diets to make more informed species-level interpretations of primate jaw morphology. For example, howlers choose less tough leaf material during feeding compared to what is available in their habitat (Teaford et al., 2006). This behavioral choice may effectively reduce mechanical loads during chewing and help account for their relatively reduced jaw robusticity compared to hard-object feeding platyrrhines.

Caliper-based measurements provide the foundation of our understanding of primate jaw shapes; however, researchers have begun using several newer technologies to expand on these traditional assessments of jaw shape. For the most part, though, these techniques have not been applied broadly to platyrrhines, leaving many available research opportunities. Significant progress has been made studying mandibular cross-sectional geometry in catarrhines (Daegling, 1989, 1993, 2001, 2002, 2007; Daegling and Grine, 1991). These analyses are important because they more accurately describe the load resisting abilities of the jaw based on the amount and distribution of bone. Still, only two cross-sectional studies of platyrrhine jaws have been conducted and both focus on specific groups of platyrrhines. Daegling (1992) demonstrated increased jaw robusticity in *Cebus apella* compared to the non-tufted *C. capucinus*, while the second study identified a lack of jaw robusticity in tree-gouging marmosets compared to non-gouging tamarins and squirrel monkeys (Vinyard and Ryan, 2006; Ryan et al., 2010).

We combine CT scans from Rossie (2006) and Vinyard and Ryan (2006) to provide a first look at variation in cortical area of the mandibular corpus across platyrrhines (Fig. 3). Ln cortical area (CA) at P₄ (least-squares

[LS] regression slope = 2.53; 95% CI = ± 0.47) scales with strong positive allometry relative to ln jaw length (Fig. 4a). Cortical area at M₂ exhibits a similar scaling pattern (LS slope = 2.60 ± 0.41) (data not shown). The scaling of these cross-sectional estimates suggest stronger positive allometry of CA compared to a caliper-based estimate of cortical area (i.e., as an ellipse using external corpus depth and width) (LS slope = 2.29 ± 0.25 , N = 18). The cross-sectional estimate suggests that cortical areas may be increasing more rapidly with size across New World monkeys than might be expected based on external appearance. Examination of cortical area shape (CA^{0.5}/jaw length) supports previous arguments based on external measurements that hard-object feeding capuchins and pitheciines tend to have relatively robust jaws (Fig. 4b; see also Fig. 3). Despite their larger size, the more folivorous *Alouatta* is intermediate in CA, while several smaller frugivorous, insectivorous, and gummivorous species maintain relatively reduced cortical areas (Fig. 4b). Interestingly, *Callicebus* exhibits a relatively large cortical area at P₄ (and M₂; data not shown) (Fig. 4b). This result is consistent with previous observations of relatively large molars in *Callicebus* (Pirie, 1978) as well as their consumption of a large percentage of leaves and seeds, with seeds being important during the cooler, lean season (Kinzey, 1974; Heiduck, 1997). Future research exploring the cross-sectional morphology of platyrrhine jaws will be important in demonstrating the functional consequences of variation in internal jaw form throughout the clade.

In addition to cross-sectional analyses, assessment of bone material properties in the jaws of catarrhines has been important in describing how bone microstructural variation impacts load resistance abilities in the mandible during feeding. Microstructural analyses of catarrhines have focused on (1) documenting variation in material properties throughout the skull during ontogeny and between species (Dechow et al., 1993, 2010; Peterson and Dechow, 2003; Rapoff et al., 2008; Wang et al., 2010), (2) describing how variation in stiffness and directionality of elastic properties relate to differences in load resistance abilities (Dechow et al., 1993, 2010; Daegling et al., 2008, 2009, 2011a,b; Daegling and McGraw, 2009; Wang et al., 2010), (3) interpreting *in vivo* strains as patterns of bone stress during mastication (Dechow and Hylander, 2000), and (4) improving finite-element modeling of jaw biomechanics (Wang and Dechow, 2006). As pointed out in several of these studies, an improved comparative dataset is needed to fully explore the functional consequences of microstructural variation in bone properties. This point is particularly relevant to platyrrhines where this level of variation in bone properties remains essentially untouched in studies of craniofacial functional morphology.

Examining how the symphysis performs in resisting *in vitro* loads represents another area of research that will improve our understanding of platyrrhine jaw functional morphology. Recently, Hogg et al. (2011) loaded platyrrhine symphyses to failure in simulated lateral transverse bending (i.e., wishboning) and dorso-ventral shear to compare symphyseal strength in tree-gouging marmosets to other non-gouging platyrrhines. They found that marmosets exhibit a relatively reduced ability to withstand external forces in their symphyses (Hogg et al., 2011). This result links symphyseal performance

Fig. 3. μ CT reconstructions of platyrrhine jaws demonstrating variation in cortical morphology of the mandibular corpus at P_4 for two hard-object feeders (*Cacajao* and *Cebus*), a folivore (*Alouatta*) and tree-

gouger (*Callithrix*). All specimens are scaled to approximately similar corporal heights. The white scale bar below each jaw indicates 1.0 cm. Reconstructions generated in Avizo 3D visualization software (6.2; VSG).

to morphological comparisons between these groups (Vinyard et al., 2003; Vinyard and Ryan, 2006), suggesting that marmoset jaws do not offer improved load resistance abilities against habitual loads generated during mastication.

To further consider the potential of *in vitro* performance studies for evaluating the functional consequences of symphyseal form in platyrrhines, we assessed whether symphyseal shape helps dictate the location of failure during simulated lateral transverse bending (Fig. 5). These preliminary data suggest that more “v-shaped” symphyses (i.e., long and narrow) are more likely to fail at the midline during lateral transverse bending com-

pared to “u-shaped” morphologies (Fig. 6). Based on this result, we hypothesize that symphyseal shape will affect where failure occurs during loading. This hypothesis builds on the argument that long and narrow jaws concentrate symphyseal stresses in lateral transverse bending (Hylander, 1984, 1985; Hylander and Johnson, 1994; Vinyard and Ravosa, 1998; Daegling, 2001). Moreover, the significant percentage of platyrrhine symphyses that failed off-midline suggest that fusion of the symphysis provides sufficient midline robusticity that other areas of the symphyses, such as segments associated with the large canines, become relatively weak (see Williams et al., 2008a).

Fig. 4. Plots of (a) cortical area (CA) and (b) cortical area shape ($CA^{0.5}$ /jaw length) at P₄ versus jaw length across 10 platyrrhine species. The regression slope estimate of $2.53 (\pm 0.47)$ suggests that $\ln$ cortical area scales with positive allometry (where isometry = 2.0) relative to $\ln$ jaw length. Similarly, the trend for cortical area shape to increase with jaw length ($r = 0.59$, $P = 0.07$) (b) tracks this size-correlated change in shape. Data for *C. jacchus*, *S. fuscicollis* and *S. sciureus* are taken from Vinyard and Ryan (2006), while data for all remaining species are taken from scans described by Rossie (2006).

These cortical areas were estimated using MacroMomentJ v1.3 (Warfel, 1997) in ImageJ. (Abbreviations: LS Slope = Least-squares regression slope; R = Product-moment correlation coefficient; *C. calvus* = *Cacajao calvus*; *C. apella* = *Cebus apella*; *A. seniculus* = *Alouatta seniculus*; *L. lagotricha* = *Lagothrix lagotricha*; *C. moloch* = *Callicebus moloch*; *L. rosalia* = *Leontopithecus rosalia*; *C. goeldii* = *Callimico goeldii*; *S. fuscicollis* = *Saguinus fuscicollis*; *S. sciureus* = *Saimiri sciureus*; *C. jacchus* = *Callithrix jacchus*).

Dental Metrics

Similar to the bones of the masticatory apparatus, there have been numerous metric analyses of platyrrhine teeth. Much of this work has addressed how tooth size and shape (Zingesser, 1973; Kinzey, 1974, 1992; Kay, 1975; Rosenberger and Kinzey, 1976; Hershkovitz, 1977; Rosenberger, 1978, 1992; Eaglen, 1984; Teaford, 1985; Greenfield, 1992; Spencer, 2003; Wright, 2005; Norconk et al., 2009) as well as dental microstructure (Gantt, 1980; Nogami and Yoneda, 1983; Nogami and Natori, 1986; Maas and Dumont, 1999; Martin et al. 2003; Hogg, 2010; Ravosa et al., 2010; Hogg et al., 2011) relate to resisting loads during feeding on different diets. Because tooth wear and breakage can significantly affect food intake, exploring the relationships between dental form and function provides important insights into platyrrhine feeding biology. Very broadly speaking, these studies show that platyrrhines subscribe to trends identified throughout primates where occlusal relief is linked to folivory and insectivory while dental robusticity is related to hard-object feeding.

Lucas et al. have recently applied engineering theory involving fracture mechanics to generate several predictions relating enamel structure to mammalian diets (Lucas et al., 2008a,b; Chai et al., 2009; Lawn et al., 2009). These efforts follow previous work exploring how dietary material properties relate to occlusal shape in the primate dentition (Lucas, 2004). This primarily theoretical work is significant because it marries enamel morphology throughout the tooth to fracture mechanics,

providing explicit predictions linking regional enamel form to dietary processing via tissue engineering principles. Fortunately, some of the basic morphological data on enamel morphology are available to test these predictions in platyrrhines (Nogami and Yoneda, 1983; Nogami and Natori, 1986; Hogg, 2010; Hogg et al., 2011). Moreover, the dietary diversity across platyrrhines makes them a compelling group for assessing whether enamel structure follows predicted patterns in this clade.

Compared to studies of dental load-resisting ability, we know much less about how the teeth act to reduce masticatory stresses (i.e., act efficiently) in platyrrhines. The effective distribution of dental material for fracturing food items can impact loads experienced in the jaws by reducing both muscular and reaction forces. Outside of platyrrhines, studies of tooth crest sharpness have been important in understanding the functional principles guiding variation in tooth form in mammals (e.g., Rensberger, 1973; Strait, 1993; Popowics and Fortelius, 1997; Evans et al., 2005; Lucas, 2004; Ang et al., 2006).

Marmoset incisors represent one case among platyrrhines where efficiency has been identified as a factor in the evolution of dental form as it relates to their derived tree-gouging behavior (Fig. 7). The thickened labial and reduced lingual enamel of marmoset incisors is hypothesized to offer a mechanism for maintaining sharpness through differential wear of dentine and enamel (Rosenberger, 1978, 1992). We briefly consider this example to highlight the potential impact of dental efficiency on helping to understand masticatory loads during feeding.

Fig. 5. Plot of the percentage of midline failures during *in vitro* lateral transverse bending versus relative symphyseal shape among platyrrhines (see Hogg et al., 2011 for loading details). Symphyseal shape is measured as the mediolateral width of the symphysis near its lingual border divided by symphysis length (primarily an AP distance). The negative Spearman's rank correlation (ρ) suggests that more "v-shaped" symphyses (i.e., smaller ratios) tend to break along the midline. This result may indicate a tendency for symphyseal shape in platyrrhines to dictate patterns of failure during *in vitro* loading. The single *C. apella* individual failed superiorly at the midline, but the crack propagated inferiorly to below the canine. This was scored as 0.5, but should be considered preliminary pending additional data for this species. (Abbreviations: *A. trivirgatus* = *Aotus trivirgatus*; *S. oedipus* = *Saguinus oedipus*; *S. sciureus* = *Saimiri sciureus*; *C. apella* = *Cebus apella*; *C. jacchus* = *Callithrix jacchus*).

The marmoset incisor is best modeled as a sharp wedge when gouging to remove pieces of bark (to stimulate exudate flow for later consumption) (Fig. 7). Separating a piece of bark is a complicated process involving initial indentation, fracture, and propagation of the initial crack (Lucas, 2004; Atkins, 2009). Hypotheses about incisor tip sharpness immediately apply to the indentation of the bark. The impact of sharpness on indentation will depend on the material properties of the substrate (i.e., bark), but the basic concept is that all else being equal a sharper incisor tip will act to reduce the relative force needed to indent (up to a threshold) (Meehan and Burns, 2007; Atkins, 2009). While the sharpness of a cutting tip is measured in several ways (Atkins, 2009), we compare the tip radius of curvature between five common marmosets and five saddle-back tamarins (see Hogg et al., 2011 for sample details). The radius of curvature in marmosets (0.119 mm) is significantly smaller than in tamarins (0.172 mm) (ANOVA, $F = 10.5$, $P = 0.012$) (Fig. 8), while both have sharpness values comparable to similar-sized mammals (Popowics and Fortelius, 1997; Evans, 2005). The significant difference between these two species supports the hypothesis that enamel modifications in marmosets help maintain tip sharpness. By focusing the bite force over relatively smaller cusp tips (i.e., elevating stresses on the bark), loads may be

reduced throughout the jaw during this initial phase of the gouge.

Atkins (2009) argues that there is little benefit of dental cusps becoming sharper than the critical distance for crack opening displacement (δ) of a dietary substrate. We can estimate the average δ for barks gouged by common marmosets by dividing average toughness (R) (1.92 kJ/m²) by yield strength (σ_y) (6.9 MPa) (where σ_y is estimated as $3 \times$ the average hardness of 2.3 MPa; Kendall, 2001) using mechanical property data from gouged barks (Vinyard et al., 2009; unpubl. data). The average δ of 0.278 mm for these barks approximates the sharpness of callitrichine teeth (i.e., $2 \times$ radius of curvature) suggesting that marmosets may have reached a beneficial sharpness threshold for gouging. Alternatively if a bark tends to collapse on itself during indentation (i.e., it exhibits a Poisson's ratio approaching 0 due to the underlying organization of cells), then the estimate of yield strength as $3 \times$ hardness is too large. Subsequently, δ would increase (up to 0.83 mm for a bark that collapses completely; Lucas, 2004) and may indicate that the increased tip width of marmoset incisors compared to tamarins (Hogg et al., 2011) helps to create the critical distance for propagating a crack through barks during gouging.

At some depth during the indentation, a flaw in the bark will develop into a crack as the incisors wedge deeper into the bark. The largest bite forces during a gouge are likely associated with this phase of the gouge as sufficient strain energy is required to develop a free running crack ahead of the teeth (Vincent et al., 1991; Atkins, 2009). In general, a relatively wider incisal tip will tend to elevate bite forces in elastic materials. The benefit of the wider tip is that it decreases the depth at which a crack propagates by widening the distance between sides of the bark, increasing stored strain energy and attaining the critical distance for crack propagation (δ) more quickly. Ang et al. (2006) recently modeled the strain energy release rate (G) for an incisor penetrating a substrate as:

$$G = \frac{F}{b} \left[1 - \frac{\mu}{\cos(\frac{\alpha}{2}) [\sin(\frac{\alpha}{2}) + \mu \cos(\frac{\alpha}{2})]} \right]$$

where F = bite force (i.e., normal force), b = incisor contact width, μ = the friction coefficient, and α = the included angle of the incisor (see also Williams, 1998). We can apply average values from *in vivo* recordings of bite forces during gouging and estimates of friction between marmoset teeth and barks to estimate how G changes as a function of the incisor included angle between marmosets and tamarins. We estimated included angles at 1 mm from the incisor tip (marmoset $\bar{\alpha} = 74$ degree, tamarin $\bar{\alpha} = 57$ degree) and for the entire crown (marmoset $\bar{\alpha} = 32$ degree, tamarin $\bar{\alpha} = 28$ degree) using data by Hogg et al. (2011). Figure 9 shows that across the range of observed friction coefficients for gouged trees ($\mu = 0.2$ – 0.65 ; Vinyard, unpubl. data), marmosets have slightly higher strain energy release rates (G) for the incisal tip at low friction, but this pattern reverses at higher friction coefficients. Marmosets maintain slightly higher G estimates relative to the included angle for the crown (Fig. 9). In both cases, the included angle has limited impact on variation in G estimates, particularly when compared to the effect of

Fig. 6. The relationship between symphyseal shape and breakage patterns in platyrrhines. Superior-view photographs of (a) a v-shaped symphysis (*Callithrix*) and (b) a u-shaped symphysis (*Aotus*). The yellow arrows demonstrate symphyseal arch width (*W*) and symphysis length (*L*) shown in Fig. 5. μ CT cross-sections of (c) a *Callithrix* sym-

physis that broke in the midline during loading in wishboning and (d) an *Aotus* symphysis that broke along the medial edge of the canine root (white arrows). Resolution of μ CT slices = 20.5 μ m. Photographs of jaws (a,b) are reproduced under Creative Commons License: Copyright to Phil Myers, Museum of Zoology, University of Michigan.

friction. This result suggests that any improvements in energy release rate based on marmoset incisor angulation are relatively small and may not markedly impact loads during a single gouge.¹ A cumulative effect of slightly

elevated strain energy release rates (*G*), however, remains possible.

Based on these results, we hypothesize that the sharpness of the incisors, the width of the incisal tip, and the included angle of the incisor crown may increase efficiency and reduce the loads experienced by the marmoset facial skeleton during gouging. While sharpness may reduce indenting forces, the wider tip may actually increase forces during the initiation of a stable crack. The ability to quickly generate and propagate a stable crack (by reaching δ sooner) may reduce the net forces required in separating a piece of bark (see Vincent et al.,

¹These results model the wedging of an elastic substrate. The introduction of plastic deformation in the substrate, which may characterize some barks (e.g., Gibson and Ashby, 1997; Xu et al., 1997), can significantly affect these estimates (Williams, et al., 1998; Ang et al., 2006; Atkins, 2009). Further work is warranted in modeling the effect of incisal wedge angle during the splitting of substrates that include a plastic deformation phase.

1991). To benefit from this design, marmosets should attempt to propagate cracks through large excursions during gouging. Both behavioral and morphological data

support this hypothesis by demonstrating that marmosets use large jaw gapes during gouging and have a masticatory apparatus that facilitates these large excursions during this behavior (Vinyard et al., 2003, 2009; Taylor et al., 2009).

Fig. 7. Photograph of a captive common marmoset (*Callithrix jacchus*) gouging a simulated tree substrate (i.e., section of sweetgum tree affixed to force platform) in a laboratory setting. A gouge proceeds by the animal anchoring the upper dentition in the tree substrate and moving the lower anterior teeth through the substrate to remove a segment as shown in the figure.

Jaw-Muscle Fiber Architecture

Muscle fiber architecture considers the arrangement of muscle fibers relative to the force-generating axis of the muscle (Gans and Bock, 1965). Holding other factors constant, muscles with long, parallel fibers tend to exhibit increased excursion while muscles with shorter, more pinnate fibers can pack more fibers together, increasing the physiologic cross-sectional area (PCSA) and force-producing capacity. Recent comparative investigations of jaw-muscle fiber architecture in platyrrhines have yielded important insights into how jaw-muscle architecture relates to masticatory apparatus form and load resistance during feeding in this clade (Taylor et al., 2009; Taylor and Vinyard, 2009).

In vivo analyses suggest that marmosets use relatively large jaw gapes, but not relatively large bite forces, during tree gouging (Vinyard et al., 2009). Metric comparisons match these *in vivo* data by showing that marmosets do not have relatively robust jaws for resisting significant bite forces compared to non-gouging platyrrhines (Vinyard et al., 2003; Vinyard and Ryan, 2006; Ryan et al., 2010). Taylor et al. analyzed the fiber architecture of the jaw-closing muscles in tree-gouging pygmy (*Cebuella pygmaea*) and common (*Callithrix jacchus*)

Fig. 8. Comparison of tip radius of curvature between common marmosets (*Callithrix jacchus*, $N = 5$) and saddle-back tamarins (*Saguinus fuscicollis*, $N = 5$). Curvature was measured as the radius of a circle fit to the cusp tip of the lower, central incisor of each individual. Central incisor segments were obtained from high-resolution μ CT

scans of jaws (see Ryan et al., 2010; Hogg et al., 2011 for details of μ CT scanning). Marmosets maintain a significantly sharper cusp tip, based on an ANOVA comparing the cusp radius of curvature ($F = 10.5$, $P = 0.012$).

Fig. 9. Plot of estimated strain energy release rate (G) in common marmosets (*C. jacchus*, closed symbols) and saddle-back tamarins (*S. fuscicollis*, open symbols) across a range of friction coefficients (μ) for barks gouged by marmosets ($\mu = 0.2$ – 0.65 ; Vinyard, unpubl. data). Estimates of G are based on Eq. (2) in Ang et al. (2006). Bite force = 10 N (Vinyard, unpubl. data) and incisor contact width (b) = 4 mm. Coefficients of friction were calculated by dragging marmoset teeth across gouged bark samples using a Lucas-Darvell HKU tester (see Lucas, 2004). Included angles were measured at 1 mm from the incisor tip (marmoset $\bar{x} = 74$ degree, tamarin $\bar{x} = 57$ degree) and for the entire crown (marmoset $\bar{x} = 32$ degree, tamarin $\bar{x} = 28$ degree) using data from Hogg et al. (2011).

marmosets and observed that tree gougers have relatively longer masseter and temporalis fibers compared to non-gouging tamarins (Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009). Because of the architectural tradeoff between fiber length and PCSA, tree gougers have relatively smaller PCSAs as the increase in jaw-muscle excursion comes at some expense to maximal force production. Thus, jaw-muscle architecture in tree-gouging marmosets fits the prediction of relatively long fibers to facilitate relatively wide jaw gapes. Moreover, marmoset jaw-muscles are not geared for producing relatively large maximal bite forces during gouging, linking the lack of jaw robusticity to a comparatively weaker set of jaw muscles.

In contrast to marmosets, tufted capuchins (*Cebus apella*) have a masticatory apparatus that has been functionally and adaptively linked to generating and dissipating relatively large bite forces during feeding on resistant food objects (Kinzey, 1974; Kay, 1981; Cole, 1992; Daegling, 1992; Masterson, 1997; Wright, 2005). Taylor and Vinyard (2009) found that *C. apella* has a masseter and temporalis architecture that favors the production of relatively large maximum muscle forces compared to untufted capuchins that feed on less-resistant foods. Importantly, the capacity to generate relatively higher muscle force is primarily a function of increased jaw-muscle mass, with little difference in fiber lengths or pinnation angles among capuchins. These findings suggest that *C. apella* can generate relatively large muscle forces without markedly compromising gape. This result agrees with behavioral observations that *C. apella* process large food items with the cheek teeth (Izawa, 1979; Terborgh, 1983; Wright, 2004; Norconk et al., 2009). Collectively, these architectural analyses of marmoset

and capuchin jaw muscles emphasize the diverse functional strategies used by these two platyrrhine groups during feeding.

The results of these two studies demonstrate an integration of musculoskeletal form suggesting that further analyses of platyrrhine jaw-muscle architecture may help us better understand the loading history of the masticatory apparatus in this clade. As a preliminary assessment, we consider the relative force producing capacity (PCSA) of the superficial masseter and temporalis across 11 platyrrhine species (Taylor et al., 2009; Taylor and Vinyard, 2009; Taylor, unpubl. data). Figure 10a suggests that relative PCSA may vary with size ($r = 0.52$, $P = 0.1$) keeping in mind that PCSA (mm^2)/jaw length (mm) retains the effect of scale (i.e., the estimate is not dimensionless). In addition to a potential size-related trend, hard object feeding taxa, such as *C. apella* and *P. pithecia*, exhibit relatively large PCSA estimates. In contrast, the more folivorous *A. seniculus* possesses a relatively reduced jaw-muscle PCSA, suggesting that large body size rather than relatively enhanced jaw-muscle force production is key to the functional morphology of feeding in howlers. At smaller body sizes, tree gouging marmosets exhibit relatively reduced PCSA compared to non-gouging taxa (Taylor et al., 2009) (Fig. 10a).

The significant correlation ($r = 0.76$, $P = 0.01$) between relative PCSA and a robusticity index computed from 10 measures of the jaws and teeth (Norconk et al., 2009) suggests that variation in jaw-muscle architecture tracks variation in the bony masticatory apparatus across platyrrhines (Fig. 10b). Hard-object feeding platyrrhines tend to possess both relatively robust jaws and relatively large PCSA, while *A. seniculus* exhibits both relatively reduced skeletal robusticity and jaw-muscle PCSA. This preliminary association between musculoskeletal measures across platyrrhines suggests that these two morphological systems are evolving together in platyrrhines as they both play integral roles in feeding performance (Vinyard and Taylor, 2010). Future work on jaw-muscle architecture exploring the details of these relationships will be important for understanding the functional morphology of the platyrrhine masticatory apparatus.

MASTICATORY BIOMECHANICS IN AN ECOLOGICAL SETTING

Characterizing natural feeding behaviors is essential to understanding the functional morphology of feeding in any species. In platyrrhines, feeding ecology research that is directly pertinent to masticatory apparatus form has focused on describing diets (e.g., Ayres, 1986; Strier, 1991; Norconk 1996; Palacios et al., 1997; Peetz, 2001; Porter, 2001; Di Fiore, 2004; Wallace, 2005; Norconk et al., 2009) and their mechanical properties (e.g., Wright, 2005; Teaford et al., 2006; Vinyard et al., 2009). For example, Norconk et al. (2009) compared jaw morphologies across platyrrhines to both the mechanical and nutritive properties of their diets. Neither dietary variable was strongly associated with morphological variation across New World monkeys. Unfortunately, the small sample sizes, particularly for the mechanical property data, preclude any definitive statements regarding these potential relationships.

Fig. 10. Plot of combined superficial masseter and temporalis physiologic cross-sectional area (PCSA) versus (a) jaw length and (b) mandibular robusticity index in 11 platyrrhine species. PCSA was estimated following methods outlined by Taylor et al. (2009) and Taylor and Vinyard (2009). Whenever possible, PCSA estimates are based on fiber lengths normalized to a resting sarcomere length, but when normalization was not possible, only individuals fixed with incisors in tip-to-tip occlusion were included. While admittedly not ideal, we anticipate that interspecific variation across this range of species will more than outpace potential variation due to these two methods of adjust-

ing for variation in fiber length fixation. Jaw length was measured as the midline distance from the mandibular condyles to infradentale. The mandibular robusticity index is taken from Norconk et al. (2009) and averages z-scores from 10 relative measures of the masticatory apparatus related to bite force production, load resistance and dental function. (Abbreviations: *C. apella* = *Cebus apella*; *C. albifrons* = *Cebus albifrons*; *P. pithecia* = *Pithecia pithecia*; *S. sciureus* = *Saimiri sciureus*; *C. jacchus* = *Callithrix jacchus*; *S. oedipus* = *Saguinus oedipus*; *C. goeldii*; *Callimico goeldii*; *A. trivirgatus* = *Aotus trivirgatus*; *A. seniculus* = *Alouatta seniculus*; *C. pygmaea* = *Cebuella pygmaea*).

Beyond improving our assessments of natural dietary properties, ecological research provides an opportunity to assess feeding behaviors in a realistic evolutionary setting. While numerous descriptions of platyrrhine feeding exist, we lack significant details on the ecological physiology—or environmentally relevant physiology—of feeding in platyrrhines that would allow us to identify how specific physiological processes help an organism cope in a given environment (e.g., Bartholomew, 1987). By conducting *in vivo* physiology studies separate from feeding ecology research, we are forced to assume that physiological data in the lab are comparable to feeding behaviors typical of free-ranging animals (Williams et al., 2008b; Thompson et al., 2011). The lack of integration between physiology and ecology likely limits our ability to advance adaptive hypotheses linking cranio-dental morphology, function, and feeding behaviors.

As a first attempt to link *in vivo* laboratory and field-based ecological research, we are recording jaw-muscle activity during feeding in free-ranging mantled howling monkeys (*Alouatta palliata*) (Williams et al., 2008b) (Fig. 11). The telemetered EMG data from the jaw muscles (Fig. 12) allows us to measure several ecologically relevant variables, such as the percentage of a feeding bout that the muscles are active (i.e., duty factors), the percentage of feeding time spent masticating foods and the daily number of loads experienced by the bony masticatory apparatus. We can also relate muscle recruitment to other ecologically relevant variables such as ranging behaviors, dental wear rates, and food mate-

rial properties. For example, in an initial comparison of jaw-muscle EMG activity and food toughness we see little association between these variables over a two-day recording period (Fig. 13). While highly preliminary, the lack of association may indicate that food material properties are not necessarily closely related to the normal physiological parameters of mastication on a day-to-day basis. A speculative implication of this result is that many of the events that ultimately determine species-level differences in form and behavior might occur as temporally discrete episodes (potentially separated by years) linked to dietary extremes in an environment (e.g., Boag and Grant, 1981; Grant and Grant, 2002). For example, this episodic evolutionary pattern could perhaps lie at the root of evolutionary “paradoxes” involving taxa, like *Paranthropus boisei* (Grine et al., 2010; Strait et al., 2009; Ungar et al., 2008), seemingly adapted to a wide range of activities, but pursuing some of them infrequently at best (Robinson and Wilson, 1998; Marshall and Wrangham, 2007). If true, then long-term feeding studies in primates will be more likely to capture these evolutionarily significant events.

From a physiological perspective, these data support the hypothesis that howlers will behaviorally modulate diets by choosing foods and bolus sizes that facilitate rhythmic mastication within a specific physiological range (see Reed and Ross, 2010). We can speculate that in howlers this physiological range emphasizes efficient processing related to their large number of daily chewing cycles. We can further hypothesize that an emphasis

Fig. 11. Photographs of free-ranging mantled howling monkeys (*Alouatta palliata*) wearing an EMG telemetry unit (and associated jacket) in their natural habitat at La Pacifica, Costa Rica. Individual photos demonstrate animals continuing their normal daily activities including (a) sitting postures, (b) resting, (c) foraging and locomotion, and (d) feeding behaviors while wearing the telemetry unit.

on efficient processing may differ from hard-object feeding platyrrhines that may need to prioritize masticatory strength (i.e., bite force and load-resistance ability) as they periodically generate large bite forces, relative to their maximum capabilities, during feeding. The implication of these differing physiological strategies for musculoskeletal form may go beyond the readily observed differences in morphology and predicted functional capacity. Musculoskeletal morphologies may be adapted to fundamentally different physiological parameters

between these dietary groups of New World monkeys. This potential difference in physiological strategies for effectively breaking down their respective diets may also help explain why the howler masticatory apparatus does not appear particularly robust among platyrrhines (Norconk et al., 2009). Furthermore, if this initial result is supported by additional eco-physiological data, then morphologists studying masticatory form may need to look beyond assessing maximal abilities (i.e., most assessments of musculoskeletal form) and separately

Fig. 12. Plot of electromyographic (EMG) activity from the right-side deep masseter of a female mantled howler (*Alouatta palliata*) during a single feeding bout in La Pacifica, Costa Rica. The feeding bout consisted of consuming *Lysiloma* sp. leaves and lasted approximately

56 min. This individual's jaw muscles were active about 60% of the feeding bout. This percentage appears to vary markedly, however, across animals, foods and days. EMG implantation and recording procedures are outlined in Williams et al. (2008b).

consider the effects of hard-object versus tough-object feeding (e.g., peak loads vs. repetitive loads) on bone and muscle. For example, recent approaches describing how dietary plasticity impacts skull growth can provide novel insights into the lifetime effects of dietary variation on skull form (Ravosa et al., 2007; Menegaz et al., 2009). Continued development of this physiological ecology approach to studying primate feeding will help us to both address these specific issues in bone and muscle physiology and ultimately build our understanding of platyrrhine masticatory apparatus loading and evolution.

SUMMARY

We briefly reviewed several ongoing projects aimed at exploring the evolutionary and functional morphology of the platyrrhine masticatory apparatus. Several of the projects highlight current gaps in our knowledge and call for new data. The need for *in vivo* data documenting loading regimes in the platyrrhine skull during mastication is clear and these data simply need to be collected. Our preliminary *in vivo* mandibular strains from capuchins suggest that Old World monkeys may not be an ideal model of jaw loading patterns for platyrrhines.

Some of the projects we discussed call for a broader examination of morphology incorporating new techniques and concepts. Technological advances should improve accuracy in quantifying morphology and provide new insights into form–function relationships. Even though we did not discuss Finite Element Analyses (FEA), this approach can help test functional hypotheses in platyrrhines not readily addressed by more traditional methods (e.g., Ross et al., 2010; Dumont et al., 2011). Finally, we reviewed several projects that integrate previously distinct research traditions in studying platyrrhine feeding biology. Whether these are studies of dental form incorporating material science engineering, analyses linking jaw muscles with their underlying skeletal form, or efforts to collect *in vivo* physiological data during feeding in natural habitats, we argue that integration of approaches will offer the greatest opportunity for advancing our knowledge of platyrrhine feeding biology. We understand that metric analyses of form will dominate functional morphology studies of the platyrrhine masticatory apparatus because of logistical limitations. Our morphometric analyses, however, would benefit from stronger links to physiology and feeding behaviors given that these data tell us how morphology behaves during feeding. The diversity in feeding across

Fig. 13. Plot of scaled EMG recruitment versus food toughness for a single female howler (*A. palliata*) from 11 separate feeding bouts over a two-day period. The product-moment correlation ($r = -0.42$, $P = 0.2$) suggests that relative EMG recruitment levels for the jaw muscles are not correlated with food toughness over this two-day period. This result suggests that animals may behaviorally modulate food intake to maintain feeding activities within a specific physiological range. EMG levels are scaled to the maximum observed value for an electrode during the two-day period (i.e., ≤ 1). We used the scissors test on a Lucas-Darvell HKU tester to estimate food toughness for dropped or similar food items (i.e., leaves) (see Lucas, 2004; Teaford et al., 2006).

platyrrhines offers researchers an excellent natural dietary experiment for understanding how primate skulls are tuned to their diets. New data and new links across research traditions will provide a clearer and more informed view of the loading profiles in the masticatory apparatus of New World monkeys and will help us to better understand how feeding shaped the platyrrhine face.

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