

# Jaw-Dropping: Functional Variation in the Digastric Muscle in Bats

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## ABSTRACT

Diet and feeding behavior in mammals is strongly linked to the morphology of their feeding apparatus. Cranio-muscular morphology determines how wide, forcefully, and quickly the jaw can be opened or closed, which limits the size and material properties of the foods that a mammal can eat. Most studies of feeding performance in mammals have focused on skull form and jaw muscles involved in generating bite force, but few explore how jaw abduction is related to feeding performance. In this study, we explored how the morphology of the digastric muscle, the primary jaw abducting muscle in mammals, and its jaw lever mechanics are related to diet in morphologically diverse noctilionoid bats. Results showed that insectivorous bats have strong digastric muscles associated with proportionally long jaws, which suggests these species can open their jaws quickly and powerfully during prey capture and chewing. Short snouted frugivorous bats exhibit traits that would enable them to open their jaws proportionally wider to accommodate the large fruits that they commonly feed on. Our results support the hypothesis that digastric muscle and jaw morphology are correlated with diet in bats, and that our results may also apply to other groups of mammals. *Anat Rec*, 301:279–290, 2018. © 2018 Wiley Periodicals, Inc.

**Key words:** feeding; Chiroptera; jaw; mammals; Noctilionoidea

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Feeding is one of the most important functions that a vertebrate's musculoskeletal system must perform. The morphology of the vertebrate feeding apparatus determines what foods can be accessed and how efficiently they can be processed, which can directly affect an organism's fitness (Boag and Grant, 1981; Price et al., 1984; Dumont, 1999; Aguirre et al., 2002; Aguirre et al., 2003; Santana and Dumont, 2009; Santana et al., 2011; Meyers and Irschick, 2015). Across the vertebrate phylogeny, similar functional morphological solutions have evolved in response to similar challenges to acquire and process food (Van Valkenburgh, 2007; Wainwright et al., 2015; McGee et al., 2016). Furthermore, the evolution of novel feeding morphologies can allow species to exploit new dietary niches, which has been linked to rapid diversification of species via adaptive radiations (Grant and Grant, 2002; Price et al., 2010; Dumont et al., 2012).

In mammals, the dimensions of the skull and the jaw musculature affect how wide, how quickly, and how forcefully the mandible can be opened and closed during prey capture and oral processing (Herring and Herring,

1974; Perry et al., 2011; Hartstone-Rose et al., 2012; Santana and Portugal, 2016). Previous studies of the mammalian feeding apparatus have primarily focused on how skull morphological differences impact the ability to generate bite force and resist bending and torsional stresses imposed by food items during jaw closure (Dumont et al., 2005; Slater et al., 2009; Santana et al., 2012; Santana and Portugal, 2016). Skulls that produce

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forceful bites and resist higher stress levels are generally characterized by short, broad rostra, and are dorsoventrally deep, with large attachment sites for the jaw adductors (Freeman, 1979; Freeman, 1981, 1988, 1998; Dumont et al., 2009; Slater et al., 2009; Santana and Cheung, 2016). Conversely, rapid jaw closure, at the cost of bite force, is often associated with proportionally longer rostra, shorter skulls dorsoventrally, and smaller jaw muscles. Differences in the size and orientation of the jaw adductor muscles (*m. temporalis*, *m. masseter*, *m. pterygoideus medius*) are well known to affect how efficiently bite force is generated at different gapes and/or different bite points along the jaw (e.g., Santana et al., 2010; Perry et al., 2011; Hartstone-Rose et al., 2012; Santana et al., 2012; Santana and Portugal, 2016). However, before a bite can occur, the jaw must be opened. To date, it is poorly understood how differences in the morphology of the structures involved in opening the jaw are related to diet and feeding performance in mammals.

The digastric muscle (*m. digastricus*) is the primary jaw abducting (opening) muscle in mammals (Gorniak, 1985). As its name implies, it typically consists of two muscle bodies connected via a central tendon. It originates on the mastoid notch of the temporal bone (also referred to as the paraoccipital process [e.g. Ewer, 1973], jugular process of the occipital bone [e.g. Scapino, 1976]), posterior to the auditory bulla, and inserts on the ventromedial margin of the dentary. Typically, the digastric muscle inserts toward the posterior portion of the dentary in mammals, but can insert as far anteriorly as the mandibular symphysis in some taxa (e.g., some rodents; Scapino, 1976; Tomo et al., 1998; Woods and Howland, 1979). Previous studies have described variation in the relative length, thickness, angle and location of insertion of the digastric muscle that may be correlated with skull shape and diet (Storch, 1968; Ewer, 1973; Scapino, 1976). However, the functional morphology of the digastric muscle has rarely been examined in a quantitative and comparative framework, and has never been analyzed within a phylogenetic framework.

Several authors have described qualitative differences in digastric muscle morphology and attachment sites that may be adaptive for particular biting and/or prey-capture modes. For example, the digastric muscle of insectivorous canids, the raccoon dog (*Nyctereutes procyonoides*) and bat-eared fox (*Otocyon megalotis*) inserts on a subangular lobe, a bony process that protrudes from the ventral margin of the dentary and is oriented directly ventral to the temporomandibular joint (Huxley, 1880; Ewer, 1973). Compared to other canids, this more posteroventral insertion on the dentary increases the angle of insertion of the digastric muscle in these species, which in turn allows faster depression of the jaw and fast mastication of insect prey (Gaspard, 1964; Ewer, 1973). A less prominent subangular process is also present in the gray fox and island gray fox (genus *Urocyon*), which also consume insects as a large proportion of their diets (Fritzell and Haroldson, 1982; Moore and Collins, 1995).

The only quantitative comparative study of digastric muscle morphology, in several carnivorans, suggests that variation in digastric muscle morphology is correlated with foraging/feeding strategy and cranial dimensions in mammals (Scapino, 1976). The digastric muscle in river otters (*Lontra canadensis*), which must rapidly

open their jaws against the resistance of water to catch fish, has proportionally larger physiological cross-sectional area (PCSA) than digastric muscles of carnivorans that do not pursue fast moving prey underwater (Scapino, 1976). Muscles with larger PCSAs are capable of generating greater forces during contraction, which may be adaptive for abducting the jaw against greater resistance in water (Scapino, 1976). The digastric muscle in felids is proportionally longer (with presumably longer muscle fibers) and inserts farther anteriorly on the dentary than in other carnivorans. This increases gape angle, which is necessary to subdue prey with a foreshortened snout (Scapino, 1976). Muscles with longer fibers are also capable of contracting more quickly due to the additive velocity of greater numbers of contractile units (Gans and de Vree, 1987). In carnivorans, rapid abduction of the jaw may be necessary while subduing prey to either quickly open the mouth prior to biting or to quickly disengage the mouth after biting (Scapino, 1976). Whether or not these patterns apply across mammals, and how digastric muscle anatomy varies among taxa with more diverse diets, remain to be studied.

Here, we used noctilionoid bats (Noctilionoidea) as a model system to investigate how digastric muscle morphology is related to diet in mammals. Noctilionoidea is a taxonomically diverse radiation of bats (~207 species) that consume a variety of foods including insects, nectar, blood, fruits, fish, and small terrestrial vertebrates (Wetterer et al., 2000; Rojas et al., 2016). The mechanical properties of food and behaviors associated with food acquisition and processing have played a dominant role in shaping cranio-muscular morphology in this clade, at least with respect to jaw adduction (Aguirre et al., 2002; Herrel et al., 2008; Santana et al., 2010; Dumont et al., 2012; Santana et al., 2012; Santana and Cheung, 2016; Santana and Portugal, 2016). We hypothesize that variation in digastric muscle and associated cranio-mandibular morphology has also evolved in tandem with dietary specialization in Noctilionoidea. We expect to find traits that facilitate wider gapes in species that specialize in consumption of large, hard fruits (e.g., *Centurio senex*, *Sphaeronycteris toxophyllum*) because, like felids, these species have foreshortened rostra and must depress their jaws to a greater degree to achieve the gape necessary to accommodate large food items. We expect to observe traits that increase the speed and strength of jaw abduction in insectivorous and piscivorous species because of their observed ability to rapidly depress the jaw during chewing (Santana et al., 2011; Ewer, 1973). Nectarivores and sanguivores do not require wide gapes or powerful jaw movements to feed, and the size of their jaw adductors is relatively reduced (Santana et al., 2010). Thus, we expect that the jaw opening apparatus in these liquid feeders will be similarly reduced relative to that of other dietary groups. The relationships among cranial shape, feeding performance, and diet in Noctilionoidea parallel those in other groups of mammals (Freeman, 1988; Santana et al., 2012; Santana and Cheung, 2016). Therefore, by exploring the poorly understood morphological variation in the digastric muscle and jaw lever mechanics involved in jaw opening, the results from this study should improve our understanding of how cranio-muscular morphology is shaped by diet in mammals.

## METHODS

Our sample included 31 species from three noctilionoid families: Noctilionidae (2 species), Mormoopidae (1 species), and Phyllostomidae (28 species) (Table 1, Fig. 1), with sample sizes ranging from 1 to 5 individuals per species (Table 1, Supporting Information Table S1). The feeding apparatus of noctilionoid bats is not sexually dimorphic, thus data from males and females were pooled together in all analyses (Santana et al., 2010). Body mass data were available for all but seven individuals, for which we obtained mean species body mass from the panTHERIA data set (Jones et al., 2009). We categorized species into six dietary categories: insectivore, omnivore, frugivore, nectarivore, sanguinivore (blood), and carnivore (fish and terrestrial vertebrates) (Table 1, Fig. 1), following previous dietary classifications (Freeman, 1998; Aguirre et al., 2003; Nogueira et al., 2009; Dumont et al., 2012; Santana et al., 2010) and quantitative analyses of stomach contents and fecal samples (e.g., Wetterer et al., 2000). We grouped species that consume fish and terrestrial vertebrates into the broader “carnivore” category due to similarities in the mechanical properties of these diets, and the low

taxonomic diversity in the more specific dietary categories in our sample and in Noctilionoidea as a whole.

## Digastric Muscle Morphology

We compiled digastric muscle mass and fiber length data from Santana et al. (2010) and Santana (2018) using the methods therein (Table 1). Muscle fiber length was obtained via chemical digestion of individual muscles, and calculated for both left and right sides as the average fiber length from both bellies of the muscle; the central tendon is very thin and both bellies are presumed to function as a single unit (Kallen and Gans, 1972; De Gueldre and De Vree, 1988). Muscle fiber length is positively correlated with muscle contraction velocity and the total distance over which a muscle can contract. We calculated physiological cross-sectional area (PCSA = muscle mass/(density  $\times$  fiber length), Lieber, 2002; density = 1.06 g/cm<sup>3</sup>, Mendez and Keys, 1960) for each species, which is correlated with how forcefully a muscle can contract. Species with longer muscle fibers forming the *m. digastricus* should be able to more rapidly abduct the jaw, and/or open the jaw to a wider gape than species with shorter muscle fibers. Species with

TABLE 1. Species sampled, sample sizes, body mass, and muscle size data

Species	N	Code	Diet	BM	MM	FL	PCSA
<b>PHYLLOSTOMIDAE</b>							
<i>Anoura geoffroyi</i>	1	Age	N	14.0	0.009	3.90	2.23
<i>Artibeus jamaicensis</i>	2	Aja	F	34.0	0.035	5.35	6.28
<i>Artibeus lituratus</i>	1	Ali	F	73.0	0.042	9.98	3.98
<i>Artibeus phaeotis</i>	1	Aph	F	13.0	0.006	6.31	0.87
<i>Brachyphylla nana</i>	1	Bna	O	36.9	0.015	8.51	1.69
<i>Carollia brevicauda</i>	4	Cbr	O	16.3	0.015	4.20	3.36
<i>Carollia perspicillata</i>	3	Cpe	F	16.9	0.012	5.08	2.35
<i>Centurio senex</i>	1	Cse	F	18.0	0.011	5.19	2.07
<i>Desmodus rotundus</i>	2	Dro	S	35.0	0.021	7.96	2.57
<i>Enchisthenes hartii</i>	2	Eha	F	15.0	0.008	4.04	1.85
<i>Gardnerycteris crenulatum</i>	3	Gcr	I	15.0	0.015	3.80	3.92
<i>Glossophaga soricina</i>	2	Gso	N	9.2	0.006	4.50	1.34
<i>Lonchophylla robusta</i>	2	Lro	N	17.5	0.021	5.25	3.90
<i>Lophostoma brasiliense</i>	3	Lbr	I	10.0	0.012	3.82	3.06
<i>Lophostoma silvicolum</i>	2	Lsi	I	30.5	0.046	4.89	9.50
<i>Macrotus waterhousii</i>	1	Mwa	I	16.1	0.021	9.82	2.00
<i>Micronycteris hirsuta</i>	4	Mhi	I	14.1	0.018	5.64	3.43
<i>Micronycteris megalotis</i>	2	Mme	I	5.0	0.005	3.26	1.48
<i>Micronycteris minuta</i>	1	Mmi	I	6.0	0.006	3.80	1.43
<i>Phylloiderma stenops</i>	2	Pst	O	50.0	0.040	8.10	5.59
<i>Phyllostomus elongatus</i>	2	Pel	O	34.5	0.048	7.66	6.19
<i>Phyllostomus hastatus</i>	2	Pha	O	105.0	0.131	10.37	11.90
<i>Sphaeronycteris toxophyllum</i>	1	Sto	F	13.0	0.009	4.46	1.82
<i>Sturnira lilium</i>	3	Sli	F	16.6	0.015	5.41	2.53
<i>Tonatia saurophila</i>	3	Tsa	I	27.3	0.034	4.52	7.10
<i>Trachops cirrhosus</i>	5	Tci	C	27.2	0.034	6.49	5.38
<i>Uroderma bilobatum</i>	2	Ubi	F	15.0	0.012	4.98	2.36
<i>Vampyressa pusilla</i>	1	Vpu	F	6.7	0.005	4.00	1.18
<b>MORMOOPIDAE</b>							
<i>Pteronotus parnellii</i>	1	Ppa	I	18.7	0.015	8.55	1.68
<b>NOCTILIONIDAE</b>							
<i>Noctilio albiventris</i>	2	Nal	I	30.0	0.031	4.48	6.55
<i>Noctilio leporinus</i>	1	Nle	C	60.3	0.031	10.58	2.80

All data represent species means. N, sample size; Code, species labels used in figures; Diet, dietary categories; N, nectarivore; S, sanguinivore (blood); F, frugivore; O, omnivore; I, insectivore; C, carnivore (vertebrates); BM, body mass (g); MM, digastric mass (g); FL, digastric fiber length (mm); PCSA, digastric physiological cross-sectional area (mm<sup>2</sup>).

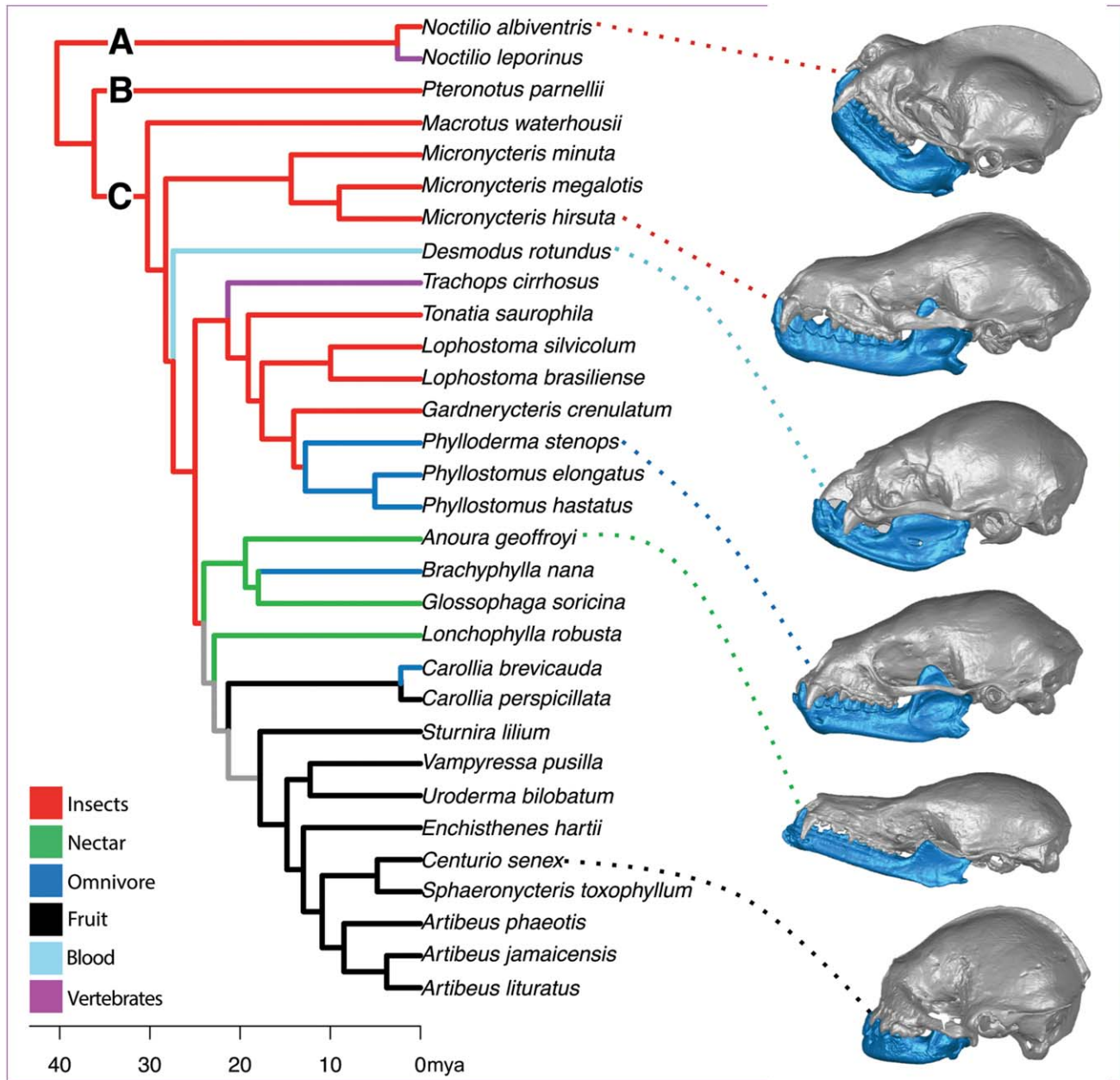


Fig. 1. Time-calibrated phylogeny of Noctilionoidea based on Rojas et al. (2016), pruned to include species in this study. Branches at the roots of each clade labeled to indicate family. **A:** Noctilionidae, **B:** Mormoopidae, **C:** Phyllostomidae. Branch colors reflect dietary category. Skulls to the right of the phylogeny were selected to illustrate cranio-mandibular shape diversity within Noctilionoidea. Skulls scaled to approximately the same basicranial length and oriented along the basicranial axis to emphasize variation in relative rostrum length and orientation.

larger PCSA for an *m. digastricus* of a given length should be capable of generating greater muscle forces to abduct the jaw than species with smaller PCSA.

### Jaw Lever Mechanics

In addition to fiber length and PCSA, jaw morphology and the angle at which the digastric muscle inserts on the dentary (angle of insertion) can also affect the mechanics of jaw abduction. To quantify the lever mechanics of the

digastric muscle, we micro-CT scanned skulls from a subset of specimens in our sample (24 species; Table 2). These had associated dissection photos in which the origin and insertion of the digastric muscle could be identified. We collected micro-CT data as .BMP image stacks using a Skyscan 1172 Microfocus X-radiographic Scanner (Skyscan, Belgium) and NRecon v. 1.5.1.4 (MicroPhotonics Inc., Allentown, PA) reconstruction software at Amherst College (Amherst, MA). Scan parameters for each specimen are available on request. We manually isolated

greyscale values representing bone, and used Mimics v. 19.0 (Materialise, Ann Arbor, MI) to generate separate three-dimensional models of crania and dentaries, which were saved as binary .STL volumes. We aligned STLs of crania and dentaries using Geomagic v. 11 (Geomagic, Research Triangle Park, NC) so that the jaws were completely closed to ensure consistency in our measurements.

The mastoid notch is quite prominent in bats, thus the origin of the digastric muscle on the cranium is easy

to identify. Conversely, the point of insertion of the digastric muscle on the dentary is ambiguous in most species because the insertion area is typically smooth. To approximate the insertion point of the digastric muscle on mandible STLs as accurately as possible, we used dissection photos including scale bars to measure the distance from the anterior margin of the insertion point of the digastric muscle to the antero-ventral most point on the mandibular symphysis (distance “x” in Fig. 2). We measured this distance five times per individual in Image J v. 1.48 (imagej.nih.gov; Abramoff et al., 2004) and calculated an average for each specimen. We then used 3-Matic v. 10.0 (Materialise) to extrapolate this measurement, from the antero-ventral point on the mandibular symphysis, on corresponding mandible STLs to locate the insertion point of the digastric muscle.

To identify how the geometry of the dentary affects jaw abduction (Greaves, 2012), we measured the angle at which the digastric muscle inserts on the dentary relative to the jaw joint (i.e., the muscle angle of action; Table 2, Fig. 3A) to the nearest 0.01 degrees. Species with larger angles of action should have better mechanical advantage for opening the jaw because a muscle’s mechanical advantage is optimal when it is pulling perpendicularly to bone (Greaves, 2012). A larger digastric muscle angle of action should also confer the ability to depress the dentary over a greater distance per unit of muscle contraction, which translates to increased velocity of jaw abduction and/or increased gape angle (Greaves, 2012).

We also determined how digastric muscle morphology is related to another proxy for mechanical advantage during jaw abduction, the ratio of inlever/outlever. We measured the distance from the mandibular condyle to the tip of the lower canine to represent the outlever, and the perpendicular distance between the jaw joint and the line of action for the digastric muscle as the inlever (Fig. 3B), both to the nearest 0.01 mm. Higher inlever/outlever values represent proportionally short jaws and potentially greater mechanical advantage for dislodging teeth from food, while lower values indicate elongate jaws that increase velocity of jaw abduction (Greaves,

**TABLE 2. Jaw lever mechanics data**

Binomial	Diet	AI	O/I
<b>PHYLLOSTOMIDAE</b>			
<i>Anoura geoffroyi</i>	N	22.38	0.11
<i>Artibeus jamaicensis</i>	F	18.48	0.15
<i>Carollia brevicauda</i>	O	13.19	0.11
<i>Carollia perspicillata</i>	F	14.78	0.12
<i>Centurio senex</i>	F	22.81	0.22
<i>Desmodus rotundus</i>	S	20.25	0.25
<i>Enchisthenes hartii</i>	F	23.92	0.18
<i>Glossophaga soricina</i>	N	21.90	0.13
<i>Lonchophylla robusta</i>	N	21.36	0.12
<i>Lophostoma brasiliense</i>	I	20.35	0.11
<i>Lophostoma silvicolum</i>	I	14.96	0.14
<i>Micronycteris hirsuta</i>	I	17.72	0.14
<i>Micronycteris megalotis</i>	I	20.63	0.14
<i>Micronycteris minuta</i>	I	22.80	0.14
<i>Gardnerycteris crenulatum</i>	I	14.12	0.15
<i>Phylloderma stenops</i>	O	31.15	0.18
<i>Phyllostomus elongatus</i>	O	14.25	0.13
<i>Sphaeronycteris toxophyllum</i>	F	23.91	0.21
<i>Sturnira lilium</i>	F	21.93	0.19
<i>Tonatia saurophila</i>	I	19.14	0.15
<i>Trachops cirrhosus</i>	V	12.80	0.10
<i>Uroderma bilobatum</i>	F	22.57	0.16
<i>Vampyressa pusilla</i>	F	24.25	0.15
<b>NOCTILIONIDAE</b>			
<i>Noctilio albiventris</i>	I	13.47	0.11

AI: angle of insertion for the digastric muscle in degrees (see Fig. 3A for diagram); I/O, inlever/outlever (see Fig. 3B for diagram and Supporting Information Table S2 for raw inlever and outlever data).

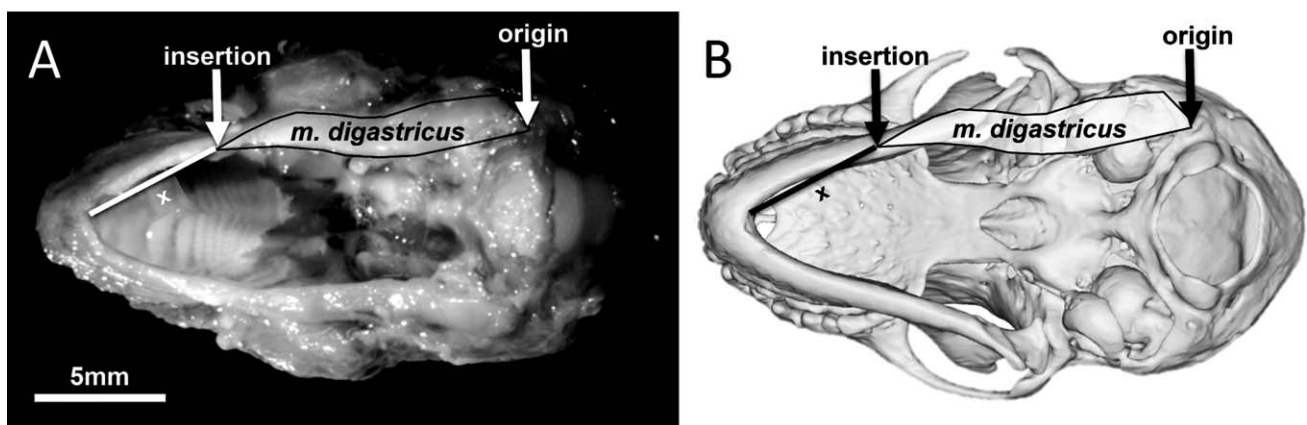


Fig. 2. Identification of digastric muscle attachment on skull STLs. **A:** Photo of *Enchisthenes hartii* in ventral view with *m. digastricus* dissected. Left *m. digastricus* is outlined in black, and its origin (mastoid notch) and insertion are indicated. *x*, distance from the anteroventral margin of the mandibular symphysis to the insertion; **B:** STL of *Enchisthenes hartii*, also in ventral view. For each skull STL, we measured distance *x* from the anteroventral margin of the mandibular symphysis to identify the digastric muscle insertion site. See Methods for further details.

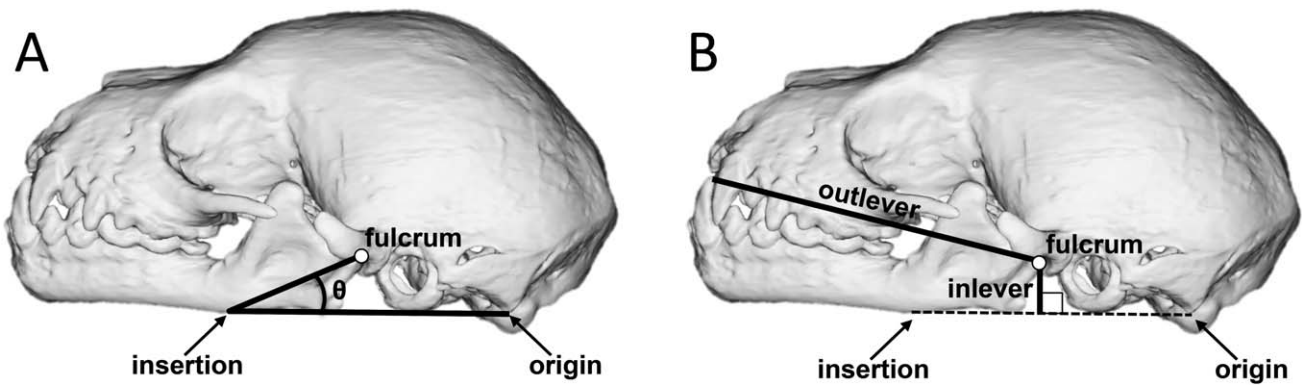


Fig. 3. Measures of jaw lever mechanics. The skull of *Enchisthenes hartii* in lateral view with the jaw completely closed showing **A**:  $\theta$ , angle of insertion, which is the angle measured between the insertion and fulcrum (temporomandibular joint) and insertion and origin for the digastric muscle. **B**: outlever, distance from the fulcrum to the tip of the lower canine, inlever, perpendicular distance from the line of action of the digastric muscle to the fulcrum.

2012). To avoid biases, a single observer (AAC) measured the angle of insertion, inlever, and outlever using tools in 3-Matic v. 10.0 (Materialise). These were measured five times and averaged for each individual. All raw measurements are provided in the Data Supplement (Supporting Information Tables S1 and S2).

### Statistics

We calculated species means for all variables described above, and  $\log_{10}$ -transformed these values prior to statistical analyses to improve normality. We conducted these, and all other statistical analyses in R v. 3.4.1 (R Core Team, 2017). We first explored the scaling relationship between digastric muscle PCSA and fiber length, respectively, and body mass using traditional ordinary least-squares (OLS) and phylogenetic generalized least squares (PGLS) regressions. OLS regressions allowed us to visualize differences in the relative size of the digastric muscle among species and the five dietary groups, as well as identify outliers, and PGLS regressions allowed us to test scaling relationships among variables while accounting for non-independence due to shared ancestry. We ran PGLS regressions using functions in the geiger package (Harmon et al., 2008) and a pruned version of a recent time-calibrated phylogeny for Noctilionoidea (Rojas et al., 2016). If rapidly chewing insects and vertebrates is associated with strong jaw abductors, we expected to observe proportionally larger digastric muscle PCSAs in insectivorous and carnivorous species (i.e., positive residuals in regressions of digastric muscle PCSA against body mass). We may observe proportionally longer muscle fibers in frugivorous species, reflected as positive residuals in a regression of fiber length against body mass, which would suggest that they are capable of achieving proportionally wider gapes.

To better understand how the morphology of the digastric muscle is related to the mechanics of jaw abduction, we used OLS and PGLS regressions to investigate the relationship between the angle of insertion and inlever/outlever of the digastric muscle. A positive correlation between these two variables would indicate that mechanical advantage is optimized in species that exhibit higher values (i.e. the jaw can be opened more

forcefully), whereas velocity of jaw abduction (at the cost of mechanical advantage) would be being optimized for in species that exhibit lower values. A negative relationship between angle of insertion and inlever/outlever would suggest that there is a tradeoff between force and velocity of jaw abduction.

To test for differences in PCSA and fiber length, respectively, among dietary groups, we first extracted size-corrected residuals of PCSA and fiber length from  $\log_{10}/\log_{10}$  OLS regressions of each variable against body mass. We then used phylogenetic Analysis of Variance (10,000 iterations), with diet as the explanatory variable, and a pruned version of the Noctilionoidea tree from Rojas et al. (2016), to test for diet-related differences in residual PCSA and fiber length, respectively, in our sample. These were conducted using the aov.phylo function in the geiger package (Harmon et al., 2008). Additionally, to test whether species with different diets can be classified based on digastric muscle morphology and lever mechanics (PCSA, fiber length, angle of insertion and inlever/outlever), we ran a linear discriminant analysis using the lda function in the MASS library. Our sample for this analysis included the 24 specimens (24 species) that had associated STLs and body size-corrected residuals for PCSA and fiber length.

### RESULTS

Results from OLS and PGLS regressions were largely similar. Therefore, we present results from traditional OLS regressions to highlight differences among individual species in our sample, and report statistics from PGLS regressions in the Data Supplement (Supporting Information Table S3).

#### Digastric Muscle PCSA

The slope from a regression of digastric muscle PCSA against body mass ( $b = 0.63 \pm 0.12$  SE, Table 3, Fig. 4A) did not differ significantly from the slope expected under isometry (slope test, expected slope = 2/3,  $F = 0.11$ ,  $P > 0.05$ ). All but two insectivorous species in our sample were above the common regression line and thus have proportionally greater PCSAs for their body masses; of

TABLE 3. OLS regression statistics

Regression	N	Slope $\pm$ SE	Intercept $\pm$ SE	$r^2$	$t$	$P$
$\log_{10}$ PCSA versus $\log_{10}$ BM	31	$0.63 \pm 0.12$	$-0.34 \pm 0.16$	0.47	5.09	< 0.0001
$\log_{10}$ FL versus $\log_{10}$ BM	31	$0.37 \pm 0.06$	$0.26 \pm 0.08$	0.58	6.38	< 0.0001
$\log_{10}$ AI versus $\log_{10}$ I/O	24	$0.63 \pm 0.17$	$1.81 \pm 0.15$	0.38	3.67	0.001

PCSA, digastric physiological cross-sectional area; FL, digastric muscle fiber length; BM, body mass; AI, Angle of insertion for the digastric muscle; I/O, inlever/outlever for jaw abduction by the digastric muscle.  $t$  values and  $P$  values are reported for a test of the null hypothesis that slope = 0.

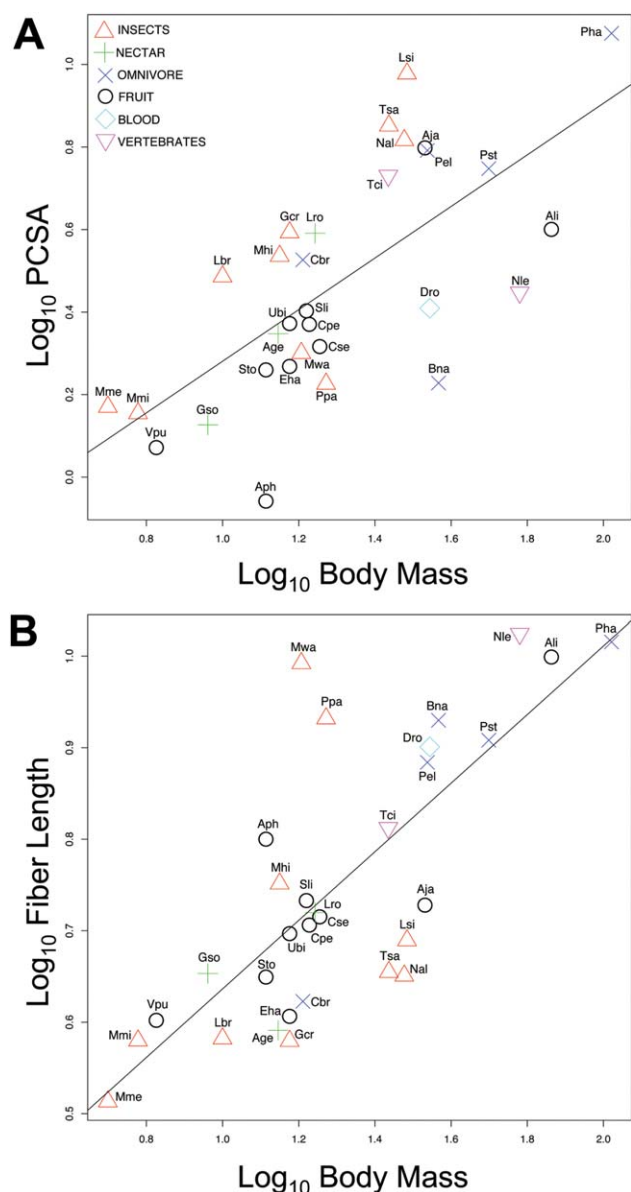


Fig. 4.  $\log_{10}/\log_{10}$  OLS regressions of species means for **A**: Digastric muscle PCSA ( $\text{mm}^2$ ) against Body Mass and **B**: Digastric muscle Fiber Length (mm) against Body Mass (g). Regression statistics are provided in Table 3. Species are coded as in Table 1, diet coded by plot symbols.

these, *Lophostoma silvicolum* has the highest PCSA relative to its body mass in (Fig. 4A). The insectivores *Macrotus waterhousii* and *Pteronotus parnellii* were below

the regression line with proportionally low PCSAs compared to other insectivorous noctilionoids of similar body mass (Fig. 4A). As expected, nectarivores (*Anoura geoffroyi*, *Glossophaga soricina*) and the sanguivore *Desmodus rotundus* all have reduced PCSAs. However, one nectarivore, *Lonchophylla robusta*, showed relatively higher digastric muscle PCSA than all other nectarivores and was closer to similarly sized insectivorous species above the regression line (Fig. 4A). Frugivorous taxa also have relatively lower digastric muscle PCSAs for their body masses, which were especially low in *Artibeus phaeotis* and *A. lituratus* (Fig. 4A). However, in contrast with other frugivores, we observed relatively high digastric muscle PCSAs in *A. jamaicensis*, which was above the common regression line. All omnivores showed proportionally high PCSAs for their body masses, except *Brachyphylla nana*, which has greatly reduced PCSA for its body mass (Fig. 4A). *Trachops cirrhosus* (carnivore) has relatively high PCSA, while *Noctilio leporinus*, a carnivore that specializes in eating fish, has substantially reduced digastric muscle PCSA for its body mass compared to nearly all other species in our sample (Fig. 4A).

### Digastric Muscle Fiber Length

Scaling of digastric muscle fiber length against body mass in noctilionoids ( $b = 0.37 \pm 0.06$  SE, Table 3, Fig. 4B) also did not differ significantly from isometry (slope test, expected slope = 1/3,  $F = 0.50$ ,  $P > 0.05$ ). Dietary groups did not segregate relative to one another or to the common regression line, but both *Macrotus waterhousii* and *Pteronotus parnellii* appear to have proportionally long digastric muscle fibers for their body masses compared to all other taxa in our sample (Fig. 4B). Notably, *Noctilio leporinus* has particularly long muscle fibers, especially compared to its insectivorous sister taxon, *Noctilio albiventris*, which has the shortest muscle fibers relative to body mass (Fig. 4B).

### Digastric Muscle Angle of Insertion and Inlever/Outlever

The angle of insertion for the digastric muscle increased with increasing inlever/outlever ratios (Table 3, Fig. 5:  $r^2 = 0.38$ ,  $P = 0.001$ ). This indicates that species in which the digastric muscle has a low angle of insertion tend to have proportionally longer outlevers. Nectarivorous species were all located above the regression line with relatively high angles of insertion associated with low inlever/outlever ratios (Fig. 5). Omnivorous *Phylloderma stenops* has a very large angle of insertion and a high inlever/outlever ratio, suggesting that

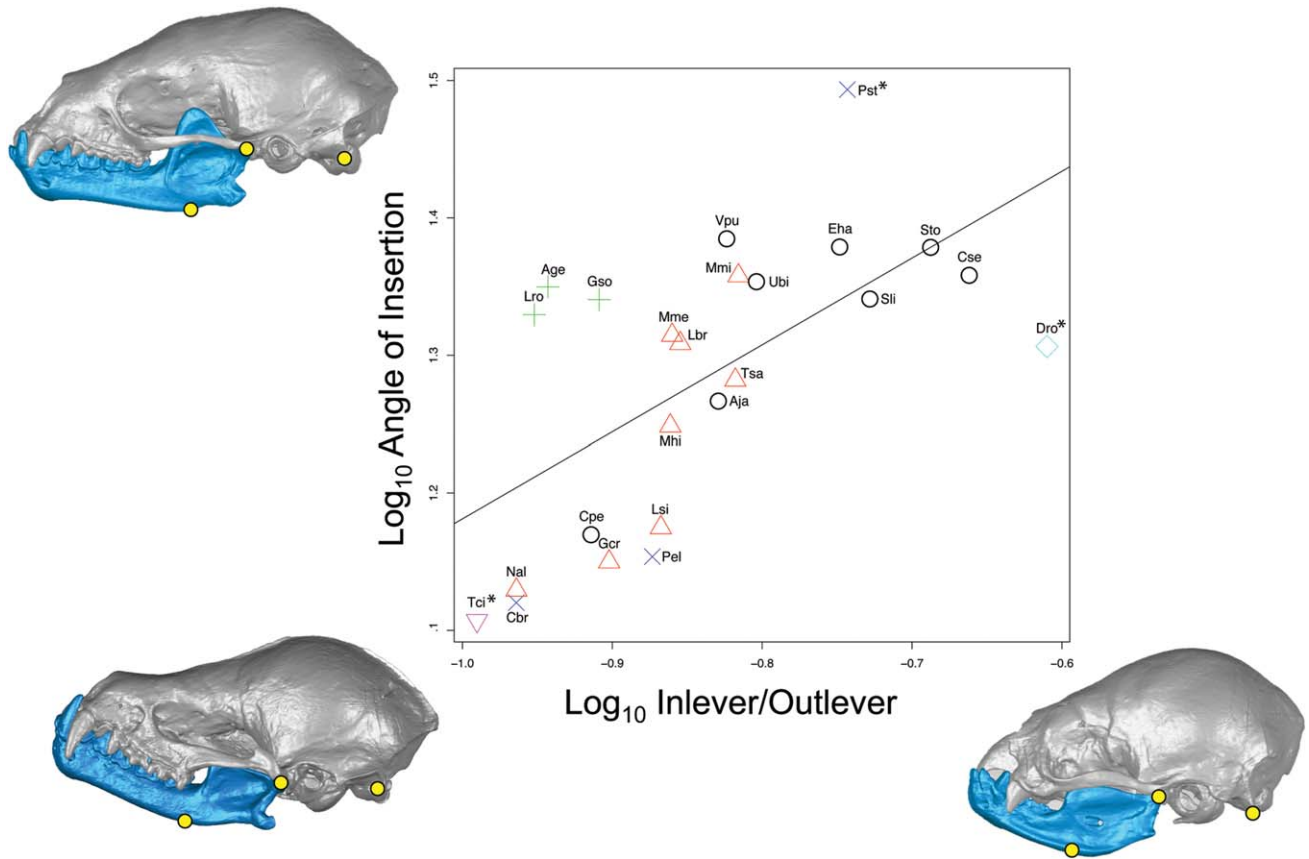


Fig. 5.  $\text{Log}_{10}/\text{Log}_{10}$  OLS regressions of angle of insertion against inlever/outlever. Regression statistics are provided in Table 3. Species are coded as in Table 1, dietary category indicated by color and plot symbols as in Figure 4. Skulls illustrating extremes for angle of insertion and inlever/outlever are shown along each axis, with representative species identified with an asterisk in the plot. Insertion, fulcrum, and origin for the digastric muscle lever system indicated by yellow points on skulls.

mechanical advantage of jaw abduction is quite high in this taxon (Fig. 5).

**Digastric Muscle Morphology, Jaw Lever Mechanics, and Diet**

We did not detect significant differences in residual digastric muscle PCSA (phylogenetic ANOVA:  $F_{5,25} = 1.65, P > 0.05$ ) and residual fiber length (phylogenetic ANOVA:  $F_{5,25} = 0.23, P > 0.05$ ), respectively, among dietary groups in our sample. However, a Linear Discriminant Analysis revealed that cranio-muscular and mechanical traits (PCSA, fiber length, angle of action, and inlever/outlever) can be used to distinguish among the six dietary categories, and correctly predicted diet for 75% of the species in our sample (Table 4). However, these results should be interpreted with caution due to the low sample sizes within dietary categories. LD1 accounted for 73.89% of the trait separation in our sample, and discriminated among dietary groups moderately well, especially nectarivores, sanguinivores, frugivores, and insectivores (Table 4, Fig. 6). LD1 predominantly reflects differences in angle of insertion, which had a positive LD coefficient for LD1, and inlever/outlever, which had a negative LD coefficient for LD1. Nectarivores had the highest positive loadings along LD1, and

**TABLE 4. LDA summary statistics**

Coefficients of Linear Discriminants				
Trait	LD1 (73.89%)	LD2 (14.16%)	LD3 (11.31%)	LD4 (0.65%)
IO	-20.28	-6.32	-8.74	-0.95
AI	17.20	8.49	-6.81	-5.36
FLresids	-1.43	-8.04	6.62	-9.03
PCSAresids	5.19	-6.82	-4.48	-4.57
Classification Analysis				
Diet	Correct	Misclassified	Total	% Correct
Nectarivore	3	0	3	100
Sanguinivore	1	0	1	100
Frugivore	6	2	8	75
Omnivore	0	3	3	0
Insectivore	7	1	8	90
Carnivore	1	0	1	100
Total	18	6	24	75

are, therefore, characterized by low inlever/outlever ratios and high angles of insertion of the digastric muscle. Sanguinivorous *Desmodus rotundus* had the lowest (negative) loadings, and thus a high inlever/outlever ratios and a low angle of insertion for the digastric.



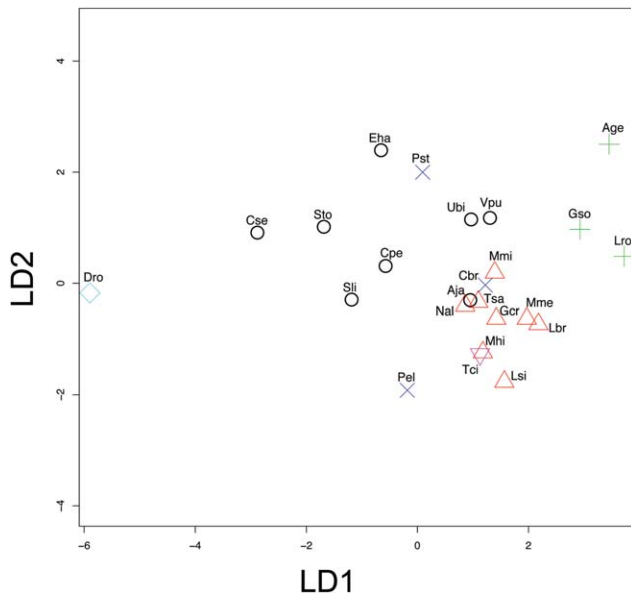


Fig. 6. Plot of LD2 against LD1. Species coded as in Table 1, dietary category indicated by color and plot symbols as in Figure 4. LDA statistics summarized in Table 4.

Insectivores, the carnivore *Trachops cirrhosus*, and frugivores overlapped along LD1, but insectivores and the carnivore tended to have higher, positive scores along LD1, whereas frugivores had lower, negative scores. Omnivores were intermediate and overlapped with both insectivores and frugivores along LD1. All nectarivores, sanguinivores, and carnivores were correctly classified. However, all omnivores (*Carollia brevicauda*, *Phyllostoma stenops*, and *Phyllostomus elongatus*) were misclassified, as well as two frugivores (*Artibeus jamaicensis* and *Carollia perspicillata*), and an insectivore (*Noctilio albiventris*).

## DISCUSSION

Functional differences in the structures related to jaw abduction are poorly understood in mammals despite their likely effects on how wide, fast, and forcefully the jaws can be opened, and, consequentially, what foods a mammal can successfully eat. In this study, we observed trends in digastric muscle morphology and jaw lever mechanics in noctilionoid bats that are likely adaptive for feeding.

The scaling relationships of digastric muscle PCSA and fiber length with body mass, described here, are consistent with prior work on digastric muscle size in bats; Herrel et al. (2008) found an isometric relationship between digastric muscle mass, PCSA, and fiber length, respectively, and skull size in a smaller set of species. Our results further suggest that the dimensions of the dentary and orientation of the digastric muscle origin and insertion may be more important than differences in PCSA and muscle fiber length in determining functional differences in jaw abduction. To verify whether this is the case, greater sampling at the specific and intraspecific level are needed, since most dietary categories contained very few species, and jaw lever mechanics were

only available for a single individual per species in our sample. Constraints on body mass related to flight and/or limited physical space for a greatly enlarged digastric muscle may limit its mass and PCSA in bats. Thus, selection may have favored changes in cranial and dentary form as a means to enable changes in the mechanical advantage of the digastric without increasing the size of the muscle itself. Results from previous work lend support to this idea; jaw muscle mass, PCSA, and fiber lengths scale isometrically or with slight negative allometry to skull size or body mass in bats (Herrel et al., 2008; Santana, 2018). Conversely, other studies indicate that a positive allometric relationship of jaw muscle traits with skull size may be typical in non-volant mammals and other vertebrates (e.g. primates [Anapol et al., 2008], fish [Herrel et al., 2005], rodents [Druzinsky, 1993], felids [Hartstone-Rose et al., 2012]).

Our results suggest that digastric muscle morphology and lever mechanics may be associated with diet in Noctilionoidea; most species can be correctly classified into their dietary categories based solely on digastric morphological and mechanical traits. Frugivory is associated with high angles of action and proportionally short outlevers for jaw abduction by the digastric muscle. This suggests that frugivores with foreshortened rostra are capable of producing proportionally wider gape angles, which would be advantageous for opening the mouth wide enough to bite into large fruits. *Artibeus jamaicensis* differed from other closely related frugivores, and appears to have proportionally higher digastric muscle PCSA and a lower angle of insertion, thus being more similar to insectivores in our sample. *Artibeus jamaicensis* was the largest frugivore for which we measured jaw lever traits, and, therefore, the fruits it eats may be smaller relative to its body size compared to other taxa in our sample, or it may use biting behaviors that do not require as large a gape (Morrison, 1980). *Carollia perspicillata* also differed from other frugivores and showed a lower angle of insertion and lower inlever/outlever ratios. This is probably related to this species' diet, which is primarily composed of fruits from the genus *Piper* (Fleming, 1988), which are long, narrow and soft, and do not require a large gape or particularly forceful jaw abduction to consume.

Insectivorous bats appear to have stronger digastric muscles than other dietary groups, as evidenced by proportionally higher PCSAs relative to body mass and proportionally long outlevers. Proportionally large digastric muscles have also been described in many carnivorans, and are thought to facilitate wide, rapid and powerful abduction of the jaws during prey capture, and/or to rapidly disengage the jaw from prey (Scapino, 1976 and sources therein). This supports our prediction that insectivores should exhibit traits associated with increased strength of jaw abduction, required to quickly depress the jaw while apprehending prey and breaking up arthropod exoskeletons via rapid and prolonged mastication (Santana et al., 2011). Interestingly, *Pteronotus parnellii*, a member of Mormoopidae, the sister taxon to Phyllostomidae, and *Macrotus waterhousii*, the most basal genus in Phyllostomidae, both have reduced PCSAs but longer muscle fibers for their body masses relative to other insectivorous species. This suggests that there may have been a shift in jaw abductor

morphology in the common ancestor of the rest of Phyllostomidae.

Exceptionally high digastric muscle PCSAs observed in insectivorous *Lophostoma silvicolum* may be related to roost excavating behavior in this taxon, rather than diet. *Lophostoma* use their incisor and canine teeth to excavate roosts inside termite nests, which are more mechanically challenging than food items they typically consume. Cranial shape and the size of the jaw abductors are linked to evolution of roost excavating behavior in *Lophostoma* (Santana and Dumont, 2011). Perhaps disengaging the jaw from tough nest material requires increased muscle force, or maybe these species use jaw abduction to pry apart termite nest pieces (Dechmann and Kerth, 2008; Dechmann et al., 2009; Santana and Dumont, 2011). Interestingly, other bat species also use their jaws for non-feeding purposes, such as bats that construct tents by making a series of bites in large leaves, and species that use wide gapes as a threat posture (Freeman, 1984; Kunz et al., 1994). Thus, these behaviors may also play a role in shaping evolution of bat jaw muscle anatomy.

Piscivorous *Noctilio leporinus* have digastric muscles with disproportionately long muscle fibers and low PCSA relative to most other noctilionoids. Its insectivorous sister taxon, *N. albiventris*, exhibits the opposite trend (high PCSA for its body mass and relatively short muscle fibers) and is more similar to more distantly related insectivorous species. Longer muscle fibers should allow *Noctilio leporinus* to abduct its jaw both wider and faster, than bats of similar size and skull shape. The digastric muscle specialization of *Noctilio leporinus* is consistent with reports of its ability to rapidly and thoroughly chew fish prey (Murray and Strickler, 1975; Schnitzler et al., 1994) despite having a skull morphology relatively unspecialized for wide gape and fast jaw closure (e.g., a short rostrum; Freeman, 1984; Santana and Cheung, 2016). While rare compared to other diets, piscivory has evolved several times in Chiroptera, which would allow future studies to investigate cranio-muscular adaptations for piscivory (Ruedi and Mayer, 2001; Fenton and Bogdanowicz, 2002). Our sample was similarly depauperate of species that commonly prey on terrestrial vertebrates, as this diet is uncommon within Noctilionoidea (Freeman, 1984, 1988; Norberg and Fenton, 1988; Santana and Cheung, 2016). However, we found that *Trachops cirrhosus* does have increased digastric muscle PCSAs, similar to insectivores, suggesting that this species relies on powerful jaw abduction while hunting. Again, expanding sampling of species to other independent origins of carnivory would help elucidate specializations associated with this diet.

As expected, most nectarivorous bats and sanguivorous *Desmodus rotundus* have reduced digastric muscles, as evidenced by proportionally lower PCSAs for their body masses. This is similar to observations of reduced jaw adductor morphology, and consequentially reduced bite force, in nectarivores and sanguivores relative to other bats (Herrel et al., 2008; Santana and Dumont, 2009; Santana et al., 2010; Santana and Portugal, 2016). However, the angle at which the digastric muscle inserts on the dentary in all nectarivorous species is relatively high, which increases the mechanical advantage of the digastric muscle during jaw abduction. This arrangement also increases the speed and distance

the jaw can be abducted per unit of muscle contraction compared to species with similar inlever/outlever ratios. Similarly high angles of action have been described in insectivorous canids and have been linked to the rapid chewing used by these species during food processing (Ewer, 1973). This suggests that nectar feeding does not require particularly powerful jaw abduction, but may entail rapid opening of the jaw. Interestingly, *Lonchophylla robusta*, showed proportionally larger digastric muscle PCSA for its body size than other nectarivores. While most nectar-feeding bats repeatedly dip their elongated tongues covered in hair-like papillae into nectar while feeding (Winter and von Helversen, 2003), *Lonchophylla robusta* and other close relatives in the subfamily Lonchophyllinae, have a smooth tongue with a longitudinal groove that is held in continuous contact with nectar while feeding (Tschapka et al., 2015). In these bats, nectar moves up the tongue groove into the oral cavity and the mouth is held open during feeding (Tschapka et al., 2015).

Our results suggest that jaw abduction is quite different in the sanguivore *Desmodus rotundus* when compared to other liquid-feeding (nectarivorous) species, although all of these species have similarly reduced jaw musculature (Herrel et al. 2008; Santana et al., 2010). *D. rotundus* has a proportionally shorter jaw and relatively low digastric angle of insertion relative to the inlever/outlever ratio, as highlighted by LDA results (Fig. 6). It is the only species in our data set that does not chew any food and feeds using its sharp incisors to cut through the skin of its prey (Greenhall, 1972). Thus, characteristics that improve strength, speed, or magnitude of jaw depression may not have been under strong selection in this species. However, other species of vampire bats are known to eat insects on occasion (Arata et al., 1967), and may show more robust digastric muscle and/or jaw lever morphology.

While most omnivores seem to be largely similar to insectivores in jaw abductor morphology, *Phylloderma stenops* appears to have a particularly high angle of insertion that makes it particularly well suited to produce wide gape with a relatively short jaw outlever. The diet of *Phylloderma* is poorly known, but this species has been observed feeding on fruits of cucurbit plants, which can be quite large (York, 2008). Omnivorous *Brachyphylla nana*, which is sister to nectarivorous *Glossophaga soricina* and *Anoura geoffroyi*, has greatly reduced digastric muscle PCSA, suggesting this species also has weak muscles for jaw abduction, possibly due to shared ancestry with nectarivores and the inclusion of nectar in its diet (Burt, 1983).

Most noctilionoid bats do not feed exclusively on one food type, which may partly explain the large overlap in digastric muscle morphology among the broad dietary groups used in our analyses. For example, many nectarivores occasionally consume insects and fruit, and many frugivores consume nectar and insects during parts of the year (Wetterer et al., 2000). In addition, insectivorous species can specialize on arthropods of different sizes, habits, and exoskeletal material properties (Freeman, 1979, 1981; Aguirre et al., 2002; Aguirre et al., 2003). Pressures from these different prey properties could explain differences in gape, strength and speed of jaw abduction among species (Freeman, 1979, 1981; Aguirre et al., 2002; Aguirre et al., 2003). To improve

our understanding of how cranio-muscular form is correlated with diet and feeding behavior, future studies would benefit from directly measuring gape angle, using continuous metrics that describe the physical properties of diet, and quantifying chewing rates among species. This kind of approach has already proven useful in studies of jaw adduction in several mammal groups (Dumont, 1999; Aguirre et al., 2003; Perry and Hartstone-Rose, 2010; Santana et al., 2012; Figueirido et al., 2013).

The trends described here support the hypothesis that dietary evolution has shaped jaw abduction morphology and function in noctilionoid bats, and sets the stage for future work on this topic in bats and other groups of mammals. We anticipate that phylogenetic comparative analyses incorporating more taxa, and multiple evolutionary origins of different diets, may reveal that the general trends observed in our sample reflect, indeed, dietary specializations in jaw abduction.

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