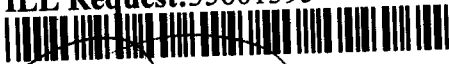


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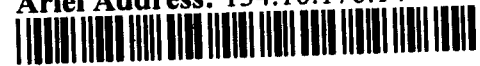
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# Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*

Andrea B. Taylor

Departments of Community and Family Medicine and Biological Anthropology and Anatomy, Duke University Medical Center,  
Box 3907, Durham, NC 27710, USA

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## Abstract

Orangutans are amongst the most craniometrically variable of the extant great apes, yet there has been no attempt to explicitly link this morphological variation with observed differences in behavioral ecology. This study explores the relationship between feeding behavior, diet, and mandibular morphology in orangutans. All orangutans prefer ripe, pulpy fruit when available. However, some populations of Bornean orangutans (*Pongo pygmaeus morio* and *P. p. wurmbii*) rely more heavily on bark and relatively tough vegetation during periods of low fruit yield than do Sumatran orangutans (*Pongo abelii*). I tested the hypothesis that Bornean orangutans exhibit structural features of the mandible that provide greater load resistance abilities to masticatory and incisal forces. Compared to *P. abelii*, *P. p. morio* exhibits greater load resistance abilities as reflected in a relatively deeper mandibular corpus, deeper and wider mandibular symphysis, and relatively greater condylar area. *P. p. wurmbii* exhibits most of these same morphologies, and in all comparisons is either comparable in jaw proportions to *P. p. morio*, or intermediate between *P. p. morio* and *P. abelii*. These data indicate that *P. p. morio* and *P. p. wurmbii* are better suited to resisting large and/or frequent jaw loads than *P. abelii*. Using these results, I evaluated mandibular morphology in *P. p. pygmaeus*, a Bornean orangutan population whose behavioral ecology is poorly known. *Pongo p. pygmaeus* generally exhibits relatively greater load resistance capabilities than *P. abelii*, but less than *P. p. morio*. These results suggest that *P. p. pygmaeus* may consume greater amounts of tougher and/or more obdurate foods than *P. abelii*, and that consumption of such foods may intensify amongst Bornean orangutan populations. Finally, data from this study are used to evaluate variation in craniomandibular morphology in *Khoratpithecus piriya*, possibly the earliest relative of *Pongo* from the late Miocene of Thailand, and the late Pleistocene Hoa Binh subfossil orangutan recovered from Vietnam. With the exception of a relatively thicker M<sub>3</sub> mandibular corpus, *K. piriya* has jaw proportions that would be expected for an extant orangutan of comparable jaw size. Likewise, the Hoa Binh subfossil does not differ in skull proportions from extant *Pongo*, independent of the effects of increase in jaw size. These results indicate that differences in skull and mandibular proportions between these fossil and subfossil orangutans and extant *Pongo* are allometric. Furthermore, the ability of *K. piriya* to resist jaw loads appears to have been comparable to that of extant orangutans. However, the similarity in jaw proportions between *P. abelii* and *K. piriya* suggest the latter may have been dietarily more similar to Sumatran orangutans.

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**Keywords:** *Pongo*; Orangutan evolution; *Khoratpithecus*; Hoa Binh; Mandibular morphology; Feeding behavior; Diet

## Introduction

Orangutans are amongst the most craniometrically variable of the extant great apes, but the nature and patterning of this variation is not completely understood (Jacobshagen, 1979; Röhrer-Ertl, 1984, 1988; Courtenay et al., 1988; Brown, 1989, 1997; Groves et al., 1992; Uchida, 1996, 1998). Along with

well known phenotypic differences in skull form between island orangutan populations, orangutans inhabiting the island of Borneo exhibit notable geographic variation in craniofacial and dental morphology that may exceed the degree of variation observed between island populations (Groves, 1986; Courtenay et al., 1988; Uchida, 1998). While inter- and intra-island differences in behavioral ecology have been documented (MacKinnon, 1974; Rodman, 1977, 1988; Rijksen, 1978; Galdikas, 1988; Leighton, 1993; Knott, 1998; van Schaik et al., 1999; Delgado and van Schaik, 2000; Fox et al., 2004), there has been no explicit

E-mail address: [andrea.taylor@duke.edu](mailto:andrea.taylor@duke.edu)

attempt to link the morphological variation with observed differences in behavioral ecology in *Pongo*, as has been done for the African apes (e.g., Groves, 1970; Shea, 1983; Daegling, 1989; Uchida, 1996; Taylor, 2002, 2003, 2005, in press).

Here I investigate the relationship between variation in mandibular morphology and diet in *Pongo*. Bornean and Sumatran orangutans are similar in adult body size (Smith and Jungers, 1997), and all orangutan populations are closely related, either as species (Xu and Arnason, 1996; Groves, 2001) or subspecies (Muir et al., 1998), suitably limiting the effects of allometry and phylogenetic history, respectively, on morphological variation. Therefore, orangutans provide an excellent context for exploring the relationship between jaw form and dietary variation.

Apart from the question of whether orangutan mandibular variation can be functionally linked to diet, the morphological data should prove to be informative with regard to the evolution of *Pongo*. Two recently reported fossils include the late Miocene *Khoratpithecus piriyai* from Thailand, represented by a fairly complete and undistorted lower jaw (Chaimanee et al., 2004), and a late Pleistocene subfossil skeleton recovered from a cave in Hoa Binh province, Vietnam, which includes a complete cranium and mandible (Bacon and Long, 2001). The *K. piriyai* mandible is described as bearing a deep and very thick lower corpus with a deep, thick, and strongly proclined mandibular symphysis, which differs from that of extant *Pongo*, bearing a deep corpus at M<sub>3</sub>, a high M<sub>3</sub> robusticity index, and an enlarged lower third molar (Chaimanee et al., 2004). The Hoa Binh specimen has been diagnosed on the basis of canine size as female, and is described as a large skull with large teeth (Bacon and Long, 2001). A detailed examination of mandibular variation in geographic populations of extant orangutans provides an opportunity to evaluate variation in the evolution of the orangutan skull, and to interpret the functional consequences of jaw form in these fossil Miocene and Pleistocene hominoids.

### Orangutan distribution, behavioral ecology, and diet

Orangutans inhabit the tropical rainforest islands of Sumatra and Borneo in Southeast Asia. Sumatran orangutans (*Pongo abelii*; Groves, 2001) today are restricted to small and fragmented populations to the north of the island (Fig. 1a). On Borneo, there are three recognized populations, geographically separated from each other by major rivers (Groves, 2001) (Fig. 1b). Two orangutan populations inhabit the western Kalimantan region: *Pongo pygmaeus pygmaeus*, distributed in northwest Kalimantan, north of the Kapuas River and extending into Sarawak; and *Pongo pygmaeus wurmbii*, distributed south of the Kapuas River and west of the Barito River. The third population, *Pongo pygmaeus morio*, ranges from northeast of the Mahakam River into the northern region of Sabah.

Orangutans are large-bodied primates that prefer ripe, pulpy fruits when available. While orangutans experience some seasonal variation in fruit availability, of greater consequence to their dietary regime is that they can experience

a lengthy period, sometimes years, during which there is little to no fruit yield. These periods are followed by periods of abundant fruiting, called masts (van Schaik, 1986; Knott, 1998). During a mast, orangutans subsist almost entirely on ripe, fleshy fruit (the pulp or mature mesocarp) and seeds, selecting for high ratios of pulp weight/fruit and pulp weight/seeds (Rodman, 1988; Leighton, 1993). Galdikas (1982) observed that orangutans frequently chew a combined mass of fruit flesh and fiber for as long as 15–20 minutes before spitting out a wad of intact seeds and/or chewed fibers. Mature seeds are generally either swallowed whole or discarded (Galdikas, 1982; Rodman, 1988), while orangutans carefully select and feed preferentially on chemically unprotected species of immature seeds (Rodman, 1988; Leighton, 1993). Leighton (1993), for example, observed that orangutans crush whole fruits, discard the husks, and swallow the small, unripe soft seed coats. Orangutans have thick enameled, crenulated molars, a morphology that has been adaptively linked in primates to feeding on hard objects such as seeds (Kay, 1981; Lucas and Luke, 1984; Martin, 1985; Kinzey, 1992). While immature seeds are visibly ingested and often times masticated (Leighton, 1993), little is known about how orangutans actually process various seed species in the wild.

When fruit yield is low, orangutans feed regularly on fibrous fruits (e.g., fig species) as well as on unripe fruits, leaves, epiphytes, lianas, bark, and on rare occasions, wood (MacKinnon, 1974; Rodman, 1977, 1988; Rijksen, 1978; Galdikas, 1988; Leighton, 1993; Ungar, 1994a,b; Knott, 1998).<sup>1</sup> Observations of bark feeding indicate that orangutans may either gnaw directly on the trunk or limbs of the tree or strip the bark from the ends of twigs. They also utilize their upper canines to split the bark and then apply their incisors to strip the bark away from the limb or twig, generating a wad which they then chew and eventually discard (Rodman, 1988; Leighton, 1993). Orangutan bark-stripping behavior has resulted in the death of trees (Rijksen, 1978; Galdikas, 1982). Rodman (1988) has suggested that orangutans exhibit an anterior maxillary dental complex, including small lateral incisors, broad central incisors, relatively short canines, and a wear pattern on the lateral maxillary incisors, which together are functionally linked to this bark-stripping behavior. It is worth noting that orangutans generally select fruits that are small in size relative to the amount of jaw opening they can generate,

<sup>1</sup> Ingestion and mastication of bark have been variously referred to in the literature as both “bark feeding” and “cambium feeding”. Tree bark comprises an outer bark layer (the cork), an intermediate layer that serves to transport sugars to various parts of the tree (the phloem), and an inner vascular growth layer (the cambium). When orangutans feed on bark, it is the phloem layer that is being sought (Rodman, personal communication, as cited in Leighton, 1993), although the animals undoubtedly acquire both the phloem and cambium layers while feeding. Rodman (1988), for example, observes that once the bark has been split and opened, orangutans gnaw at the cambium layer from the inside of the piece of bark. Given that the cambium is a thin cell layer of undifferentiated tissue, and the nutritional value is derived from the phloem layer, it is probably misleading to utilize the terms bark-feeding and cambium-feeding interchangeably. Therefore, I will describe this behavior as “bark feeding”.

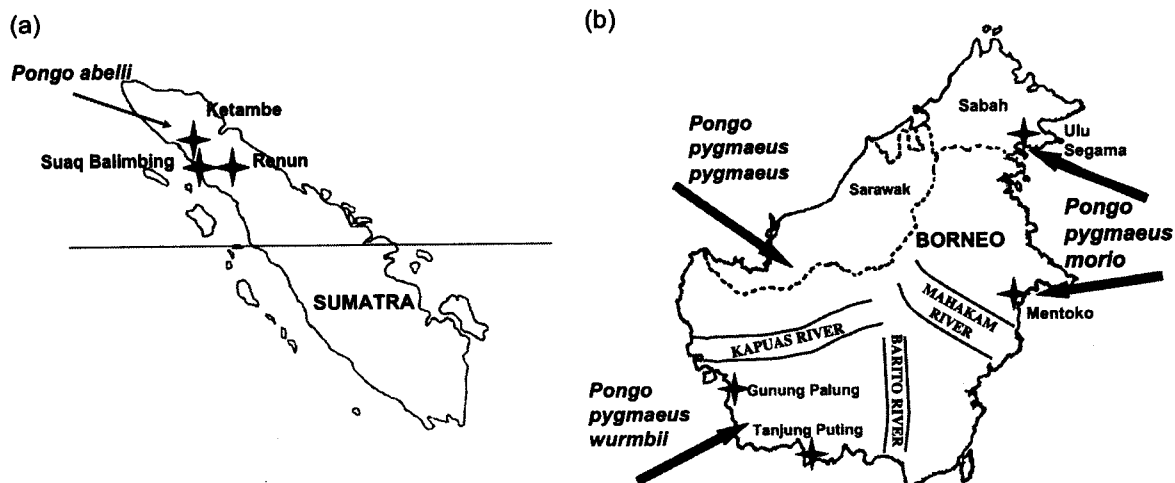


Fig. 1. Current distribution and study sites for (a) *Pongo abelii*, and (b) *Pongo pygmaeus*. Adapted from Delgado and van Schaik (2000).

and thus do not appear to have feeding requirements that require wide jaw gapes (Rodman, 1988).

Data on feeding behavior and diet compiled from multiple sites reveal inter-island differences in dietary composition (Table 1). As estimated by the percentage of total feeding time, Sumatran orangutans spend more time feeding on fruit than do Bornean orangutans. By contrast, Bornean orangutans allocate a considerably greater percentage of their feeding time to bark and vegetation than do Sumatran orangutans. In some months, Bornean orangutans may spend as much as 67% of their feeding time on bark, and as much as 77% on vegetation (e.g., *P. p. morio* at Mentoko and Ulu Segama, respectively; MacKinnon, 1974; Rodman, 1988; Knott, 1998; Fox et al., 2004; Wich et al., in press). According to MacKinnon (1977), Bornean orangutans fed on a greater number of fruit species compared to Sumatran orangutans observed during the same months. These data suggest that Bornean orangutans feed on a broader range of foods and may be less selective feeders. More fine-grained details on dietary proportions by food classes and species are needed.

Table 1  
Average dietary percentages for orangutan populations<sup>1</sup>

	Fruit	Vegetation	Bark
<i>Pongo p. morio</i>	57.9 (16.7–89.9)	26.3 (6.4–66.3)	12.4 (0–52.8)
<i>Pongo p. wurmbii</i>	63.9 (18.2–98.1)	12.8 (0–37.8)	10.4 (0–42.1)
<i>Pongo abelii</i>	66.9 (60.1–70.6)	16.0 (11.7–19.2)	1.9 (1.5–2.4)

<sup>1</sup> Average percentages (monthly ranges in parentheses). Data for *Pongo pygmaeus morio* averaged from Mentoko and Ulu Segama. Data for *P. p. wurmbii* averaged from Tanjung Puting and Gunung Palung. Data for *P. abelii* averaged from Ketambe and Suaq Balimbing. Data represent percentages based on total minutes feeding, with the exception of data from Ulu Segama, which represent percentages of feeding observations. Data compiled from Wich et al. (in press; 18,472 hours collected 1984–2001), MacKinnon (1974; collected June 1968 – November 1968 and October 1969 – August 1971), Rodman (1988; collected April 1970 – August 1971), Knott (1998; collected September 1994 – September 1995), and Fox et al. (2004; collected January 1995 – July 1998). Monthly ranges reflect observations from months of both high and low fruit abundance, and so are not skewed toward only low-fruiting years.

The dietary data are consistent with observed habitat and density differences between Sumatran and Bornean orangutans (Delgado and van Schaik, 2000). For example, soil fertility and consequent production of soft-pulp fruit are higher on Sumatra (van Schaik and Mirmanto, 1985). Furthermore, where Sumatran orangutans inhabit alluvial and swamp forest, masting events are less pronounced because fewer mast-fruiting species are present (van Schaik, 1996). Thus, orangutan densities are higher in Sumatra, even controlling for habitat differences, because of the greater spatiotemporal abundance of fruiting trees. Meijaard and Groves (2004) hypothesize that these same ecological differences may explain unusual distributional patterns of *Presbytis*.

Data for Bornean populations suggest minor differences in dietary composition between *P. p. morio* and *P. p. wurmbii* (Table 1). To date, ecological and dietary data have been collected from study sites south of the Kapuas River (*P. p. wurmbii*) and northeast of the Mahakam River (*P. p. morio*). These data indicate roughly similar averages and monthly ranges of time spent feeding on bark for *P. p. morio* and *P. p. wurmbii*, with *P. p. morio* spending a greater average percentage of feeding time on vegetation than *P. p. wurmbii* (Table 1). However, these differences, and, in particular, the maximum percentage time spent feeding on bark and vegetation in a given month, are relatively minor when compared to between-island differences. Unfortunately, little is known about the behavioral ecology and diet of *P. p. pygmaeus*.

### Morphological predictions

Bark and some vegetation are more obdurate and mechanically difficult to process than fruit pulp (Elgart-Barry, 2004; Lambert et al., 2004; Lucas, 2004; Wright, 2005). If some orangutan populations allocate a greater percentage of feeding time to relatively tougher, more obdurate foods, these taxa may incur more frequent mechanical loading of the jaws, possibly with greater forces. These populations, therefore, would be expected to exhibit an increased capacity to resist such

loads. Several biomechanical predictions can be made regarding the expected jaw shapes for improving load resistance capabilities. The null hypothesis is that there is no predictable pattern of morphological differentiation between orangutan populations of divergent feeding behaviors and diets. Alternatively, assuming the percentage dietary intake data reflect a tougher and/or more obdurate diet, *P. p. morio* and *P. p. wurmbii* would be predicted to exhibit jaw morphologies that are functionally linked to relative increases in load resistance abilities. This alternative is best viewed as a working hypothesis that requires further testing, given that material properties data are needed to substantiate that foods ingested and masticated more frequently by Bornean orangutans are actually tougher than foods consumed by Sumatran orangutans. Because the behavioral ecology of *Pongo p. pygmaeus* is poorly known, no informed *a priori* morphological predictions can be generated for this subspecies.

*Prediction 1: Relatively vertically deeper mandibular corpora*

Experimental studies (Hylander, 1979a,b, 1981) demonstrate that the macaque mandible is bent in a parasagittal plane during mastication and incision. Parasagittal bending places the alveolar and basilar portions of the corpus in tension and compression, respectively. Theoretically, improved resistance to parasagittal bending loads is best achieved by increasing the vertical depth of the corpus. In addition, comparative studies (Bouvier, 1986a,b; Ravosa, 1991; Daegling, 1992) reveal that primates engaged in routine, forceful incisal biting exhibit relatively deeper mandibles than primates that do not engage in such behavior.

*Prediction 2: Relatively thicker (buccolingually) mandibular corpora*

Experimental studies (Hylander, 1979a,b) demonstrate that the macaque mandibular corpora are twisted about their long axes during incision and mastication. Improved resistance to axial torsion is achieved by increasing the transverse thickness of the mandibular corpus.<sup>2</sup>

*Prediction 3: Relatively vertically deeper mandibular symphyses*

Torsional loads incurred along the corpus during incision and mastication produce vertical bending of the symphysis in the coronal plane (Hylander, 1984, 1985). Vertical bending compresses the alveolar symphysis and places tension on the basilar symphysis. In a primate with a fused mandibular symphysis, improved resistance to vertical bending is best achieved by

increasing the vertical depth of the symphysis. The same effect may be achieved by adding a transverse torus (Hylander, 1988).

*Prediction 4: Relatively thicker (labiolingually) mandibular symphyses*

Experimental studies (Hylander, 1984, 1985) demonstrate that the macaque mandibular corpus is bent laterally in a transverse plane. Lateral transverse bending (wishboning) is produced by the late-phase activity of the balancing-side deep masseter during the power stroke of mastication, coupled with the laterally directed working-side muscle and bite force. Wishboning at the corpus places high tensile loads on the lingual aspect of the symphysis and lower compressive loads on the labial aspect of the symphysis. A number of anthropoid, but not strepsirrhine, primates demonstrate the muscle-firing pattern for wishboning, suggesting that wishboning may be an anthropoid loading pattern (Hylander and Johnson, 1994; Hylander et al., 2000, 2002, 2004; Vinyard et al., 2005). There is also indirect evidence to support the hypothesis that wishboning comprises a significant component of the loading regime at the symphysis in all extant hominoids (Daegling, 2001; but not humans: Hylander and Johnson, 1994). In primates with fused symphyses, an efficient way to resist wishboning loads is to increase the labiolingual thickness of the symphysis. Additional solutions include developing a transverse torus and/or reorienting the symphysis from a vertical to an oblique inclination (Hylander, 1984, 1985; Daegling, 2001).

*Prediction 5: Relatively larger mandibular condylar articular surfaces*

During incision and mastication, macaque mandibular condyles are loaded in compression (Hylander and Bays, 1979). An increase in the articular surface area of the condyles is an effective way to counter repetitive and/or large condylar reaction forces incurred during incision and mastication of tougher, more obdurate foods (Hylander, 1979c; Smith et al., 1983; Bouvier, 1986a,b; Wall, 1999; Taylor, 2005).

## Materials and methods

### Samples

The sample comprises 248 adult *Pongo* representing four geographically distinct populations: *Pongo p. morio* (n = 16), *P. p. wurmbii* (n = 25), *P. p. pygmaeus* (n = 167), and *Pongo abelii* (n = 40). Males and females were combined in all analyses, based on similarity in degrees and patterns of mandibular dimorphism among orangutan populations (Taylor, 2006).<sup>3</sup> Excepting *P. p. pygmaeus*, these samples represent

<sup>2</sup> Theoretically, resistance to torsion is maximized with a cylindrically-shaped corpus. However, in orangutans and most other primates, the height of the mandible exceeds mandibular width. Given this initial configuration, a relative increase in the transverse thickness of the corpus will improve resistance to torsion.

<sup>3</sup> If sex ratios are unbalanced, as they are for *P. p. morio*, one population may appear larger or smaller simply due to sampling. Nevertheless, sexes were combined in this case to maximize small group samples. Importantly, sex-specific patterns of morphological differentiation are similar to the pattern of morphological differentiation with the sexes combined.

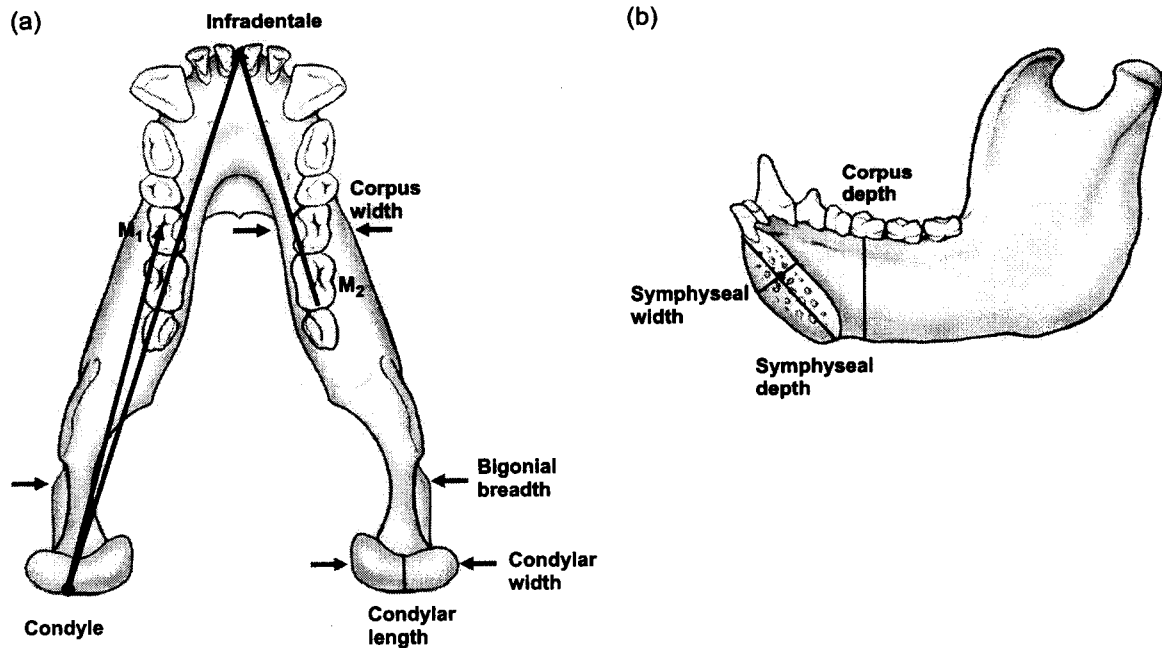


Fig. 2. Measurements employed in this study as defined in Taylor (2002, 2003, 2005): (a) Mandibular condyle – M<sub>1</sub> length, mandibular condyle – infradentale length, M<sub>1</sub> corpus width, bigonial breadth, condylar width, and condylar length. Infradentale – M<sub>2</sub> length adapted from Hylander (1988). (b) Mandibular corpus depth at M<sub>1</sub>, symphyseal depth, and symphyseal width.

most of the available wild-caught specimens of known locality, and are the largest ever presented for these populations (cf. Courtenay et al., 1988; Uchida, 1996, 1998). Determination of adult status was based on a fully erupted dentition in complete occlusion combined with partial to complete fusion of the basilar suture (Taylor, 2002, 2003).<sup>4</sup> Specimens with any obvious pathology were excluded from data analysis.

#### Measurements and shape variables

Mandibular dimensions were measured to the nearest 0.001 mm with Mitutoyo digital calipers (as defined in Taylor, 2002, 2003, 2005) (Fig. 2). Condylar area was computed using the formula for an ellipse (Bouvier, 1986a; Vinyard et al., 2003; Taylor, 2005), where condylar area =  $\frac{1}{2}$  (condylar length)  $\times$   $\frac{1}{2}$  (condylar width)  $\times$   $\pi$ . I generated a series of biomechanical shape variables (Vinyard et al., 2003) by dividing selected linear or areal measurements by a relevant biomechanical standard and multiplying each shape variable by 100. To evaluate relative load resistance capabilities during postcanine mastication, I used the distance between M<sub>1</sub> and the condyle. To evaluate relative load resistance capabilities during incision, I used mandibular length (condyle – infradentale).

<sup>4</sup> There is evidence that growth of the skull and tooth root development extend beyond the period at which the teeth are fully erupted and in occlusion (Markham and Groves, 1990; Uchida, 1996; Brown, 1997). Based on paired t-tests, I observed no differences ( $p > 0.05$ ) in jaw dimensions between dentally adult males with or without complete fusion of the basilar suture, and the patterns of differentiation between orangutan groups were comparable at both stages of growth. Therefore, samples used here include a mix of dentally and craniodentally adult males in order to achieve robust sample sizes.

These two variables reflect load arms for creating bite force at the M<sub>1</sub> and at the incisors, respectively (Hylander, 1985; Bouvier, 1986a; Daegling, 1990). Additionally, I used bigonial breadth as an estimate of the load arm for vertical bending at the symphysis during incision (Daegling, 1990).

I used published values for corpus, symphyseal, and mesiodistal dental dimensions for *Khoratpithecus piriyai* (Chaimanee et al., 2004). Values for infradentale-M<sub>2</sub> length and buccolingual width at M<sub>3</sub> were obtained by digitizing data directly from the published photograph and adjusting to scale. Skull and mandibular values for the Hoa Binh subfossil are from Bacon and Long (2001).

#### Statistical analyses

I tested the hypothesis that compared to *P. abelii*, *P. p. morio* and *P. p. wurmbii* exhibit jaw morphologies that provide increased load resistance capacity during incision and mastication. For each functional hypothesis, one-tailed Mann-Whitney U tests were performed to test for significant differences in biomechanical shape ratios between taxa. The sequential Bonferroni correction was used to guard against Type I error associated with multiple pairwise comparisons (Rice, 1989). Because differences in feeding behavior and diet between Bornean orangutan populations are relatively minor, I performed two-tailed Mann-Whitney U tests to evaluate the null hypothesis of no differences in jaw shapes between *P. p. morio* and *P. p. wurmbii*. Likewise, in the absence of ecological data for *P. p. pygmaeus*, I used two-tailed statistical tests to compare jaw shapes between *P. p. pygmaeus* and the other

orangutan populations. In all comparisons, I considered both the direction and degree of pairwise differences in jaw shapes.

Sample ranges were used to evaluate variation in mandibular dimensions within and between extant and fossil/subfossil orangutans. To evaluate *Khoratpithecus*, adult values for the corpus, symphysis, and some dental dimensions are presented for combined sexes of *Pongo pygmaeus* and *P. abelii*. Because the Hoa Binh specimen is diagnosed as a female based on canine size (Bacon and Long, 2001), evaluation of craniodental dimensions for this specimen is based only on female sample ranges.

I used ordinary least-squares (OLS) regression analysis and 95% prediction intervals to test the null hypothesis that mandibular dimensions of *Khoratpithecus* and the Hoa Binh specimen do not differ significantly from those predicted by an adult interspecific trajectory (employing all available data points from the four orangutan populations) derived from extant *Pongo*.<sup>5</sup> For the Hoa Binh specimen, mandibular length was used as the independent variable. However, as *Khoratpithecus* lacks an ascending ramus and condyle, I used infradentale-M<sub>2</sub> length (Hylander, 1988) (Fig. 2a). Systat (version 10.0) was used to generate all statistical analyses and box plots. Regression lines and 95% prediction intervals were generated in SigmaPlot (version 6.1).

## Results

### Pairwise comparisons between extant *Pongo*

*Pongo p. morio* has absolutely larger ( $p < 0.05$ ) corpus, symphyseal, and condylar dimensions compared to *Pongo abelii* (Table 2). *Pongo p. wurmbii* is significantly larger than *P. abelii* in symphyseal dimensions and condylar length. There are no significant differences in jaw dimensions between *P. p. morio* and *P. p. wurmbii*, and no pairwise differences in any of the three load-arm estimates.

Group differences are generally similar regardless of load-arm estimate (Table 2). To avoid repetition, only representative jaw shapes are presented (Fig. 3). Based on the Bonferroni-adjusted results, *Pongo p. morio* exhibits all but one of the jaw shapes predicted to provide improved load resistance capabilities (Table 2 and Fig. 3). Relative to all load-arm estimates, *P. p. morio* has a deeper mandibular corpus, deeper and wider mandibular symphysis, and greater condylar area, compared to *P. abelii* (Fig. 3a, c–e). Corpus width is significantly greater only prior to the Bonferroni correction, and degree of overlap amongst taxa is greatest for this jaw shape (Table 2 and Fig. 3b). The greater condylar area is a function of relative increases in both condylar length and width (Table 2). In the absence of significant differences in moment arm lengths between taxa, the more robust lower jaws of *P. p. morio* can be principally attributed to both absolutely and relatively larger corpus, symphyseal, and condylar dimensions (Table 2).

<sup>5</sup> Reduced major axis regression yields lower y-intercepts and higher slopes, but does not alter the pattern of results.

*Pongo p. wurmbii* exhibits some shapes that reflect relative increases in load resistance abilities (Table 2 and Fig. 3). With respect to incisal loads, *P. p. wurmbii* has a relatively deeper mandibular corpus and larger condylar area. Improved resistance to masticatory loads is reflected in a relatively wider mandibular symphysis. *Pongo p. wurmbii* also has a relatively deeper mandibular corpus and larger condylar area relative to mandibular length but these differences only achieve statistical significance prior to the Bonferroni correction. As expected, there are no differences in shape variables between the two Bornean orangutan populations.

Comparisons of jaw shapes between *P. p. pygmaeus* and the other orangutan groups are presented in Table 3. *Pongo p. pygmaeus* and *Pongo abelii* differ most frequently, the former generally (but not always) exhibiting relatively more robust jaw dimensions compared to the latter. These include a relatively deeper corpus, wider symphysis, and larger condylar area. However, relative to the load arms for mastication and incision, *P. p. pygmaeus* has a thinner corpus compared to one or more of the three orangutan populations.

### *Khoratpithecus piriyai*

In symphyseal dimensions, mandibular corpus depth, and mesiodistal dimensions of the lower postcanine dentition from P<sub>3</sub> – M<sub>2</sub>, *Khoratpithecus piriyai* falls within the observed sample ranges for extant *Pongo* (Fig. 4). Both M<sub>3</sub> corpus width and M<sub>3</sub> mesiodistal length exceed the observed ranges of variation for *Pongo*. The corpus robusticity index of *K. piriyai* also exceeds the observed range of variation for *Pongo* (Fig. 4a). Excepting M<sub>3</sub> corpus width, *K. piriyai* has corpus and symphyseal proportions that align closer with those of *P. abelii* than with the relatively more robust *P. p. morio* (Fig. 5).

Regression statistics for *Pongo* are presented in Table 4. Correlation coefficients for measures of the mandibular corpus and symphysis relative to jaw length (infradentale – M<sub>2</sub>) are all significant. The values for *Khoratpithecus piriyai* for symphyseal dimensions and corpus depth fall within the range of predicted values (95% prediction intervals) for an extant orangutan of similar jaw length (Fig. 6a–c). The observed value for *K. piriyai* is extremely close to the predicted value determined for the adult interspecific regression of symphyseal width (labiolingual thickness) on jaw length (Fig. 6c). Only M<sub>3</sub> corpus width deviates outside of the range of predicted values (95% prediction intervals) for the orangutan trajectory (Fig. 6d). Thus, *K. piriyai* has a relatively wider (buccolingually thicker) corpus for a given jaw length, and consequently, a relatively higher corpus robusticity index, compared to extant *Pongo* (Fig. 6e).

### The Hoa Binh subfossil orangutan

The Hoa Binh specimen exceeds the ranges of variation when compared to extant female orangutans for all dimensions evaluated in this study (Fig. 7). Though not shown, the Hoa Binh specimen does fall within the range of variation for extant male *Pongo*. Correlations are significant for skull and

Table 2

Means, standard deviations (in parentheses), and results of tests for statistical differences in linear dimensions and jaw shapes between orangutan taxa<sup>1–3</sup>

Linear Dimensions	<i>P. p. morio</i>	<i>P. p. wurmbii</i>	<i>P. abelii</i>	<i>P. p. morio</i> vs. <i>P. abelii</i>	<i>P. p. wurmbii</i> vs. <i>P. abelii</i>	<i>P. p. morio</i> vs. <i>P. p. wurmbii</i>
Mandibular length	168.14 (17.0)	159.21 (18.7)	159.09 (14.5)	NS	NS	NS
Bigonial breadth	104.23 (13.4)	104.37 (14.9)	96.34 (13.0)	NS	NS	NS
Condyle-M <sub>1</sub> distance	105.73 (12.4)	102.15 (17.4)	100.90 (11.9)	NS	NS	NS
M <sub>1</sub> corpus depth	41.21 (4.0)	37.87 (4.6)	36.04 (4.6)	<b>0.000</b>	NS	NS
M <sub>1</sub> corpus width	15.51 (3.7)	13.37 (3.5)	12.88 (3.6)	0.044	NS	NS
M <sub>1</sub> symphyseal depth	63.19 (6.3)	60.12 (10.1)	53.63 (7.2)	<b>0.000</b>	0.006	NS
M <sub>1</sub> symphyseal width	21.99 (2.3)	21.21 (3.4)	18.75 (3.6)	<b>0.003</b>	0.014	NS
Condylar length	17.30 (2.0)	16.21 (2.8)	14.29 (2.3)	<b>0.000</b>	0.007	NS
Condylar width	32.30 (4.3)	28.96 (5.4)	28.41 (3.3)	<b>0.008</b>	NS	NS
<b>Jaw Shapes</b>						
M <sub>1</sub> corpus depth shape (m)	38.84 (3.6)	37.62 (4.2)	35.83 (3.5)	<b>0.0025</b>	0.0435	NS
M <sub>1</sub> corpus depth shape (i)	24.35 (1.8)	23.89 (1.9)	22.56 (1.9)	<b>0.0030</b>	<b>0.0070</b>	NS
M <sub>1</sub> corpus width shape (m)	14.85 (3.6)	13.64 (4.6)	12.90 (3.6)	0.0410	NS	NS
M <sub>1</sub> corpus width shape (i)	9.30 (2.2)	8.53 (2.4)	8.04 (2.1)	0.0390	NS	NS
Symphyseal depth shape (i)	60.98 (4.9)	58.02 (5.7)	56.05 (6.9)	<b>0.0040</b>	0.0870	NS
Symphyseal width shape (m)	13.11 (1.2)	13.30 (1.6)	11.71 (1.7)	<b>0.0010</b>	<b>0.0000</b>	NS
Condylar area shape (m)	39.76 (3.5)	37.73 (4.1)	35.42 (3.1)	<b>0.0000</b>	0.0155	NS
Condylar area shape (i)	24.93 (1.9)	23.98 (2.0)	22.28 (1.6)	<b>0.0000</b>	<b>0.0005</b>	NS

<sup>1</sup> Results of tests for differences in linear dimensions are based on one-way analyses of variance followed by the post-hoc Bonferroni correction. Results of tests for differences in jaw shapes between Bornean (*P. p. morio*, *P. p. wurmbii*) and Sumatran (*P. abelii*) groups are based on one-tailed Mann-Whitney U-tests on log-transformed ratios followed by the sequential Bonferroni correction. Results of tests for differences in jaw shapes between *P. p. morio* and *P. p. wurmbii* are based on two-tailed Mann-Whitney U-tests on log-transformed ratios. Boldfaced p-values represent statistical differences following the Bonferroni correction. Non-boldfaced p-values represent differences that did not achieve statistical significance following the Bonferroni correction. NS, not statistically different.

<sup>2</sup> Indicates the shape is with respect to the load-arm estimate for mastication (m) or incision (i).

<sup>3</sup> To achieve proportional equivalence, the square root of condylar area shape is used in tests of significance between taxa.

jaw dimensions relative to mandibular length (Fig. 8). The Hoa Binh specimen, though absolutely larger than extant female *Pongo*, falls within the 95% prediction intervals for bicondylar and bizygomatic breadths for an extant orangutan extrapolated to larger terminal mandibular size (Fig. 8).

## Discussion

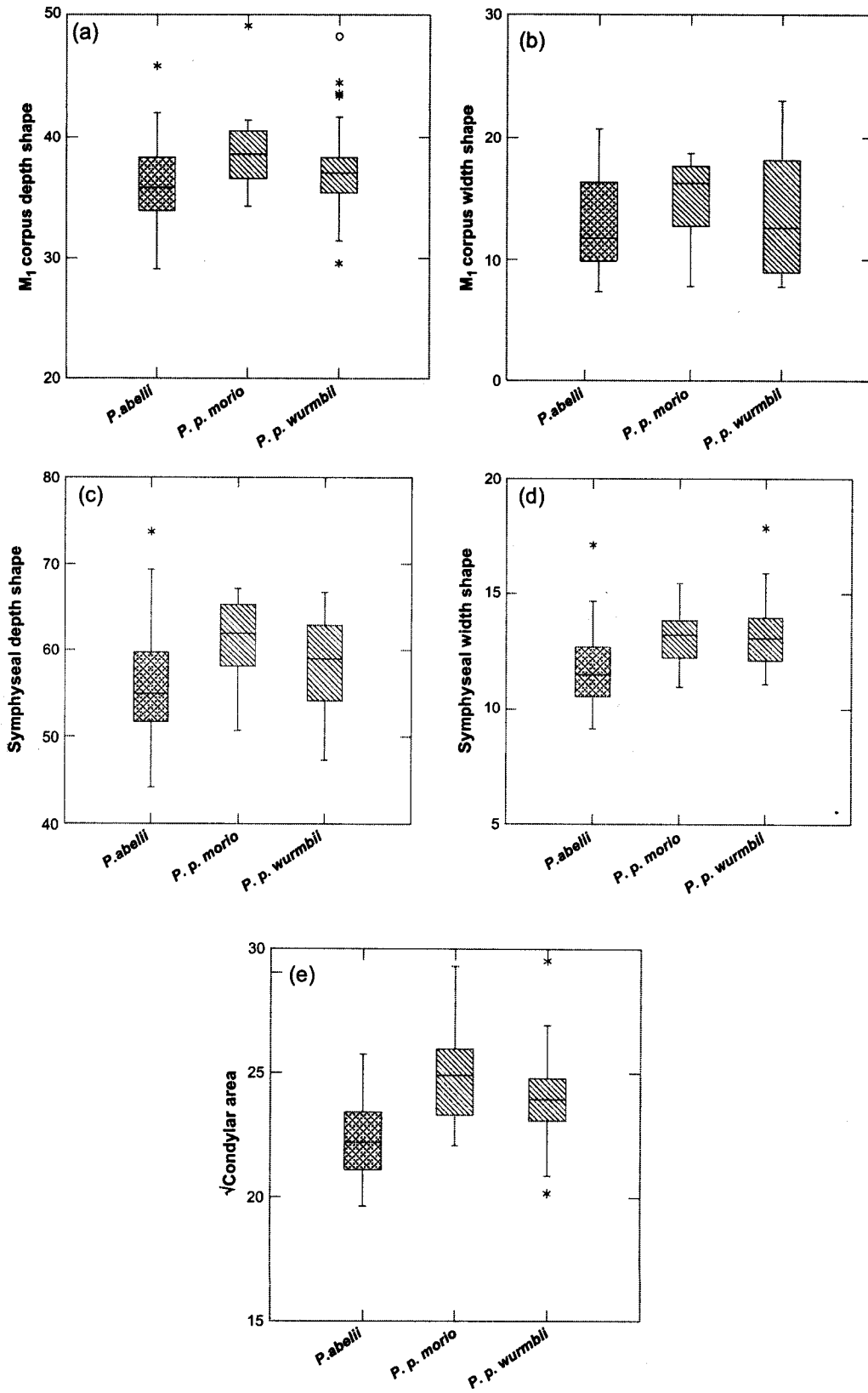
### Variation in jaw morphology in *Pongo*

*Pongo p. morio*, and to a lesser extent *P. p. wurmbii*, exhibit structural features of the mandible that provide the capacity for increased resistance to masticatory and incisal loads compared to *P. abelii*. The relatively deeper corpus suggests that *P. p. morio* is well suited to counter parasagittal bending loads along the corpus during mastication and incision; *P. p. wurmbii* is similarly suited to counter parasagittal bending loads during incision. The relatively deeper symphysis indicates that *P. p. morio* has the capacity to better resist vertical bending loads at the symphysis. The relatively wider mandibular symphysis indicates that *P. p. morio* and *P. p. wurmbii* are better able to counter wishboning loads at the symphysis. Size-correlated changes in symphyseal curvature may augment wishboning loads at the symphysis, independent of dietary influences (Vinyard and Ravosa, 1998). As orangutans do not vary in either mandibular length (Table 2) or breadth ( $F = 0.663$ ,  $df = 2,79$ ,  $p = 0.518$ ), there is little morphological evidence to suggest that larger orangutans experience size-related increases in symphyseal curvature. Therefore, differences

in symphyseal width proportions can be principally attributed to variation at the symphysis. Relatively larger condylar areas indicate that both taxa are better able to counter condylar loads during mastication and incision.

Given a greater reliance by some orangutan populations on bark and vegetation during low-fruited years, it is tempting to interpret the observed differences in jaw shapes as reflecting morphological responses to resisting loads generated during exploitation of fallback foods—that is, as serving a critical, rather than common, function (sensu Kinzey, 1978; Rosenberger, 1992). Some studies (Janson and Boinski, 1992; Lambert et al., 2004; Wright, 2005) have argued that reliance on fallback foods provides the selective pressure in shaping cranial and dental differences amongst primates. However, pinpointing the selective importance of routine versus fallback feeding behaviors in shaping orangutan morphological variation requires systematic data on their feeding behaviors and material food properties. In addition, the capacity for osteonal modeling with alterations in food consistency, though it tapers off with age, underscores the difficulties associated with attributing differences in orangutan jaw shapes to genetic, rather than epigenetic, factors (Bouvier and Hylander, 1981, 1984). Heavy reliance on leaves, lianas, and barks for a period of five or more months during the year (MacKinnon, 1974) may provide sufficient time for mandibular remodeling. Ontogenetic studies would serve to address whether these morphological differences are present at or near birth, or whether they follow the onset of mastication (e.g., Cole, 1992; Taylor, 2002, 2003).





Compared to *P. abelii*, *P. p. pygmaeus* has the structural capacity to counter repetitive and/or large parasagittal bending loads along the corpus, wishboning loads at the symphysis, and condylar loads. However, *P. p. pygmaeus* does not show improved resistance to either torsional loads along the corpus or vertical bending loads at the symphysis. It should be noted that *P. p. morio*, significantly more robust than *P. p. pygmaeus* in some jaw shapes (Table 3), demonstrates a consistent trend toward a relatively more robust jaw compared to *P. p. pygmaeus* in all jaw shapes evaluated (not shown). These data suggest that *P. p. pygmaeus* may be less able to resist masticatory and incisal loads than *P. p. morio*. *P. p. pygmaeus*, therefore, appears morphologically intermediate between *P. abelii* and *P. p. morio*. Whether *P. p. pygmaeus* engages in feeding or dietary behaviors that reflect their load resistance capabilities is yet to be explored.

Finally, apart from alterations in symphyseal proportions, wishboning and vertical bending loads at the mandibular symphysis may also be countered by the presence of a transverse torus (Hylander, 1985). Variation in the presence, expression, and position (i.e., superior versus inferior) of a transverse torus in *Pongo* is well documented (Brown, 1997). Previous evaluation of the anterior mandibular corpus demonstrates that *P. pygmaeus* has larger and thicker symphyses with robust superior transverse tori compared to those of Sumatran orangutans, which are anteroposteriorly thinner but bear more extensive inferior transverse tori (Brown, 1997). These general shape differences are confirmed here (Table 3). Brown (1997) concluded that, all things being equal, because *P. pygmaeus* and *P. abelii* maintain equivalent symphyseal surface areas, the observed shape differences are probably of minimal biomechanical significance. Findings from this study suggest that for a given load arm, orangutan populations differ in their capacity to counter wishboning loads at the symphysis, while the question of whether some orangutan populations actually generate large or repetitive wishboning loads must be addressed experimentally.

#### The functional link between jaw form and diet

Patterns of morphological divergence as observed in this study demonstrate that some orangutan populations are better able to resist repetitive and/or large loads sustained during incision and mastication. These load resistance abilities may be functionally linked to divergent feeding behaviors in orangutans, possibly related to differential exploitation of bark, vegetation, or other potentially tough or obdurate plant tissues, such as seeds. A number of investigators have linked variation in primate craniodental and mandibular morphology to

processing requirements related to a more obdurate diet in general, and bark feeding in particular (Bouvier, 1986a; Demes and Creel, 1988; Hylander, 1988; Cole, 1992; Daegling, 1992; Jablonski, 1993; Anapol and Lee, 1994; Antón, 1996; Taylor, 2002, 2003, 2005, in press; Lambert et al., 2004; Wright, 2005). Antón (1996), for example, found that Japanese macaques have relatively deeper (and possibly wider) mandibular corpora compared to other macaque species, and argued that gnawing or chiseling bark directly off of tree branches is likely to impose the greatest masticatory stresses.

To date, however, few such studies have functionally linked feeding behavior and material food properties to morphological variation. Lambert et al. (2004) provide material properties data demonstrating that the dietary repertoire of *Lophocebus albigena* is more puncture resistant compared to that of *Cercocebus ascanius*. These investigators functionally link thick dental enamel in *L. albigena* to their exploitation of bark and seeds as fallback foods. Wright (2005) found that *Cebus apella* processes plant tissues, including legume pods and palm leaves, which are two to four times as tough as the toughest plant tissues processed by *C. olivaceus*. Wright (2005) concluded that specific aspects of *C. apella* craniodental morphology are explained by the high bite forces they generate when occasionally selecting extraordinarily tough plant tissues.

Contrasting previous studies linking morphological variation to loads sustained during bark feeding is *in vivo* experimental work by Vinyard et al. (2001) on tree gouging in common marmosets (*Callithrix jacchus*). Vinyard et al. (2001) show that, contrary to longstanding theoretical predictions, the forces generated by common marmosets when they gouge trees in order to stimulate the flow of exudates are significantly lower than their ability to generate bite forces. This work is accompanied by data on skull morphology (Vinyard et al., 2003; Vinyard and Ryan, in press) and jaw-muscle fiber architecture (Taylor and Vinyard, 2004; Eng et al., 2005) which substantiate that tree-gouging marmosets do not differ from nongouging tamarins in their ability to generate or dissipate bite forces. These findings suggest that if orangutans and common marmosets ingest bark in roughly similar fashion, processing bark with the anterior masticatory apparatus may play a less important functional role in shaping the observed differences in orangutan mandibular morphology than other tougher or harder foods.

At present, there is a paucity of data on the material properties of foods ingested and masticated by orangutans in the wild (but see Lucas et al., 1994). Likewise, extra-oral manipulation of foods prior to ingestion, as well as feeding behaviors associated with ingestion and mastication, are yet to be systematically and comprehensively documented, either between

Fig. 3. Box plots comparing jaw shapes in *Pongo p. morio*, *P. p. wurmbii*, and *Pongo abelii*. Comparisons of (a)  $M_1$  corpus depth shape; (b)  $M_1$  corpus width shape; (c) symphyseal depth shape; (d) symphyseal width shape; and (e) condylar area shape (square root). Compared to *P. abelii*, *P. p. morio* has relatively larger jaw shapes, significantly ( $p < 0.05$ ) so for all but corpus width shape. *Pongo p. wurmbii* has a relatively deeper mandibular corpus, wider symphysis, and larger condylar area than *P. abelii*. These results indicate that *P. p. morio*, and to a lesser extent *P. p. wurmbii*, have greater load resistance abilities compared to *P. abelii*. All plots represent jaw shapes relative to the load arms for mastication except condylar area shape, which is relative to the load arm for incision. The center vertical line marks the median of the sample. The length of each box shows the range within which the central 50% of the values fall, with the box edges (hinges) at the first and third quartiles. The asterisks and open circles indicate that one or more data points reside outside the fence for the individual data points.

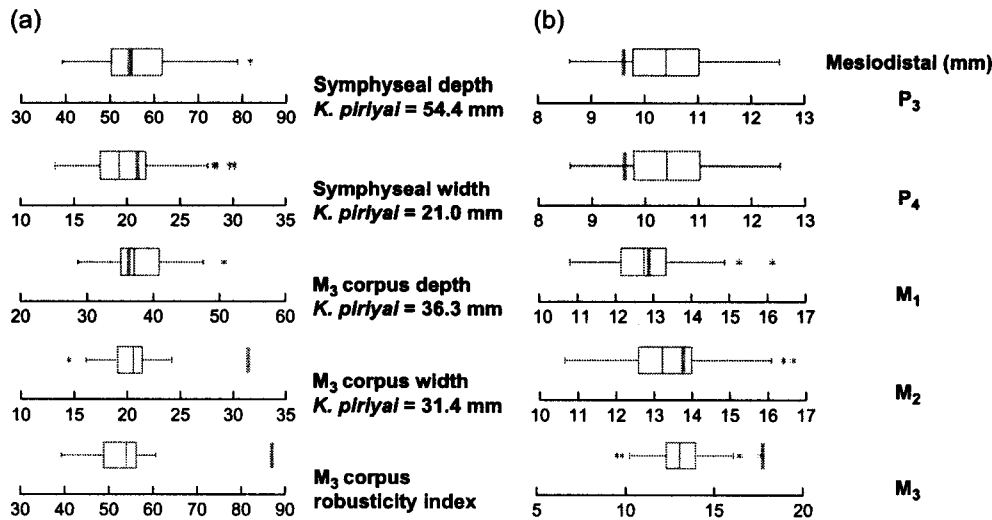


Fig. 4. Box plots comparing extant *Pongo* (both sexes, all four geographic populations combined) and *Khoratpithecus piriyai*. Values for *K. piriyai* are represented by red vertical tick marks. (a) Mandibular dimensions. *K. piriyai* falls within the observed sample ranges for extant *Pongo* for symphyseal depth, symphyseal width, and corpus depth. *M*<sub>3</sub> corpus width falls outside of the observed sample range, resulting in a larger corpus robusticity index. (b) Dental dimensions. *K. piriyai* falls within the extant *Pongo* sample range for all dental dimensions except *M*<sub>3</sub> mesiodistal length.

sites representing the same orangutan population, or between populations. As previously noted, orangutans also feed on hard and/or unripe fruits and seeds. Captive orangutans can break *Macadamia* seeds in a single bite, and experimental work shows that loading these seeds requires average bite forces of 2,000 N in order to accomplish this task (Lucas et al., 1994). If these bite force estimates are accurate, and if future field studies substantiate feeding on tough or hard seeds in the wild, it seems likely that seed-eating will be an important determinant of maximum load resistance abilities in orangutans. The importance of parsing the differential influence of various foods in order to better understand the relationship between diet and skull form argues for fine-grained field studies of orangutan feeding behavior combined with studies of food mechanical properties.

A related question is whether incisal behaviors are more or less critical than postcanine mastication in accounting for the observed differences in jaw shapes (Yamashita, 2003). Given the similarity in findings regardless of load

arm estimate, differences in load resistance abilities are not easily partitioned into specific incisal versus masticatory behaviors. However, primate taxa that are known to load their anterior dentition frequently exhibit incisor and canine morphologies that facilitate this behavior. Common and pygmy marmosets, for example, have a well-known canine-incisor complex that provides an effective wedge for gouging trees (Coimbra-Filho and Mittermeier, 1977). According to Rosenberger (1992), pitheciines share derived features of the anterior dentition that are linked to their sclerocarpic feeding behavior. Their styliiform lower incisors and anteriorly inclined upper and lower incisors form an effective wedge for cutting, while their laterally splayed canines facilitate breaking open hard fruits. The hard-object feeder *Cebus apella* has lower canines and incisors with larger basal cross-sectional areas than does *C. olivaceus*, which Wright (2005) functionally linked to improved resistance to bending stresses associated with processing hard or tough foods. The lower incisors of *C. apella* also exhibit greater wear

Table 3

Results of statistical tests of differences in jaw shapes between *P. p. pygmaeus*, *P. abelii*, *P. p. wurmbii*, and *P. p. morio*<sup>1,2</sup>

<i>P. p. pygmaeus</i> versus	<i>P. abelii</i>	<i>P. p. wurmbii</i>	<i>P. p. morio</i>	Direction of significant difference
<i>M</i> <sub>1</sub> corpus depth shape (m)	0.000	NS	NS	<i>P. p. pygmaeus</i> > <i>P. abelii</i>
<i>M</i> <sub>1</sub> corpus depth shape (i)	0.012	NS	NS	<i>P. p. pygmaeus</i> > <i>P. abelii</i>
<i>M</i> <sub>1</sub> corpus width shape (m)	NS	NS	0.001	<i>P. p. pygmaeus</i> < <i>P. p. morio</i>
<i>M</i> <sub>1</sub> corpus width shape (i)	0.029	0.003	0.000	<i>P. p. pygmaeus</i> < <i>P. p. morio</i> , <i>P. p. wurmbii</i> , <i>P. abelii</i>
Symphyseal depth shape (i)	NS	NS	NS	NS
Symphyseal width shape (m)	0.001	NS	NS	<i>P. p. pygmaeus</i> > <i>P. abelii</i>
Condylar area shape (m)	0.000	NS	NS	<i>P. p. pygmaeus</i> > <i>P. abelii</i>
Condylar area shape (i)	0.026	NS	0.000	<i>P. abelii</i> < <i>P. p. pygmaeus</i> < <i>P. p. morio</i>

<sup>1</sup> Results based on two-tailed, one-way analyses of variance on log-transformed shape variables followed by the post hoc Bonferroni correction. Though not always statistically significant, *P. p. morio* demonstrates a trend toward relatively more robust jaws than *P. p. pygmaeus* in all comparisons. NS, not significant.

<sup>2</sup> Indicates the jaw shape is with respect to the load arm for mastication (m), or incision (i).

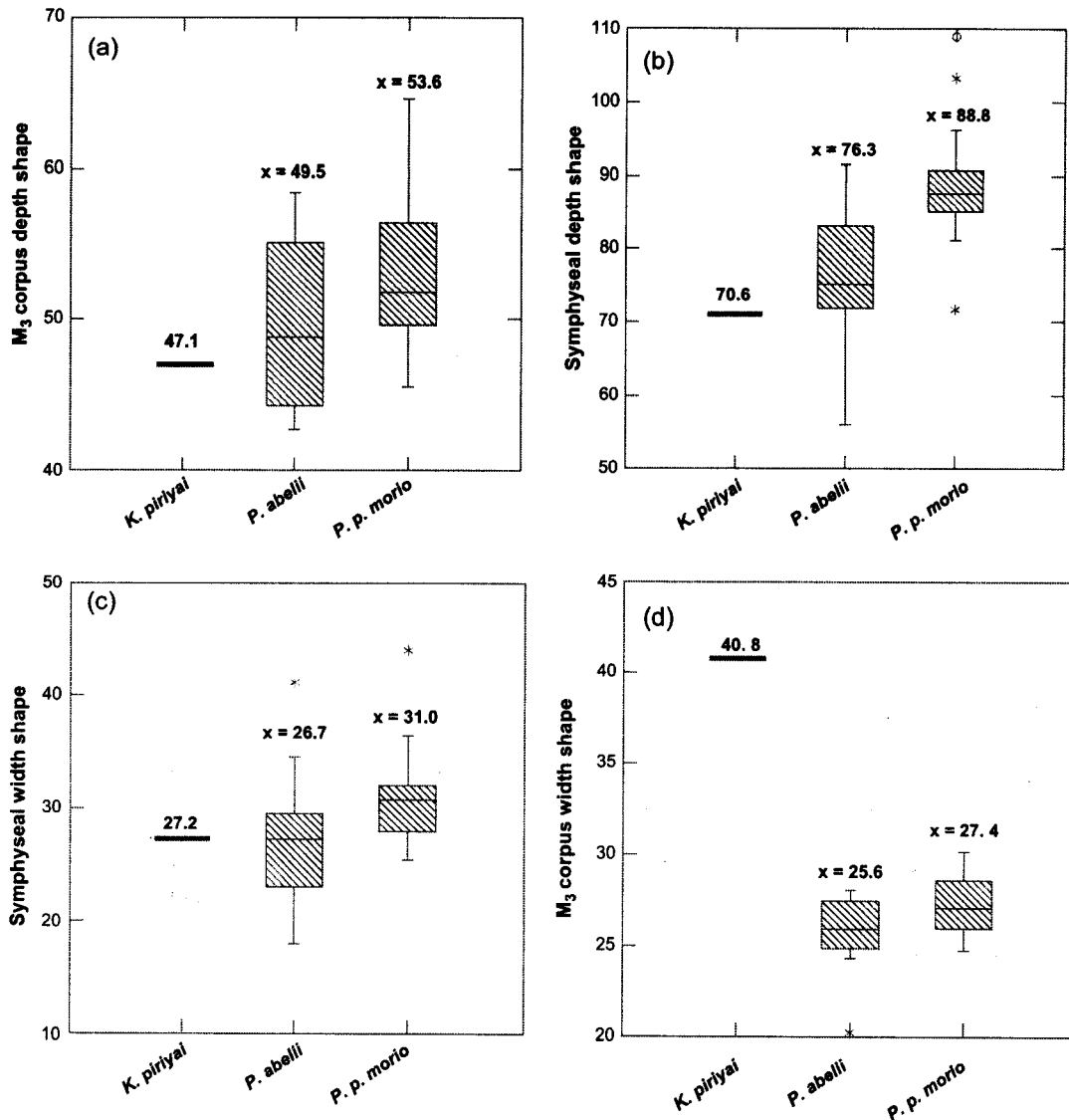


Fig. 5. Box plots comparing jaw shapes for *Khoratpithecus piriyai*, *P. p. morio*, and *P. abelii* (sexes combined). *K. piriyai* falls within the observed sample ranges for extant *Pongo* for (a)  $M_3$  corpus depth shape; (b) symphyseal depth shape; and (c) symphyseal width shape. (d) *K. piriyai* exceeds the observed sample range for extant *Pongo* for  $M_3$  corpus width shape. Note also that *K. piriyai* falls closer to the median values for *P. abelii* in all comparisons except  $M_3$  corpus width shape. These data suggest that *K. piriyai* had less load resistance abilities than *P. p. morio*, and may have been characterized by a diet more similar to that of *P. abelii*.

compared to *C. olivaceus*, which is argued to further reflect intensive processing with the anterior dentition (Wright, 2005). While inter-population differences in molar cusp proportions amongst orangutans have not been explained in terms of feeding behavior or diet (Uchida, 1996, 1998), data from other primates suggest that future studies seeking

to determine the relative importance of incisal versus postcanine masticatory behaviors in orangutans should focus on the anterior dentition.

#### *Tool use, feeding behavior, and morphological divergence*

One intriguing hypothesis for the observed pattern of morphological divergence between Sumatran and Bornean orangutans may relate to differences in feeding behavior as a function of tool use. *Neesia* are large, woody fruits that are well protected by a tough, outer woody husk, and by stinging hairs that develop when the fruits open (dehisce). The seeds form a key orangutan food source (Knott, 1998). While

Table 4

Adult interspecific regression statistics for dimensions of the corpus and symphysis relative to mandibular length (infradentale –  $M_2$  length) for *Pongo*

vs. Mandibular length	n	r	k	(SE)	y-intercept	(SE)	P
$M_3$ corpus depth	80	0.46	0.56	$\pm 0.12$	1.23	$\pm 0.52$	0.000
$M_3$ corpus width	45	0.56	0.63	$\pm 0.14$	0.30	$\pm 0.60$	0.000
Symphyseal depth	286	0.51	0.78	$\pm 0.08$	0.67	$\pm 0.33$	0.000
Symphyseal width	284	0.41	0.68	$\pm 0.09$	0.06	$\pm 0.38$	0.000

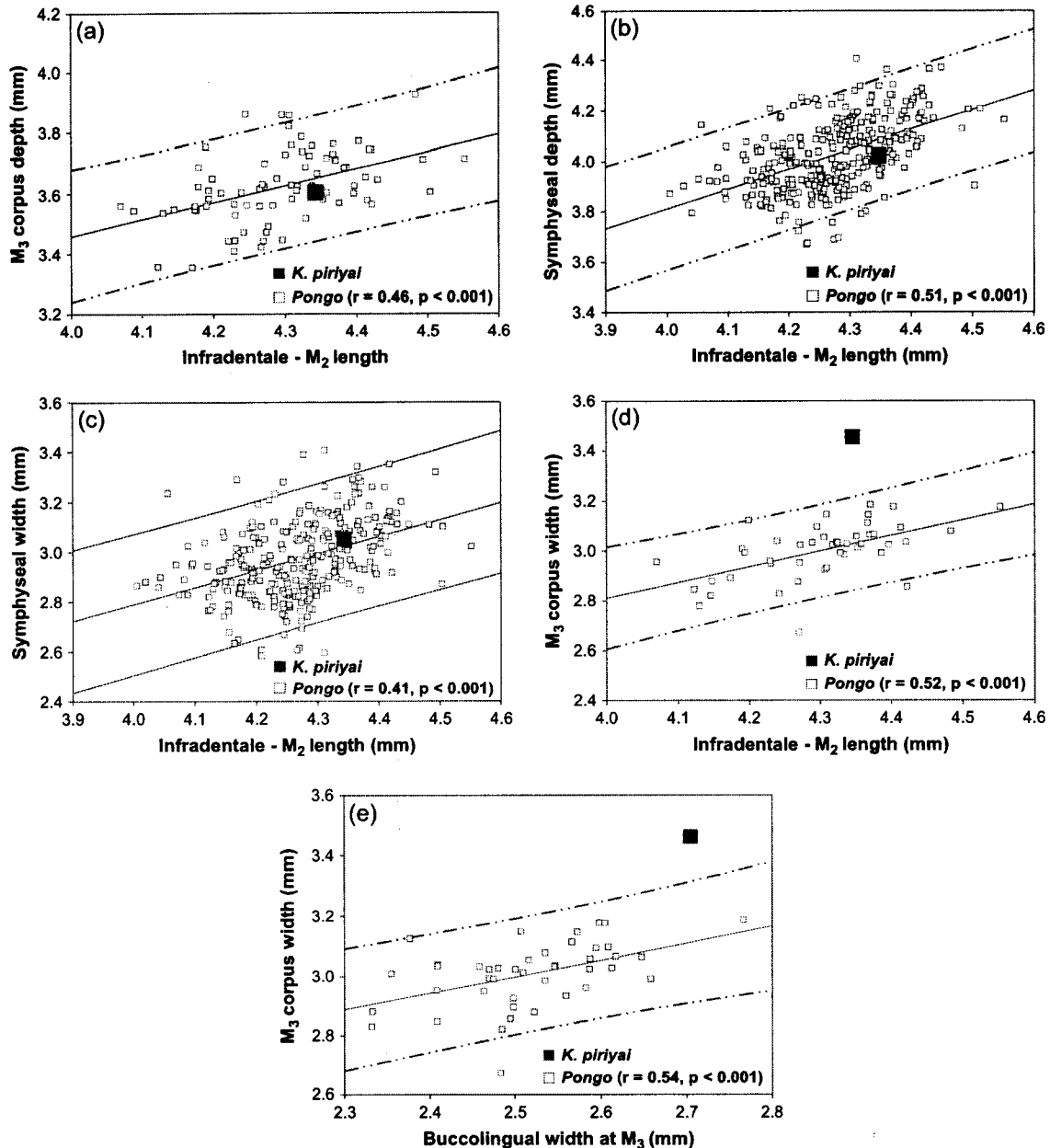


Fig. 6. Regressions and 95% prediction intervals for log-transformed jaw dimensions for *Pongo* (both sexes, all four geographic populations combined). *Khoratpithecus piriyai* has mandibular dimensions that fall within the predicted ranges for an extant orangutan of comparable jaw length (infradentale –  $M_2$  length) for (a) corpus depth; (b) symphyseal depth; and (c) symphyseal width. *K. piriyai* falls outside of the range of predicted values for  $M_3$  corpus width relative to (d) jaw length; and (e)  $M_3$  buccolingual width.

both Sumatran and Bornean orangutans feed on *Neesia*, only orangutans at Suaq Balimbing in Sumatra habitually employ the use of tools (van Schaik and Knott, 2001; van Schaik et al., 2003; Fox et al., 2004), “short straight branches with the bark stripped off, to overcome the fruit’s defense of stinging hairs” (van Schaik and Knott, 2001:336). These tools are used as an extra-oral means of facilitating access to *Neesia* seeds. By contrast, tool use by Bornean orangutans for purposes of extracting *Neesia* seeds has never been observed. Alternatively, feeding observations at Gunung Palung on Borneo

reveal that orangutans utilize their jaws to break open *Neesia* fruits to access the large seeds. The orangutan, typically an adult male (R. Delgado, pers. comm.), “hangs by one arm and uses the other arm and both its feet to tear a valve off the fruit, which is held tight between its clenched jaws” (van Schaik, 2004:122). Orangutans may engage in this behavior even before dehiscence (van Schaik and Knott, 2001). Once extracted, all orangutans appear to ingest and mechanically process *Neesia* seeds in similar fashion (R. Delgado, pers. comm.). However, percentage of feeding time and caloric

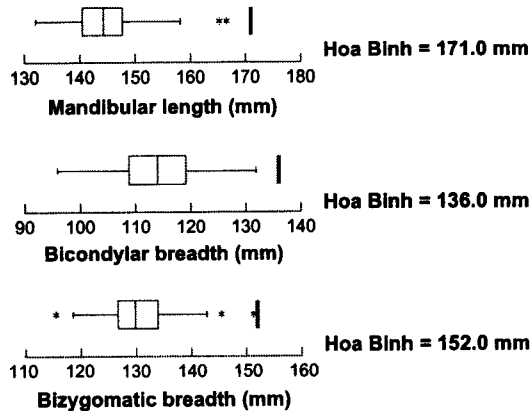


Fig. 7. Box plots comparing jaw and skull dimensions for extant *Pongo* (females only, all four geographic populations combined) and the Hoa Binh specimen. Values for the Hoa Binh specimen are represented by thick black vertical tick marks. The Hoa Binh specimen exceeds the observed sample ranges for extant *Pongo* for all dimensions.

intake of *Neesia* are greater in Sumatran compared to Bornean orangutans, and difficulty accessing *Neesia* seeds without the benefit of tools is thought to be a limiting factor in this regard (van Schaik and Knott, 2001). Thus, it would be worthwhile to

explore whether differences in feeding behavior as a function of tool use may also underlie some of the observed patterning of mandibular variation in Sumatran versus Bornean orangutans.

The use of tools to exploit food sources has been demonstrated by several primate species, including capuchin monkeys (*Cebus apella*), macaques, baboons, and chimpanzees (*Pan troglodytes*) (Beck, 1980; Candland, 1987; Tomasello and Call, 1997; Moura and Lee, 2004). However, tool use can be a regional phenomenon; that is, some populations have been observed to customarily employ the use of tools (e.g., *Cebus apella libidinosus*; Moura and Lee, 2004), while other populations of the same species have not (e.g., Langguth and Alonso, 1977). Amongst orangutans, habitual tool use has been observed by Sumatran orangutans at Suaq Balimbing, but not at Ketambe (van Schaik et al., 2003). Thus, one test of the hypothesis that tool use may play a role in morphological divergence of the primate masticatory system would involve morphological comparisons between tool-using and non-tool-using populations of the same species that are otherwise characterized by similar diets; such data could have important implications for understanding the role of tool use and production in the evolution of early hominids (e.g., Leakey, 1961; Tobias, 1965; Robinson, 1972). Their relatively restricted geographic distribution makes it difficult to test such a hypothesis

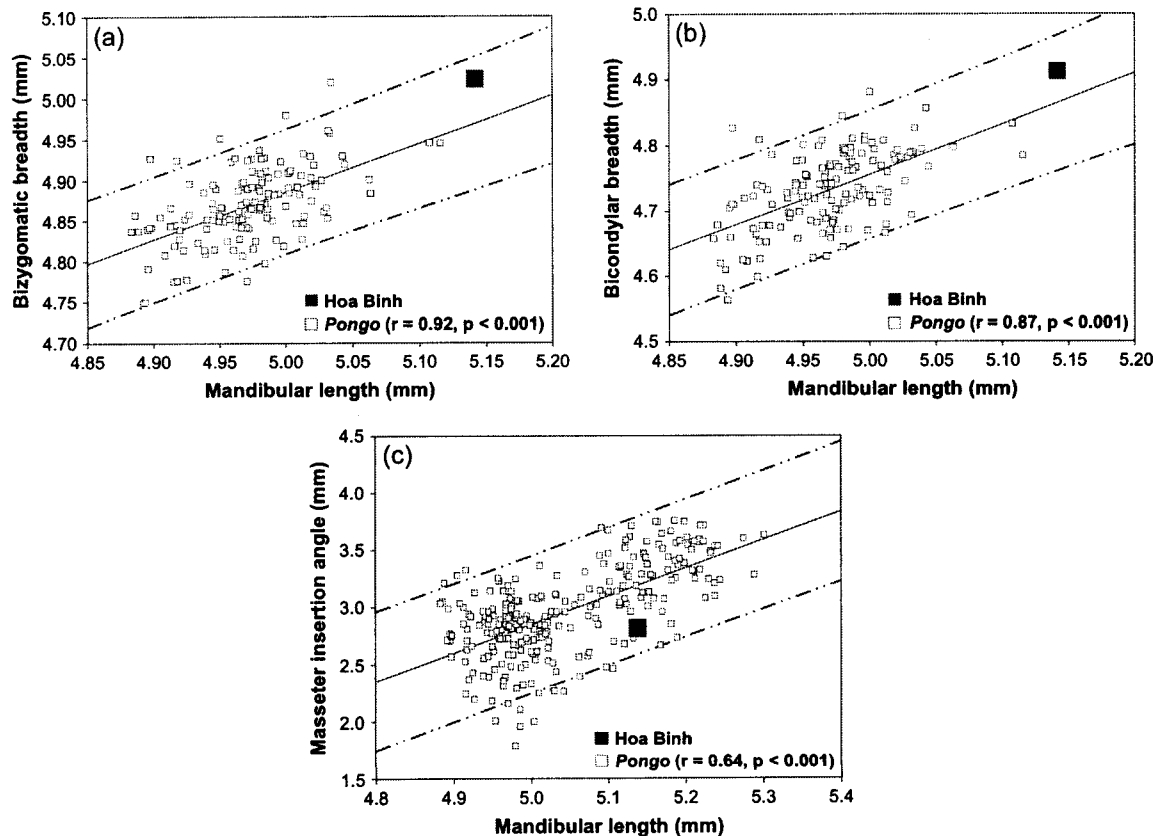


Fig. 8. Regressions and 95% prediction intervals for *Pongo* for (a) bizygomatic breadth, and (b) bicondylar breadth, relative to mandibular length. All data are log-transformed. In both analyses, the Hoa Binh specimen falls within the range predicted for an extant female orangutan extrapolated to larger mandibular size. (c) The Hoa Binh specimen falls within the 95% predictions intervals for *Pongo*, suggesting that the horizontal component of masseter muscle force is what would be expected for an extant orangutan of similar jaw length.

on Sumatran orangutans, given that locality data for orangutan specimens do not readily map to field study sites. However, other primates comprising multiple geographic populations across a broader geographic range, such as *Cebus*, may provide suitable models for testing this hypothesis.

### Implications for the evolution of *Pongo*

A re-evaluation of *Khoratpithecus piriyai* against large samples of extant orangutans representing multiple populations indicates that for the dimensions analyzed in this study, only  $M_3$  tooth dimensions and corpus width exceed the values observed based on sample ranges and 95% prediction intervals for extant orangutans. All other differences in tooth and jaw dimensions between *K. piriyai* and extant orangutans are allometric, and do not reflect proportion alterations independent of increase in jaw size. The authors (Chaimanee et al., 2004) correctly observe that *K. piriyai* does have a relatively high  $M_3$  robusticity index. However, data from this study demonstrate that the high robusticity index is explained by the thick  $M_3$  corpus, given that corpus depth at  $M_3$  is no greater than that observed in extant *Pongo*.  $M_3$  corpus width and  $M_3$  buccolingual width are significantly correlated in extant *Pongo* (Fig. 6e), suggesting that at least some of the thickness of the  $M_3$  corpus can be explained by molar width. It therefore seems reasonable to hypothesize that some of the thickness of the mandibular corpus in *K. piriyai* may also be explained by the enlarged  $M_3$ . It is noteworthy that in *K. piriyai*, the anterior margin of the ascending mandibular ramus is positioned at the level of the  $M_3$ , as it is in some extant *Pongo* (Taylor, unpublished data); this position is likely to inflate the estimate of corpus width in this region. Using a finite element approach to model the biomechanical performance of molars, Macho and Spears (1999) suggest that compared to humans and *Pan*, the posterior molars in *Pongo* appear better suited to resisting loads than the first molar. These findings may be relevant to the enlarged  $M_3$  in *K. piriyai*, and have implications for postcanine masticatory behavior in fossil *Pongo*.

The Hoa Binh specimen is absolutely larger in all dimensions compared to extant female orangutans based on observed sample ranges, and presumably larger than *Khoratpithecus piriyai*.<sup>6</sup> However, in bizygomatic and bicondylar breadths, the Hoa Binh specimen falls within the 95% prediction intervals for an extant female orangutan extrapolated to larger mandibular size. Thus, as was the case for *K. piriyai*, differences in bicondylar and bizygomatic breadths between the Hoa Binh subfossil and extant orangutans are likely accounted

for by differences in size. The difference between bizygomatic and bicondylar breadths (the masseter insertion angle) has been used as an estimate of the horizontally-directed masseter adductor muscle force (Antón, 1996; Taylor, 2002), which should influence the amount of axial torsion along the postcanine corpus (Hylander, 1985). The masseter insertion angle for the Hoa Binh specimen also falls within the 95% prediction intervals for extant female *Pongo* (Fig. 8c), suggesting that torsional loads incurred along the postcanine corpus are what would be expected for an extant orangutan of comparable jaw length.

In sum, there is little evidence to indicate that *Khoratpithecus piriyai* differs in mandibular proportions from extant *Pongo*, independent of the effects of increase or decrease in jaw size. Therefore, *K. piriyai* appears to have had load resistance abilities comparable to those of extant orangutans. Paleoenvironmental evidence indicates that *K. piriyai* evolved in a more tropical environment than either *Lufengpithecus* or *Sivapithecus* (Chaimanee et al., 2004). The similarity in jaw proportions between *P. abelii* and *K. piriyai*, coupled with the latter's tropical environment, suggest that *K. piriyai* may have been less able to resist repetitive or large loads than extant Bornean orangutans, and may have been characterized by a diet more similar to that of *P. abelii* than *P. p. morio*.

### Conclusions

Orangutan populations differ in their capacity to counter large and/or repetitive loads during mastication and incision. These differences in load resistance abilities may be linked to variation in feeding behavior and diet, and account for some of the previously observed intra- and inter-island variation in skull morphology (e.g., Courtenay et al., 1988; Uchida, 1996). A re-evaluation of *Khoratpithecus piriyai* and the Hoa Binh subfossil orangutan against large samples of extant *Pongo* indicates that the fossil taxa exhibit jaw and skull proportions (both observed and predicted) that would be expected for an extant orangutan of comparable jaw size. The similarity in jaw proportions between *K. piriyai* and *P. abelii* indicate that *K. piriyai* was less able to resist incisal or masticatory loads than extant Bornean orangutans. In conjunction with the paleogeographic evidence in support of a relatively tropical environment, results suggest that *K. piriyai* may have been dietarily more similar to *P. abelii* than to *P. p. morio*.

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<sup>6</sup> The absence of published values for similarly defined skull or mandibular measurements makes it impossible to compare any specific dimension between *K. piriyai* and the Hoa Binh specimen.  $P_4 - M_2$  mesiodistal dimensions are larger in the Hoa Binh specimen. No sex is suggested for *K. piriyai* by the authors, but the published value for mesiodistal length of the lower canine (13.71 mm) is very close to the mean value for extant male *Pongo* ( $x = 13.66$  mm,  $sd = 1.4$ ,  $n = 88$ ), and would represent the second largest outlier when compared to extant female *Pongo* ( $x = 10.27$  mm,  $sd = 1.1$ ,  $n = 99$ ). Taken together, these data suggest that the female Hoa Binh specimen is larger than *K. piriyai*.

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