Craniodental Sexual Dimorphism Among Hylobatids

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Abstract

Sexual dimorphism has been widely documented in primates, however craniodental sexual dimorphism among hylobatids has not been well researched. In this study, I investigate interspecific differences in the presence and pattern of craniodental sexual dimorphism among gibbons and siamang using data taken from eight species representing all four hylobatid genera (*Hoolock leuconedys*, *Hylobates agilis*, *Hy. klossi*, *Hy. lar*, *Hy. muelleri*, *Hy. pileatus*, *Nomascus gabriellae*, and *Symphalangus syndactylus*). I sampled 17-30 cranial specimens for each species. I quantified cranio-facial and upper canine crown height dimorphism using morphometric data taken from 3D surface models and directly from dry specimens to examine the presence and pattern of craniodental sexual dimorphism among hylobatids. *Hoolock leuconedys* shows statistically significant sex differences across all craniofacial shape and form measures investigated. Although *Hy. lar*, *Ho. leuconedys*, and *S. syndactylus* all show statistically significant cranial form dimorphism, there are interspecific differences in how this dimorphism is expressed. *Hoolock leuconedys*, *Hy. lar*, and *S. syndactylus* are unique in showing upper canine crown height dimorphism, and *Ho. leuconedys* show a high level of browridge dimorphism in which white fur highlights this region in males, in contrast to their black body and facial pelage. The finding of male-biased sexual dimorphism in only some hylobatid taxa suggests that although male craniofacial morphology of some gibbon and siamang species may be associated with sex-specific agonistic interactions, this effect is not ubiquitous among hylobatids. Further research is required to understand these findings in the context of the socioecology of individual hylobatid taxa.

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Introduction

Sexual dimorphism (i.e., the morphological differences between males and females) has been widely documented in the primate order, with most primate taxa showing sex differences in body mass, skeletal morphology, canine size, or soft tissue (Balolia *et al.* 2013, 2017; Clutton-Brock *et al.* 1977; Cobb and O'Higgins 2007; Dixson *et al.* 2005; Gordon 2006; Hens 2002, 2003, 2005; Kay *et al.* 1988; Leutenegger and Cheverud 1982; Leutenegger and Kelly 1977; Leutenegger and Masterson 1989a,b; Leutenegger and Shell 1987; Lockwood 1999; Lynch-Alfaro 2012; Masterson and Leutenegger 1990, 1992; Mitani *et al.* 1996; O'Higgins *et al.* 1990a,b, 1993; Oxnard 1983; Plavcan 2001, 2002, 2004, 2011, 2012; Plavcan and van Schaik 1992, 1993, 1997; Schaefer *et al.* 2004; Wood 1976; Wood *et al.* 1991). Among sexually dimorphic anthropoids, males tend to be the larger sex and the degree of sexual size differences among taxa varies largely in response to socioecological factors (Clutton-Brock *et al.* 1977; Leutenegger and Cheverud 1982; Leutenegger and Kelly 1977; Mitani *et al.* 1996; Plavcan 2004, 2012; Plavcan and van Schaik 1992, 1997). These studies show that variation in sexual body size and canine dimorphism is associated with various surrogate measures of sexual selection including breeding system, male contest competition, socionomic sex ratio, and operational sex ratios. The nature of female relationships can also influence the degree of sexual size dimorphism, where selection for larger body size among females is associated with competition for ecological resources (Gordon 2006; Leigh and Shea 1995; Lindenfors 2002; Martin *et al.* 1994). Alternatively, smaller female body size may be selected for based on conferred advantages such as faster or earlier breeding and fewer metabolic demands associated with a larger body size (Clutton-Brock and Huchard 2013; Plavcan 2011; Tobias *et al.* 2012).

Sexual dimorphism in the skull and dentition has been widely documented among the great apes, with low to moderate craniofacial dimorphism observed in *Pan paniscus* and *Pan troglodytes*, in contrast to *Gorilla* spp. and *Pongo* spp., who show a high degree of craniofacial size dimorphism (Balolia *et al.* 2013, 2017; Cobb and O'Higgins 2007; Hens 2002, 2003, 2005; Lockwood 1999; Masterson and Leutenegger 1990, 1992; O'Higgins *et al.* 1990a,b, 1993; Plavcan and van Schaik 1992; Schaefer *et al.* 2004; Wood 1976; Wood *et al.* 1991). A similar trend exists for body mass dimorphism among the apes, with *Pan* showing moderate body mass dimorphism, whereas *Gorilla* and *Pongo* show substantial body mass dimorphism (Leutenegger and Cheverud 1982; Leutenegger and Kelley 1977; Plavcan and van Schaik 1997). The pattern of canine dimorphism among these taxa is also similar, with the lowest degree of sexual dimorphism observed in *Pan paniscus*, and more pronounced canine dimorphism observed in *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus* (Leutenegger and Cheverud 1982; Leutenegger and Kelley 1977; Plavcan and van Schaik 1992).

Compared to research documenting craniodental dimorphism among the great apes, sexual dimorphism among hylobatids has been less well studied. This is likely because although the relevance of studying the great apes in the context of human evolution is well established based on their larger bodies and close phylogenetic relationships with hominins, the derived nature of the small apes has made their relevance to understanding human origins less clear (Zichello 2018). Research conducted to date indicates that the hylobatids show slight craniofacial sexual dimorphism relative to the great apes (Plavcan 2001). Among hylobatids, male size exceeds female size for the majority of

documented craniofacial measures among *Hoolock hoolock*, *Hylobates agilis*, *Hy. klossii*, *Hy. lar*, *Hy. moloch*, *Hy. muelleri*, *Hy. pileatus*, *Nomascus concolor*, and *Symphalangus syndactylus* (Electronic Supplementary Material [ESM] Table SI; Balolia *et al*. 2013; Creel and Preuschoft 1976, 1984; Plavcan 2002; Schultz 1940, 1941, 1944, 1962, 1973). For a minority of craniofacial measures, female size exceeds male size among *Ho. hoolock*, *Hy. lar*, *Hy. moloch*, *Hy. pileatus*, and *S. syndactylus*, and several measures among *Hy. lar*, *Hy. moloch*, *Hy. muelleri*, *Hy. pileatus*, *N. concolor*, and *S. syndactylus* are monomorphic (Creel and Preuschoft 1976, 1984; Schultz 1973). Male upper canine crown height exceeds female crown height among *Ho. hoolock*, *Hy. agilis*, *Hy. klossii*, *Hy. lar*, *Hy. moloch*, *Hy. muelleri*, *Hy. pileatus*, *N. concolor*, and *S. syndactylus* (Frisch 1963, 1973; Plavcan 2004; Plavcan and van Schaik 1992; Schultz 1973). There are no documented instances in which male upper canine crown height is equal to, or lower than, female upper canine crown height among hylobatids (ESM Table SII). In assessing the strength of evidence for craniodental dimorphism among hylobatids, the craniodental sexual dimorphism estimates that have been published have not been tested for statistical significance (the published data consist of species averages only), and some sexual dimorphism estimates are based on relatively small sample sizes (ESM Tables SI and SII).

Creel and Preuschoft were the first researchers to test the statistical significance of craniofacial dimorphism estimates among hylobatids (Creel and Preuschoft 1976). Based on a dataset of 90 craniofacial landmarks, these authors report that regional samples of 10 hylobatid species (*S. syndactylus*, *Hy. muelleri*, *Hy. agilis*, *Hy. lar entelloides*, *Ho. hoolock*, *N. concolor*, *Hy. klossi*, *Hy. moloch*, *Hy. lar vestitus*, *Hy. pileatus*) show statistically significant variance–covariance matrix male–female distances, noting that the sample for each species comprises individuals from more than one breeding population, and where some researchers recognize more than one subspecies being included in some taxonomic samples. When conducting their analyses, these authors used an α level of $P < 0.1$, which exceeds today's accepted threshold for statistical significance, and used an equation to correct for sample size. Following the application of this equation, male–female distances were recorded as zero in the variance-covariance matrix for *Hy. klossii*, *Hy. lar vestitus*, and *Hy. pileatus* (Creel and Preuschoft 1976). Using the same taxonomic samples, the authors of this study further show that intersexual craniofacial differences are negligible in comparison to interspecific differences, and discriminant function analyses show sexual dimorphism among all hylobatid groups, where *S. syndactylus* show the most pronounced male-biased sexual dimorphism (males are larger and more robust than females), and *Hy. pileatus* show the opposite pattern (female mean scores exceed male mean scores) (Creel and Preuschoft 1976). Considering all hylobatids together, these authors show that males, relative to females, show tendencies toward a taller face, a longer and narrower cranial vault, more forward protrusion of the bony bar forming the lateral border of the orbit, a more robust zygomatic arch, more pronounced supramastoid crests, and larger canines (Creel and Preuschoft 1976). More recently, researchers found that although young *Hy. lar* adults show significant sexual dimorphism in linear measurements of craniofacial size (male size exceeds female size), older adults do not due to female craniofacial growth throughout adult life (Balolia *et al*. 2013). To date, the presence of canine crown height dimorphism among hylobatids has not been tested for statistically (ESM Table SII).

In addition to hard tissue dimorphism, there is evidence of sexual dimorphism in the soft tissue of hylobatids. Sexual dichromatism has been well documented in some hylobatid taxa, with sex-specific pelage color differences observed in three of the four known hylobatid genera (Bradley and Mundy 2008; Groves 1972; Ma *et al.* 1988; Mootnick 2006; Mootnick and Fan 2011). All known *Nomascus* and *Hoolock* species are sexually dichromatic; by contrast, *Hylobates* species show no substantial pelage sex differences, except for *Hy. pileatus* (Mootnick 2006; Mootnick and Fan 2011). All four hylobatid genera show interspecific variation in light facial markings (Geissmann 1993, 2003), but there is currently no consensus as to why facial markings vary among species, or what role sexual dichromatism plays among the hylobatids. Some researchers have suggested that sex differences in pelage coloration in primates are associated with sexual selection or act as indicators of sexual maturity, specifically in the context of dark pelage in males (Bradley and Mundy 2008; Gerald 2003; Neville *et al.* 1988). Alternatively, research suggests that the lighter colored pelage observed in *Hoolock* and *Nomascus* females may be associated with camouflage for the adult females themselves in lightly colored branches, or to camouflage their lightly colored offspring (Mootnick and Fan 2011). Although the selective pressures surrounding the presence and pattern of sexual dichromatism in hylobatids are yet to be elucidated, sex-specific selection exists for pelage and facial coloration among some hylobatid taxa. It is possible that hard tissue morphology in the hylobatid facial skeleton may respond to similar selective pressures.

Although previous studies have shown evidence of slight craniofacial and canine crown height dimorphism among hylobatid taxa (Balolia *et al.* 2013; Creel and Preuschoft 1976, 1984; Frisch 1963, 1973; Plavcan 2002, 2004; Plavcan and van Schaik 1992; Schultz 1940, 1941, 1944, 1962, 1973), no study has provided a detailed quantitative analysis of variation in the magnitude and pattern of craniodental dimorphism among hylobatids. In the present study, I assess whether there is interspecific variation in the presence and pattern of craniodental sexual dimorphism among hylobatids. I quantify craniofacial and upper canine crown height sexual dimorphism among eight hylobatid species (*Ho. leuconedys*, *Hy. agilis*, *Hy. klossi*, *Hy. lar*, *Hy. muelleri*, *Hy. pileatus*, *N. gabriellae*, and *S. syndactylus*). For taxa showing sex differences in cranial and facial form, I investigate whether sexual dimorphism is expressed as size or shape dimorphism, or a combination of both. I further investigate whether there are interspecific differences in the presence of canine dimorphism among hylobatid taxa. Given the well-established association between the degree of sexual size dimorphism and the nature of male intrasexual relationships among primates, findings of interspecific variation in the presence and pattern of craniodental sexual dimorphism among hylobatids would improve our understanding of selection on craniodental morphology in gibbons and siamang in response to socioecological variables.

Methods

Specimens

The sample consists of 187 dentally mature specimens belonging to eight hylobatid species, representing all four hylobatid genera (Table I). I only included specimens with

light or moderate canine wear for canine dimorphism analyses. I or J. Michael Plavcan obtained sex information from museum records and confirmed this using pelage coloration where available.

3D Scanning and Processing

I obtained 3D surface models for five of the eight hylobatid species (*Ho. leuconedys*, *Hy. lar*, *Hy. muelleri*, *N. gabriellae*, *S. syndactylus*) using a NextEngine 2020i Desktop scanner, a Creaform Go!Scan 20 or from CT data. I processed 3D surface scan data using each scanner's proprietary software. All specimens were scanned at a resolution of <0.5 mm. Differences in how 3D models were generated are unlikely to have produced substantial measurement error (Balolia and Massey 2021; Fruciano *et al.* 2017; Marcy *et al.* 2018).

Table I Geographical locations, repositories, and sex breakdown of the hylobatid specimens used in the present study

Species	Males	Females	Geographical location	Repository
Hoolock leuconedys	15	15	Myanmar: Kachin and Sagaing (East Bank)	Natural History Museum, London; American Museum of Natural History, New York
Hylobates agilis	16	9	Sumatra: Boekit	American Museum of Natural History, New York
Hylobates klossi	13	12	Indonesia, Mentawi Islands, South Pagi	Natural History Museum, London; American Museum of Natural History, New York; Smithsonian National Museum of Natural History, Washington, DC; Field Museum of Natural History, Chicago; Museum of Comparative Zoology, Harvard
Hylobates lar	14	11	Myanmar and Thailand	Natural History Museum, London; American Museum of Natural History, New York; Smithsonian National Museum of Natural History Washington, DC
Hylobates muelleri	10	13	Malaysia: Sarawak and Sabah	Field Museum of Natural History, Chicago
Hylobates pileatus	9	8	Cambodia and Thailand	Natural History Museum, London; Smithsonian National Museum of Natural History Washington DC; Natural History Museum, Stockholm; Institute for Anthropology, University of Zurich; Rijksmuseum van Natuurlijk Histoire, Leiden
Nomascus gabriellae	8	8	Vietnam and Laos	Natural History Museum, London; American Museum of Natural History, Field Museum of Natural History, Chicago
Symphalangus syndactylus	13	13	Indonesia: Sumatra	Natural History Museum, London; American Museum of Natural History, New York; Smithsonian National Museum of Natural History Washington, DC

Data Collection and Craniodental Measures

Craniofacial Form and Shape I obtained craniofacial form and craniofacial shape data for *Ho. leuconedys*, *Hy. lar*, *Hy. muelleri*, *N. gabriellae*, and *S. syndactylus* from 3D landmarks using Stratovan Checkpoint v. 2017.03.03.0771. I quantified cranial form and shape using 27 cranial landmarks and I quantified facial form and shape using 20 facial landmarks (Table II, Fig. 1).

Craniofacial size and canine crown height For the five hylobatid taxa for which 3D surface models were available (*Ho. leuconedys*, *Hy. lar*, *Hy. muelleri*, *N. gabriellae*, *S. syndactylus*), I collected 20 craniodental linear measurements from 3D landmarks using Stratovan Checkpoint v. 2017.03.03.0771 (Table III). For bilateral measurements (orbital breadth, orbital height, vertical thickness of the supraorbital torus, and canine crown height), I took measurements from both the left and right side. For craniofacial measures, I included the measurements taken from the side with the highest number of well-preserved specimens in statistical analyses. For analyses of canine crown height, I included the maximum upper canine crown height value (i.e., the tooth exhibiting the least amount of dental wear) for each specimen. I collected linear measurements for these five taxa by calculating the interlandmark distances of 3D landmarks obtained from 3D surface models using Microsoft Excel for Office 365 MSO (16.0.12527.20612) (Table III).

To increase the hylobatid taxonomic sample, I obtained additional craniodental data for *Hy. klossi*, *Hy. pileatus*, and *Hy. agilis* specimens from J. Michael Plavcan (Plavcan 1990, 2002, 2003). I used up to nine craniodental linear measurements for each specimen from these datasets (Table III). J. Michael Plavcan collected craniofacial linear measurements using a pair of Fowler digital calipers (Plavcan 2002). The definitions for craniofacial measurements for the dataset compiled using digital calipers refer to the same measurement termination points as those taken by calculating the interlandmark distance of 3D landmarks (Plavcan 2003; Table III). Combining caliper measurements with those taken from 3D surface models is unlikely to introduce error based on the size of specimens being used in this study and the resolution at which these specimens were scanned (Balolia and Massey 2021). J. Michael Plavcan collected canine crown height measurements using a calibrated reticle in the eyepiece of a Wild binocular microscope (Plavcan 1990). The dental measurements derived from this device are comparable to those made using standard calipers, and the differences in data collection technique to the landmark-based approach adopted here are unlikely to introduce error into the combined sample. J. Michael Plavcan measured canine crown height as the distance from the cemento-enamel junction to the apex of the tooth on the mesiobuccal face of the tooth (Plavcan 1990), which is almost identical to the canine crown height measurement using the interlandmark distance (Table III). I quantified cranial size for the seven hylobatid taxa for which craniofacial data were available using the geometric mean of eight linear measurements (Table III). Similarly, I quantified facial size for these same seven hylobatid taxa using the geometric mean of six linear measurements (Table III). I performed geometric mean calculations in Microsoft Excel for Office 365 MSO (16.0.12527.20612).

Cranial Form and Shape Analysis

For the five hylobatid taxa for which 3D surface models were available (*Ho. leuconedys*, *Hy. lar*, *Hy. muelleri*, *N. gabriellae*, *S. syndactylus*), I quantified

Table II 3D landmarks used to quantify craniofacial form and shape in five hylobatid taxa (*Hoolock leuconedys*, *Hylobates lar*, *Hy. muelleri*, *Nomascus gabriellae*, *Symphalangus syndactylus*). Landmarks are depicted in Fig. 1

LM no.	Landmark and definition	Cranial form and shape	Facial form and shape
1	Glabella: the most anterior point between the orbits	X	X
2	Nasospinale: the point on the lower rim of the nasal cavity	X	X
3	Prosthion: the most anterior point on the premaxilla between the two central incisors	X	X
4	Staphylion: the point on the median palatine suture that crosses a line drawn from the deepest part of the arches of the horizontal plate of the palatine bones, or the most posterior point of the median palatine suture when no arches are present	X	X
5	Basion: the anteriormost point of the foramen magnum	X	
6	Opisthion: the posteriormost point of the foramen magnum	X	
7	Opisthocranion: the most posterior point of the cranium at the Frankfurt horizontal	X	
8	Superior cranial vault: the point on the sagittal plane of the cranial vault that intersects with the posterior limits of the zygomatic process in Frankfurt horizontal	X	
9	Point of maximal curvature on the outer orbital rim (lateral) (left)	X	X
10	Point of maximal curvature on the inner orbital rim (lateral) (left)	X	X
11	Point of maximal curvature on the inner orbital rim (medial) (left)	X	X
12	The most superior point on the upper orbital rim (left)	X	X
13	The most superior point on the supraorbital torus, perpendicular to the most superior point on the upper orbital rim	X	X
14	The most inferior point on the lower orbital rim, perpendicular to the most superior point on the upper orbital rim	X	X
15	The point corresponding to the largest width of the piriform aperture (left)	X	X
16	Maximum curvature of the anterior upper margin of the zygomatic arch (left)	X	X
17	The most inferior termination point of the zygomaticomaxillary suture (left)	X	X
18	Anterior limit of the zygomatic process (left)	X	X
19	The most anterior point on the buccal side of the canine alveolus, projected onto the alveolar margin (left)	X	X
20	The most distal point on the buccal side of the canine alveolus, projected onto the alveolar margin (left)	X	X
21	The most mesial point on the alveolar margin of the buccal side of the fourth premolar (left)	X	X
22	Midpoint of the alveolar margin of the buccal side of the upper M1 (left)	X	X
23	Midpoint of the alveolar margin of the buccal side of the upper M2 (left)	X	X
24	Midpoint of the alveolar margin of the buccal side of the upper M3 (left)	X	X
25	Midpoint of the zygomatic arch at the widest point (left)	X	
26	Porion: the most superior and lateral point of the external auditory meatus (left)	X	
27	Maximum curvature of the lateral edge of the foramen magnum (left)	X	

craniofacial shape and form using Generalized Procrustes Analysis (GPA) on 3D landmarks for each taxon separately. For shape analyses, I scaled 3D landmarks to a standard centroid size, and translated and rotated them to minimize the squared distance
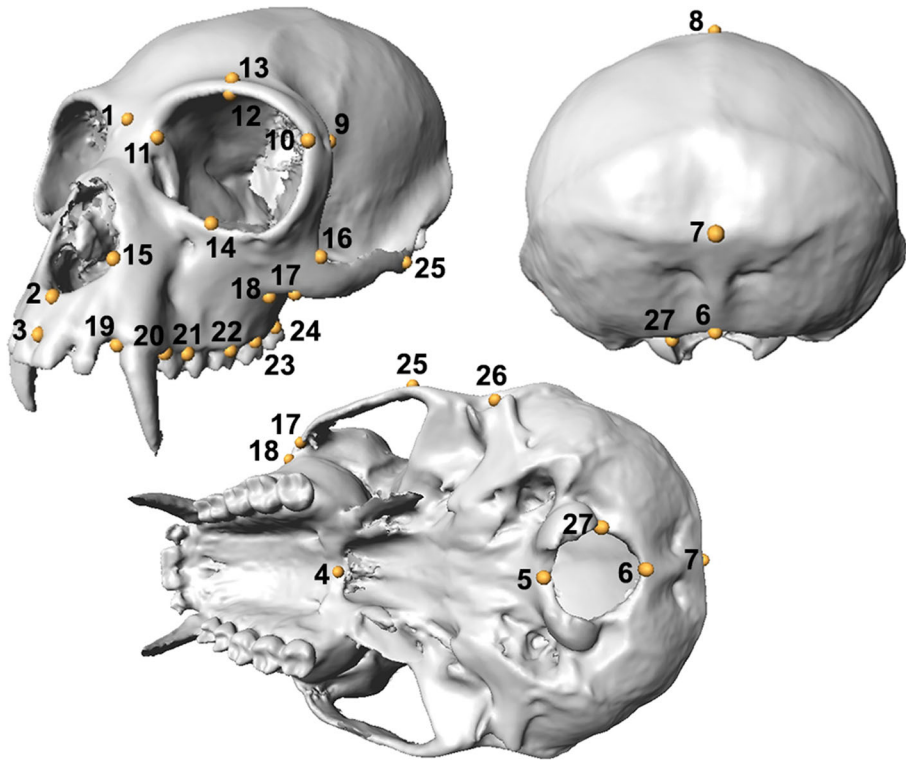
Fig. 1 3D landmarks used to quantify craniofacial shape and form, applied to a *Hoolock leuconedys* 3D surface model. Landmarks are defined in Table II.

between landmark sets (Baab *et al.*, 2012; Rohlf and Slice, 1990). For form analyses, I included the natural log of centroid size as part of the GPA. I performed Principal Components Analysis (PCA) to obtain Principal Component (PC) scores. I used these PC scores to conduct Discriminant Function Analysis (DFA) and to visualize the data in form space (PC1 vs. PC2) for sexually dimorphic species. I conducted GPAs and PCAs using the EVAN Toolbox v. 1.71.

Sexual Dimorphism Quantification and Analysis

I quantified sexual size dimorphism using the index of sexual dimorphism (ISD = male mean/female mean) and tested for statistically significant sexual size dimorphism using Student's *t*-tests. I tested for statistically significant craniofacial form dimorphism by conducting Students' *t*-tests on PC1 scores obtained using the form analysis described in the previous section. I performed Student's *t*-tests using SPSS v. 26. I did not calculate sexual form dimorphism estimates because calculating the ISD based on the male and female mean PC scores used for significance testing does not provide meaningful sexual dimorphism estimates. I used Bonferroni corrections to account for the possibility that multiple *t*-tests of sexual dimorphism yield significant *P* values (i.e., are a result of type I error).

Table III Linear measurement definitions and measurements used for composite size variables and independent cranial measurements analyses

Measurement	Definition	Cranial size	Facial size
Superior facial breadth (SUFB)[a]	The distance between the left and right points of maximal curvature on the outer orbital rim		
Biorbital breadth (BOBR)[b]	The distance between the left and right points of maximal curvature on the lateral inner orbital rim (alternatively defined as biorb: Plavcan 2003)	X	X
Interorbital breadth (IOBR)[b]	The distance between the left and right points of maximal curvature on the medial inner orbital rim (alternatively defined as interorb: Plavcan 2003)	X	X
Orbital breadth (ORBR)[a]	The distance between the point of maximal curvature on the medial inner orbital rim and the lateral medial inner orbital rim		
Bimaxillary breadth (BMBR)[a]	The distance between the left and right most inferior termination point of the zygomaticomaxillary suture		
Bizygomatic breadth (BZBR)[b]	The distance between the left and right midpoints of the zygomatic arch at the widest point (alternatively defined as bizyg-br: Plavcan 2003)	X	X
Nasal breadth (NABR)[a]	The maximum breadth of the piriform aperture		
Anterior maxillary breadth (AMBR)[b]	The maxillary breadth at the most distal point on the buccal side of the canine alveolus, projected onto the alveolar margin (alternatively defined as bicanine: Plavcan 2003)	X	X
Posterior maxillary breadth (PMBR)[a]	The maxillary breadth at the midpoint of the alveolar margin on the M2 buccal side		
Porion breadth (PORB)[a]	The distance between left and right porion		
Foramen magnum breadth (FMBR)[a]	The distance between the left and right points of maximum curvature of the lateral edge of the foramen magnum		
Orbital height (ORBH)[b]	The distance between the most superior point on the upper orbital rim and the most inferior point on the lower orbital rim, measured perpendicularly (alternatively defined as orb-hgt: Plavcan 2003)	X	X
Glabellar height (GLAH)[b]	The distance between glabella and prosthion (alternatively defined as face-hgt: Plavcan 2003)	X	X
Alveolar height (ALVH)[a]	The distance between nasospinale and prosthion		
Palate length (PALE)[b]	The distance between prosthion and staphylion (alternatively defined as pal-ln: Plavcan 2003)	X	
Vertical thickness of supraorbital torus (VTST)[a]	The distance between the most superior point on the upper orbital rim and the most superior point on the supraorbital torus		
Foramen magnum length (FMLE)[a]	The distance between basion and opisthion		
Cranial height (CRAH)[a]	The distance between basion and the point on the sagittal plane of the cranial vault that intersects with the posterior limits of the zygomatic process in Frankfurt horizontal		
Cranial length (CRAL)[b]	The distance between glabella and opisthion (alternatively defined as neuro-ln: Plavcan 2003)	X	
Canine crown height (CANHEIGHT)[c]	The distance between the midpoint on the labial surface of the canine crown, at the alveolar margin and the most inferior point of the canine crown (canine tip)		

[a] *Hoolock leuconedys*, *Hylobates lar*, *Hy. muelleri*, *Nomascus gabriellae*, *Symphalangus syndactylus*.

[b] *Hoolock leuconedys*, *Hy. klossi*, *Hy. lar*, *Hy. muelleri*, *Hy. pileatus*, *N. gabriellae*, *S. syndactylus*.

[c] *Hoolock leuconedys*, *Hy. agilis*, *Hy. klossi*, *Hy. lar*, *Hy. muelleri*, *N. gabriellae*, *S. syndactylus*.

I calculated sexual shape dimorphism using the male–female Procrustes distance, i.e., the Procrustes distance between the male and female mean shapes, obtained using the GPA procedure described earlier. I used permutation tests (1000 permutations for each analysis) to statistically test for significant sex differences using software developed by the UCL Anatomy Department (Strand Viðarsdóttir *et al.* 2002).

I performed DFA to assess correct sex classification rates for craniofacial form. For each test, I included PCs representing at least 5% of the sample variation, which resulted in the inclusion of between five and seven PCs in each analysis, representing between 66% and 84% of the variation for each sample. I report "Leave-one-out" (i.e., cross-validated) classification results, which is the most conservative application of this test. I performed DFA analyses in SPSS v. 26.

Ethical Note

No ethical clearance was required for this study.

Data Availability The data set analyzed during the current study is available from the corresponding author on request.

Results

Craniofacial Form, Shape, and Size Dimorphism: Composite Measures

Of the five species for which craniofacial shape and form data are available, *Ho. leuconedys* shows statistically significant sex differences across all craniofacial shape and form measures investigated (male > female cranial and facial size by 5%) (Tables IV–VII). *Hylobates lar* and *S. syndactylus* also show cranial form dimorphism, which is driven by both size and shape in *Hy. lar* (male > female cranial size by 4%) and by size alone in *S. syndactylus* (male > female cranial size by 7%) (Tables IV and V). *Hylobates lar* shows facial shape dimorphism and *S. syndactylus* shows facial size dimorphism, similar to what is observed for the cranium (Tables VI and VII). Neither *Hy. muelleri* nor *N. gabriellae* show craniofacial size or shape dimorphism. Similarly, neither *Hy. klossi* nor *Hy. pileatus* show significant craniofacial size dimorphism (Tables IV–VII).

The three taxa for which cranial form dimorphism is found (*Ho. leuconedys*, *Hy. lar*, and *S. syndactylus*), are visibly separated by sex along the first two PCs (Fig. 2). These taxa show high correct sex classification rates of 88% (*Hy. lar*), 93% (*Ho. leuconedys*), and 85% (*S. syndactylus*). Shape differences include a wider and longer cranium in *Ho. leuconedys* and *Hy. lar* males, and a smaller face relative to cranial vault size in *Ho. leuconedys* females. *Hylobates muelleri* and *N. gabriellae*, which do not show statistically significant sex differences in either cranial or facial form, show relatively poor sex classification rates of 42.1% (*Hy. muelleri*) and 71.4% (*N. gabriellae*). These results are consistent with the observed lack of craniofacial form dimorphism in *Hy. muelleri* and *N. gabriellae* (Tables IV and VI). I did not conduct DFA for *Hy. klossi* or *Hy. pileatus*, as form data were not available for these taxa.

Table IV Hylobatid cranial form and shape sexual dimorphism. 3D landmarks used for cranial form and shape measures are provided in Table II

Species	Sex	N	PC1 scores (cranial form)		Student's *t-test* (male vs. female)			Male–female PD (cranial shape)	
			Mean	SD	t	df	P	PD	P
Hoolock leuconedys	Male	14	0.147	0.323	**3.029**	**25**	**0.006**	**0.0258**	**0.003**
	Female	13	−0.016	0.017					
Hylobates lar	Male	12	0.023	0.027	**4.662**	**19**	**<0.001**	**0.0447**	**<0.001**
	Female	9	−0.031	0.025					
Hylobates muelleri	Male	7	0.018	0.034	1.553	17	0.139	0.0267	0.286
	Female	12	−0.010	0.039					
Nomascus gabriellae	Male	6	−0.005	0.018	−0.542	12	0.598	0.0317	0.17
	Female	8	0.004	0.037					
Symphalangus syndactylus	Male	9	0.028	0.027	**3.671**	**18**	**0.002**	0.0239	0.283
	Female	11	−0.023	0.034					

Significant results following correction for multiple comparisons and results that are significant based on results of permutation tests are presented in bold. PC1 = Principal Component 1; PD = Procrustes Distance.

Table V Hylobatid cranial size sexual dimorphism. Linear measurements used for cranial size measures are provided in Table III

Species	Sex	N	Geometric mean (cranial size)		ISD	Student's *t-test* (male vs. female)		
			Mean	SD		t	df	P
Hoolock leuconedys	Male	14	39.74	1.11	**1.05**	**4.835**	**23**	**< 0.001**
	Female	11	37.97	0.55				
Hylobates klossi	Male	12	34.45	0.88	1.02	1.382	19	0.183
	Female	9	33.89	0.99				
Hylobates lar	Male	9	37.97	0.84	**1.04**	**3.110**	**20**	**0.006**
	Female	13	36.51	1.21				
Hylobates muelleri	Male	6	36.66	1.03	1.04	1.877	16	0.079
	Female	12	35.30	1.60				
Hylobates pileatus	Male	9	36.04	1.08	1.02	1.271	14	0.225
	Female	7	35.38	0.96				
Nomascus gabriellae	Male	7	37.25	1.09	0.99	-0.748	13	0.468
	Female	8	37.70	1.23				
Symphalangus syndactylus	Male	9	45.04	1.08	**1.07**	**4.146**	**18**	**< 0.001**
	Female	11	42.29	1.73				

Significant results following correction for multiple comparisons are presented in bold. ISD = Index of Sexual Dimorphism; SD = Standard Deviation.

Table VI Hylobatid facial form and shape sexual dimorphism. 3D landmarks used for facial form and shape measures are provided in Table II

Species	Sex	N	PC1 scores (facial form)		Student's *t-test* (male vs. female)			Male–female PD (facial shape)	
			Mean	SD	t	df	P	PD	P
Hoolock leuconedys	Male	14	0.018	0.033	**3.199**	**25**	**0.004**	**0.0299**	**0.033**
	Female	13	−0.019	0.267					
Hylobates lar	Male	12	0.020	0.028	**3.096**	**21**	**0.005**	0.0331	0.227
	Female	11	−0.022	0.038					
Hylobates muelleri	Male	10	−0.019	0.042	−1.694	21	0.105	0.0243	0.873
	Female	13	0.014	0.049					
Nomascus gabriellae	Male	7	0.010	0.017	0.868	13	0.401	0.0362	0.167
	Female	8	−0.008	0.053					
Symphalangus syndactylus	Male	11	0.222	0.038	1.955	21	0.064	0.0304	0.276
	Female	12	−0.012	0.046					

Significant results following correction for multiple comparisons and results that are significant based on results of permutation tests are presented in bold. PC1 = Principal Component 1; PD = Procrustes Distance.

Table VII Hylobatid facial size sexual dimorphism. Linear measurements used for facial size measures are provided in Table III

Species	Sex	N	Geometric mean (facial size)		ISD	Student's *t-test* (male vs. female)		
			Mean	SD		t	df	P
Hoolock leuconedys	Male	15	34.63	0.99	**1.05**	**5.250**	**24**	**<0.001**
	Female	11	32.84	0.63				
Hylobates klossi	Male	12	29.98	0.93	1.02	1.386	19	0.182
	Female	9	29.40	0.94				
Hylobates lar	Male	9	33.25	1.00	1.04	2.735	20	0.013
	Female	13	31.90	1.22				
Hylobates muelleri	Male	8	31.94	0.99	1.04	2.059	18	0.054
	Female	12	30.72	1.47				
Hylobates pileatus	Male	9	31.37	1.10	1.02	1.266	14	0.226
	Female	7	30.72	0.92				
Nomascus gabriellae	Male	7	32.35	1.04	0.99	−0.560	13	0.585
	Female	8	32.68	1.20				
Symphalangus syndactylus	Male	12	38.66	1.22	**1.07**	**4.131**	**21**	**<0.001**
	Female	11	36.34	1.46				

Significant results following correction for multiple comparisons are presented in bold. ISD = Index of Sexual Dimorphism; SD = Standard Deviation.

Craniofacial Size Dimorphism: Individual Measurements

Three out of the seven taxa for which craniofacial measurements were available show sexual size dimorphism for individual cranial measurements (Table VIII). *Hoolock leuconedys* shows statistically significant sexual dimorphism for 6 of 19 individual craniofacial size measurements. Five of these measurements represent craniofacial breadth (superior facial breadth, biorbital breadth, interorbital breadth, bizygomatic breadth, and posterior maxillary breadth) and one measurement quantifies supraorbital thickness (Table VIII). *Hoolock leuconedys* show particularly high ISD values for browridge thickness and the interorbital region (ISD = 1.24 and ISD = 1.12 respectively). I found statistically significant sexual dimorphism for bizygomatic breadth in *S. syndactylus*, and for anterior maxillary breadth in *Hy. pileatus*, with male size exceeding female size for both of these measurements (Table VIII). Interpretations of these statistical test results that do not correct for multiple comparisons show that sexual dimorphism may exist for other craniofacial dimensions, particularly those associated with facial breadth in *Ho. leuconedys*, *Hy. klossi*, *Hy. lar*, and *S. syndactylus*. Similarly, interpretations of these statistical tests results that do not correct for multiple comparisons also show browridge thickness and interorbital region sexual dimorphism in *S. syndactylus* (ISD = 1.32 and ISD = 1.13 respectively), indicating a similar pattern of dimorphism to what is found in *Ho. leuconedys* in the upper facial region. This less conservative interpretation of results also suggests the presence of glabellar and alveolar height sexual dimorphism in *Ho. leuconedys* and *Hy. lar* and negative sexual dimorphism for orbital height (i.e., female size exceeds male size) in *N. gabriellae* and *S. syndactylus* (Table VIII). Consistent with the results of
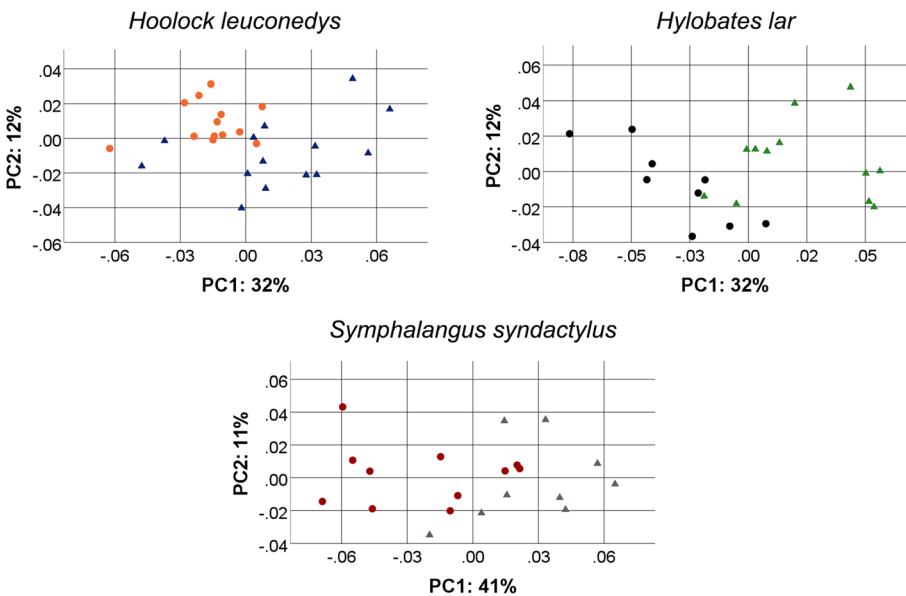

Fig. 2 Cranial form sexual dimorphism in *Hoolock leuconedys*, *Hylobates lar*, and *Symphalangus syndactylus*. *Hoolock leuconedys*: males = blue triangles, females = orange circles; *Hylobates lar*: males = green triangles, females = black circles; *Symphalangus syndactylus*: males = gray triangles, females = red circles. PC = Principal Component.

form and shape analyses previously described, these combined results show interspecific differences in the pattern of sexual dimorphism across craniofacial regions among hylobatids.

Canine Crown Height Dimorphism *Hoolock leuconedys*, *Hy. lar*, and *S. syndactylus* show statistically significant canine crown height dimorphism, with male canine crown height exceeding female canine crown height by 12% for *Ho. leuconedys*, 19% for *Hy. lar*, and 20% for *S. syndactylus* (Fig. 2, Table IX). Statistically significant canine crown height dimorphism is not detected in any other hylobatid species (Table IX).

Discussion

The results of this study show that there is interspecific variation in the presence and pattern of craniodental sexual dimorphism among hylobatids. *Hoolock leuconedys* ubiquitously shows craniofacial size and shape across all composite measures and canine crown height dimorphism, and shows sexual size dimorphism in six individual craniofacial measurements. *Hylobates lar* and *S. syndactylus* also show clear craniofacial dimorphism, where craniofacial form dimorphism among *Ho. leuconedys*, *Hy. lar*, and *S. syndactylus* are differentially driven by size, shape, or a combination of both. *Hoolock leuconedys*, *Hy. lar*, and *S. syndactylus* are the only three taxa to show significant canine crown height dimorphism, and no other hylobatid taxon shows notable sexual dimorphism for any other craniofacial measure. The finding of a relatively high magnitude of sexual dimorphism in *S. syndactylus* (males are 7% larger than females) is consistent with results of pronounced sexual dimorphism in this taxon relative to other hylobatids (Creel and Preuschoft 1976). Similarly, the finding of no significant sexual size dimorphism in the *Hy. lar* facial skeleton is consistent with findings of no significant sexual dimorphism in a dentally mature *Hy. lar* sample (Balolia *et al.* 2013).

Together, the results of this study show that the presence and pattern of craniodental dimorphism among gibbons and siamang is more diverse than had been previously recognized and suggest that sex-specific selection pressures on craniodental morphology are not uniform across hylobatid groups. This notion can be further considered in the context of ecological and behavioral complexity, flexibility in grouping patterns, and social behavioral plasticity observed among hylobatid taxa (Fuentes 2000; Malone and Fuentes 2009; Morino 2009; Palombit 1996). Under an ecological model of behavioral flexibility, even subtle differences in the Southeast Asian habitats occupied by hylobatids are likely to promote interspecific variation in the nature of their social relationships (Malone and Fuentes 2009; Palombit 1996; Wrangham 1979). The results of this study showing interspecific variation in craniofacial and canine crown height dimorphism is consistent with this proposition. Some authors have argued that the tendency to categorize hylobatids as territorial and pair-living has led to an underestimation of the degree of social variation among taxa, where social organization may be more accurately viewed as a more dynamic process than is currently recognized (Malone and Fuentes 2009; Palombit 1996). Understanding differences in the expression of hylobatid sexual dimorphism using a framework emphasizing that hylobatids

Table VIII Hylobatid sexual size dimorphism (individual measurements). Measurement definitions are provided in Table III. Descriptive statistics and full reporting of statistical test results are provided in ESM Table SIII

Measurement	Hoolock leuconedys	Hylobates klossi	Hylobates lar	Hylobates muelleri	Hylobates pileatus	Nomascus gabriellae	Symphalangus syndactylus
Superior facial breadth (SUFB)	**ISD = 1.06, p < 0.001**	N/A	ISD = 1.05, p = 0.012	ISD = 1.02, ns	N/A	ISD = 1.02, ns	ISD = 1.06, p = 0.008
Biorbital breadth (BOBR)	**ISD = 1.05, p < 0.001**	ISD = 1.02, ns	ISD = 1.04, ns	ISD = 1.02, ns	ISD = 1.01, ns	ISD = 0.99, ns	ISD = 1.03, ns
Interorbital breadth (IOBR)	**ISD = 1.12, p < 0.001**	ISD = 1.01, ns	ISD = 1.03, ns	ISD = 1.02, ns	ISD = 0.95, ns	ISD = 1.04, ns	ISD = 1.13, p = 0.016
Orbital breadth (ORBR)	ISD = 1.01, ns	N/A	ISD = 1.03, ns	ISD = 1.02, ns	N/A	ISD = 0.97, ns	ISD = 0.99, ns
Bimaxillary breadth (BMBR)	ISD = 1.05, p = 0.003	N/A	ISD = 1.02, ns	ISD = 1.03, ns	N/A	ISD = 1.02, ns	ISD = 1.03, ns
Bizygomatic breadth (BZBR)	**ISD = 1.07, p < 0.001**	ISD = 1.04, p = 0.017)	ISD = 1.05, p = 0.011	ISD = 0.93, ns	ISD = 1.05, ns	ISD = 1.03, ns	**ISD = 1.09, p < 0.001**
Nasal breadth (NABR)	ISD = 1.04, ns	N/A	ISD = 1.07, ns	ISD = 0.83, ns	N/A	ISD = 0.98, ns	ISD = 1.05, ns
Anterior maxillary breadth (AMBR)	ISD = 1.04, p = 0.009	ISD = 1.03, ns	ISD = 1.02, ns	ISD = 1.02, ns	ISD = 1.06, p < 0.001)	ISD = 0.97, ns	ISD = 1.04, p = 0.02
Posterior maxillary breadth (PMBR)	**ISD = 1.04, p = 0.002**	N/A	ISD = 1.04, ns	ISD = 1.02, ns	N/A	ISD = 0.96, ns	ISD = 1.01, ns
Porion breadth (POBR)	ISD = 1.04, p = 0.005)	N/A	ISD = 1.03, ns	ISD = 1.01, ns	N/A	ISD = 1.03, ns	ISD = 1.05, p = 0.022
Foramen magnum breadth (FMBR)	ISD = 1.03, ns	N/A	ISD = 1.03, ns	ISD = 1.14, ns	N/A	ISD = 1.01, ns	ISD = 0.94, ns
Orbital height (ORBH)	ISD = 1.02, ns	ISD = 1.00, ns	ISD = 1.00, ns	ISD = 0.99, ns	ISD = 1.04, ns	ISD = 0.95, p = 0.043)	ISD = 0.95, p = 0.029
Glabellar height (GLAH)	ISD = 1.05, p = 0.008	ISD = 1.03, ns	ISD = 1.06, p = 0.022	ISD = 1.05, ns	ISD = 1.03, ns	ISD = 0.98, ns	ISD = 1.04, ns
Alveolar height (ALVH)	ISD = 1.20, p = 0.015	N/A	ISD = 1.18, p = 0.048	ISD = 1.10, ns	N/A	ISD = 1.15, ns	ISD = 0.93, ns
Palate length (PALE)	ISD = 1.02, ns	ISD = 1.02, ns	ISD = 1.04, p = 0.011	ISD = 1.04, ns	ISD = 1.03, ns	ISD = 0.98, ns	ISD = 1.03, ns
Vertical thickness of supraorbital torus (VTST)	**ISD = 1.24, p < 0.001**	N/A	ISD = 1.11, ns	ISD = 1.00, ns	N/A	ISD = 1.10, ns	ISD = 1.32, p = 0.01
Foramen magnum length (FMLE)	ISD = 1.03, ns	N/A	ISD = 1.06, ns	ISD = 1.07, ns	N/A	ISD = 1.01, ns	ISD = 1.01, ns
Cranial height (CRAH)	ISD = 1.03, ns	N/A	ISD = 1.03, ns	ISD = 1.00, ns	N/A	ISD = 0.99, ns	ISD = 1.03, p = 0.019
Cranial length (CRAL)	ISD = 1.03, p = 0.018	ISD = 1.00, ns	ISD = 1.03, ns	ISD = 1.00, ns	ISD = 1.00, ns	ISD = 0.99, ns	ISD = 1.03, p = 0.037

Significant results following correction for multiple comparisons are presented in bold and the corresponding cell is highlighted in dark gray. Significant results with no correction for multiple comparison appear in normal font and the corresponding cell is highlighted in light gray. ISD = Index of Sexual Dimorphism; ns = not significant; N/A = Not Applicable (data not available for analysis).

live in variable communities, where intergroup behavioral differences are driven by ecological variation (e.g., Fuentes 2000), may provide increased scope to understand

Table IX Hylobatid upper canine crown height sexual dimorphism

Species	Sex	N	Geometric mean (upper canine height)		ISD	Student's *t-test* (male vs. female)		
			Mean	SD		t	df	P
Hoolock leuconedys	Male	14	20.08	2.05	**1.12**	**3.137**	**26**	**0.004**
	Female	14	17.93	1.55				
Hylobates agilis	Male	16	16.81	2.61	1.08	1.310	23	0.203
	Female	9	15.52	1.84				
Hylobates klossi	Male	9	16.40	2.71	1.02	0.214	16	0.833
	Female	9	16.08	3.58				
Hylobates lar	Male	12	18.18	2.34	**1.19**	**3.928**	**14.073**	**0.002**
	Female	7	15.33	0.71				
Hylobates muelleri	Male	6	17.10	1.13	1.06	1.458	17	0.163
	Female	13	16.18	1.34				
Nomascus gabriellae	Male	7	17.44	1.66	1.05	1.075	11	0.306
	Female	6	16.63	0.85				
Symphalangus syndactylus	Male	9	20.38	2.17	**1.20**	**4.341**	**18**	**<0.001**
	Female	11	17.04	1.23				

Significant results following correction for multiple comparisons are presented in bold. ISD = Index of Sexual Dimorphism; SD = Standard Deviation.

morphological differences among hylobatids in the context of the specific circumstances of the population or species under investigation.

There is a paucity in our understanding about whether and how the nature of intermale relationships among hylobatid communities vary. The frequency and intensity of intermale competition are widely acknowledged as being the predominant selective pressures driving body size and canine crown height dimorphism among primates (Plavcan and van Schaik 1992, 1997). The relatively low magnitude of sexual dimorphism that has been previously documented in hylobatids is thought to be a product of males and females undergoing similar selective pressures surrounding body size and canine crown height, with no apparent obvious reproductive advantage for differential selection on male morphology (Plavcan 2001). However, even individuals living in two-adult clusters engage with other adults, participate in intergroup interactions, and individually travel among clusters as part of their daily activities (Brockelman *et al.* 1998; Fuentes 2000). There is also good evidence to suggest that hylobatid social organization can be explained by the need for males to protect infants from infanticide (Fuentes 2000; Morino 2009; Sommer and Reichard 1997; van Schaik and Dunbar 1990; van Schaik and Kappeler 1997), where even low frequencies of infanticide are sufficient to maintain pair bonds among hylobatids (Fuentes 2000). Alternative arguments suggest that mate guarding may be an important selective pressure to explain hylobatid pair bonds, a behavior that has arisen among hylobatid males because females are widely dispersed and males are able to monopolize mating access to females (Emlen and Oring 1977; Fuentes 2000; Morino 2009; Palombit 1996, 1999). Under both the infanticide prevention hypothesis and the mate guarding

hypothesis, there is scope for selection for increased male body size and craniodental features that act as signals of potential aggression. Although the majority of hylobatid taxa live in pairs (Bartlett 2009; Brockelman et al. 2014; Reichard 2003), some hylobatid species live in unifemale/multimale groups, which afford an increased scope for behavioral complexity and the frequency of aggressive encounters, associated with increased body size and canine crown height dimorphism (Plavcan and van Schaik 1992, 1997). Other hylobatid species are known to live in multimale/multifemale groups that allow increased potential for agonistic interactions among males (Malone and Fuentes 2009). Despite a strong theoretical basis to suggest that selection pressures favoring increased sexual dimorphism are present in some hylobatid groups, no research has yet been conducted to systematically investigate whether interspecific differences in the presence and pattern of sexual dimorphism among hylobatids are associated with differences in social organization, mating system, and the nature of intermale or interfemale competition.

A further noteworthy finding is the presence of craniofacial size, shape, and canine crown height dimorphism in *Ho. leuconedys*, whose males also show increased size in upper orbital regions and aspects of facial breadth relative to females. The underlying causes for the high degree of sexual dimorphism in some craniofacial regions of *Ho. leuconedys*, and for differences in the pattern of craniodental dimorphism among other gibbon and siamang groups, have not yet been elucidated. However, some evidence suggests that differences in patterns of sexual dimorphism among non-human primates may reflect selection for craniofacial characteristics based on positive allometry for some facial dimensions and increased facial breadth among males of some primate taxa (Balolia et al. 2017; Borgi and Majolo 2016; Klopp 2012; Lefevre et al. 2014; Plavcan 2002, 2003; Weston et al. 2004; Wilson et al. 2020). Recent research also indicates that circumorbital morphology among some colobus monkeys may have evolved in response to intrasexual male competition and that circumorbital dimorphism among anthropoids is not strongly associated with overall sexual size dimorphism (Fannin et al. 2021). These findings further suggest that browridge morphology may play a role in social signaling among primates.

Despite a paucity of behavioral data among *Hoolock* gibbons, differences have been observed in some specific aspects of *Hoolock* socioecology compared with the other three hylobatid genera. For example, some *Hoolock* groups live in a pine/broadleaf forest habitat, where some males form all-bachelor groups of up to five individuals, allowing increased potential for intermale encounters and male–male competition (Geissmann et al. 2013; Malone and Fuentes 2009; Mukjerjee et al. 1991–1992). Furthermore, the finding that browridge thickness in *Ho. leuconedys* males is 24% larger than that of females can be considered in the context of facial marking dimorphism. *Hoolock leuconedys* males have white hair accentuating the browridge, in contrast to females, whose white coloring on the entire browridge and crown does not specifically highlight this facial region (Mootnick 2006). The results of the present study additionally show that the males of some hylobatid taxa have a wider bizygomatic region than do females. These findings can be considered in the context of research suggesting that wide faces are associated with increased aggression among primates (Borgi and Majolo 2016; Lefevre et al. 2014; Weston et al. 2004; Wilson et al. 2020). An alternative explanation is that a wide bizygomatic breadth in males could be a dietary adaptation, associated with sex differences in temporalis muscle

architecture and size. However, this suggestion seems unlikely as no such dietary sex differences have been documented to date. The available evidence supports the hypothesis that sex differences in hard tissue facial morphology among some hylobatid groups may evolve to facilitate visual communication, similar to the role that large canine crowns play among some primate species (Plavcan 2012; Plavcan and van Schaik 1997).

The findings that among *Ho. leuconedys*, *Hy. lar*, and *S. syndactylus*, male cranial size exceeds that of females, and that all three taxa show male-biased canine crown height dimorphism is consistent with the pattern of dimorphism found in other apes (Balolia *et al*. 2013; Lockwood 1999; Plavcan and van Schaik 1992; Wood 1976). Among primates, increased male body size and canine crown height is associated with the frequency and intensity of intermale aggression and primate social organization (Clutton-Brock *et al*. 1977; Kay *et al*. 1988; Leutenegger and Cheverud 1982; Leutenegger and Kelley 1977; Plavcan 2004, 2012; Plavcan and van Schaik 1992, 1997). Accordingly, the most likely explanation for the findings of the present study is that increased male-biased hard tissue sexual dimorphism in *Ho. leuconedys*, *Hy. lar*, and *S. syndactylus* may be driven by intrasexual male competition. An alternative scenario may be that the observed patterns of sexual dimorphism in these hylobatid species is *not* exclusively driven by male–male competition, a suggestion that may allow the development of alternative hypotheses surrounding the variation and complexity of hylobatid socioecology and biology and associated morphological variation. However, for the reasons outlined earlier surrounding increased scope for male–male competition and/or agonistic encounters associated with infanticide prevention and mate guarding (Fuentes 2000; Morino 2016; Palombit 1996, 1999; Setchell and Kappeler 2003; Sommer and Reichard 1997; van Schaik and Dunbar 1990; van Schaik and Kappeler 1997), it is likely that the observed presence of sexual dimorphism is driven by intermale competition in some hylobatid groups. The finding that the other hylobatid taxa investigated in this study are sexually monomorphic across the majority of craniodental measures (i.e., do not show sexual dimorphism) suggests that differences in selective pressures among hylobatid taxa exist, even within genera, on male and female craniodental morphology.

Conclusion

This article presents evidence of distinct craniodental sexual dimorphism in three hylobatid species. Although the precise reasons for sex-specific morphological differences in these taxa remain elusive, available information surrounding hylobatid socioecology indicates that aspects of the social behavior of some taxa, including increased scope for competition for access to females, infanticide prevention, and mate guarding, allow increased scope for high rates of intermale aggression and associated selection on male hard tissue morphology. The results presented in this study suggest that sex-specific craniodental morphology among some gibbon and siamang groups may be associated with visual signaling among males and indicate that craniofacial hard tissue morphology may be a useful source of information in reconstructing aspects of social behavior in extant and extinct primates.

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