Acrodont tooth implantation via severe ankylosis as an adaptation of strong bite force (#45825)

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Acrodont tooth implantation via severe ankylosis as an adaptation of strong bite force

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Extant and extinct reptiles exhibit numerous combinations of tooth implantation and attachment. Tooth implantation ranges from those possessing roots and lying within a socket (thecodonty), to teeth lying against the lingual wall of the jawbone (pleurodonty), to teeth without roots or sockets that are attached to the apex of the marginal jawbones (acrodonty). Attachment may be ligamentous or via ankylosis (i.e., fusion). Adaptative reasonings are proposed as an underlying driver for evolutionary changes in some forms of tooth implantation and attachment. However, a substantiated adaptive hypothesis is lacking for the state of acrodonty via severe ankylosis that is seen in several lineages of Lepidosauria, a clade that is plesiomorphically pleurodont. We hypothesize that acrodonty via severe ankylosis, as seen in *Sphenodon punctatus* and acrodontan lizards, is an adaptation either resulting from or allowing for a stronger bite force. We use bite force data gathered from the literature to show that those taxa possessing acrodont dentition attached via severe ankylosis possess a stronger bite force than those taxa with pleurodont dentition. Furthermore, we discuss the evolution of acrodonty and potential behaviors related to strong bite force that influenced the evolution of acrodonty within Rhynchocephalia, Acrodonta, and Trogonophidae. Implications for the evolution of different forms of tooth implantation and attachment include ancient behavioral shifts.

Acrodont Tooth Implantation Via Severe Ankylosis as an Adaptation of Strong Bite Force

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Abstract

Extant and extinct reptiles exhibit numerous combinations of tooth implantation and attachment. Tooth implantation ranges from those possessing roots and lying within a socket (thecodonty), to teeth lying against the lingual wall of the jawbone (pleurodonty), to teeth without roots or sockets that are attached to the apex of the marginal jawbones (acrodonty). Attachment may be ligamentous or via ankylosis (i.e., fusion). Adaptative reasonings are proposed as an underlying driver for evolutionary changes in some forms of tooth implantation and attachment. However, a substantiated adaptive hypothesis is lacking for the state of acrodonty via severe ankylosis that is seen in several lineages of Lepidosauria, a clade that is plesiomorphically pleurodont. We hypothesize that acrodonty via severe ankylosis, as seen in

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Introduction

Acrodont tooth implantation, where the tooth rests at the summit of the tooth-bearing bone, evolved multiple times within Lepidosauria. It appears at least twice within squamate reptiles, as seen in acrodontan lizards (Romer, 1956) and trogonophid amphisbaenians (Gans, 1960), and once within Rhynchocephalia (Jenkins et al., 2017). In Acrodonta and *Sphenodon punctatus,* the only living representative of Rhynchocephalia, the dentition is severely ankylosed (i.e., fused) to the adjacent bone. In those taxa, teeth and surrounding tissues have been investigated thoroughly via histological studies (Cooper & Poole, 1973; Smirina & Ananjeva, 2007; Kieser et al., 2009, 2011; Haridy, 2018), CT data (Dosedělová et al., 2016), and developmental research (Buchtová et al., 2013). However, the evolution of acrodont tooth implantation is seldom discussed in an adaptive context.

Smith (1958) suggested that acrodonty and thecodonty (i.e., where the tooth is implanted in a socket) are traits associated with anchoring permanent dentition. However, the fossil record shows that some reptiles possessing acrodont dentition replaced their teeth regularly (Gow, 1977; Haridy, LeBlanc & Reisz, 2018). Furthermore, it is unknown if acrodonty and severe ankylosis are truly associated with anchoring permanent dentition, or if those combined traits somehow inhibit tooth replacement. While it is possible that thecodonty evolved to anchor permanent dentition in mammals, it is well known that toothed archosaurs, which also possess thecodont implantation, replace their teeth with some regularity (e.g., Edmund, 1962; D'Emic et al., 2019).

There are a suite of traits commonly associated with acrodont tooth implantation. Reduced tooth count, severe tooth wear, and a loss of the alveolar foramen are also commonly associated with acrodont tooth implantation (Augé, 1997; Zaher & Rieppel, 1999; Haridy, 2018). A slowing or lack of tooth replacement, called monophyodonty, is also commonly associated with acrodont tooth implantation (Smith, 1958; Cooper et al., 1970). Even with monophyodont dentition, additional teeth are typically still added to the posterior end of the tooth row throughout ontogeny, as is the plesiomorphic condition within Reptilia (Robinson, 1976; Gow, 1977; Rieppel, 1992; Reynoso, 2003). Severe ankylosis accompanies acrodonty in acrodontan squamates and in *Sphenodon punctatus*. Typically, ankylosis is severe in those taxa and the tooth and bone lose identity from one another (Fig. 1). Herein, we call those combined traits acrodonty via severe ankylosis (AVSA). AVSA caused some to erroneously propose that *S. punctatus* lacks teeth entirely, instead possessing a serrated jawbone (Mlot, 1997). ~~On the contrary~~, severe wear may obscure the anterior dentition in older, acrodont, monophyodont lepidosaurs, causing them to appear to be absent.

The ancestral state of tooth implantation and attachment in the reptile line involved a tooth set in a shallow socket (i.e., subthecodonty) attached via ankylosis. However, reptiles have since explored all forms of tooth implantation (acrodonty, pleurodonty, and thecodonty) and attachment (ankylosis and gomphosis) in varying combinations (Bertin et al., 2018). Adaptive interpretations are frequently used to explain why reptiles may stray from the ancestral state. For example, dentine infoldings, called plicidentine, evolved independently multiple times within

Reptilia, and it is interpreted to be a mechanism to strengthen tooth attachment in kinetic-feeding predators (Maxwell, Caldwell & Lamoureux, 2011). Even the loss of teeth seems to be a response to the evolution of other adaptive structures, like the keratinous beak in birds and turtles (Davit-Béal, Tucker & Sire, 2009). The evolution of AVSA as seen in acrodontans and *Sphenodon punctatus* lacks any adaptive hypothesis. Here we suggest that AVSA is an adaptation associated with strong bite force.

Anecdotal evidence suggests that acrodont taxa possess a strong bite force: *S. punctatus* is said to possess a powerful, painful, and 'vice-like' bite (Robb, 1977; Daugherty and Cree, 1990), and one of the authors (KMJ) notes from personal experience that the veiled chameleon, *Chamaeleo calyptratus*, also possesses a painful bite and is reluctant to release its victim. Bite-force analyses also indicate agamids have a stronger bite than *S. punctatus*, relative to body size (Schaerlaeken et al., 2008; Jones and Lappin, 2009). The literature concerning bite force in lepidosaurs is numerous and implies a multitude of benefits for increased bite force. For instance, increase bite force is thought to improve prey capture and handling, particularly for the consumption of hard-bodied prey (Herrel et al., 1999; Herrel et al., 2001; Verwaijen, Van Damme & Herrel, 2002; Meyers et al., 2018). High bite force may also aid in territory defense and dominance (Herrel, Meyers & Vanhooydonck, 2001; Lailvaux et al., 2004; Huyghe et al., 2005; Husak et al., 2006; Jones & Lappin, 2009), and mating success (Lappin & Husak, 2005; Husak et al., 2009; Herrel et al., 2010). Higher bite force in lizards is often accompanied by skeletal correlates in the cranium and increased mass of the adductor musculature compared to those with lower bite force (Herrel, McBrayer & Larson, 2007; Fabre et al., 2014).

We hypothesize that taxa possessing acrodont dentition also possess a higher bite force, compared to those with pleurodont dentition, relative to body size. Furthermore, we suggest that

AVSA as seen in Acrodonta and *Sphenodon punctatus* protects teeth from the risk of breakage during strong biting and allows for effective feeding in older individuals with severely worn dentition. In order to test our hypothesis, we compared bite force among lepidosaurian taxa. We found that size-normalized bite force was significantly greater in acrodont lepidosaurs than pleurodont lepidosaurs. Furthermore, we discuss the evolution of AVSA within an adaptive context in response to high bite force.

Materials & Methods

To assess the relationship between bite force and tooth implantation, we collected data from thirty-eight peer-reviewed papers that record lepidosaurian bite force data (Supplementary Files). Publications that do not record metrics used in these statistical analyses and were excluded. The metrics recorded are the means of snout-vent length (SVL), head depth (HD), and bite force (BF). SVL, HD, and BF were all log-transformed and inspected for normality, following previous studies (Erickson et al., 2004; Wroe et al., 2005; Sellers et al., 2017).

We focused on the relationship between SVL and BF, as SVL is the most commonly reported measure of size in reptiles. However, many squamate reptiles possess elongate body forms that are not necessarily correlated to cranial allometry, and thus may not strongly correlate with bite force. Because of this, we also standardized by head depth in separate analyses. Multiple studies evaluating lepidosaur bite force suggest that head depth is a good predictor of bite force because it accommodates the adductor muscles (Herrel, de Grauw & Lemos-Espinal, 2001; Lappin, Hamilton & Sullivan, 2006; McBrayer & Anderson, 2007; Herrel et al., 2010). Tooth implantation was assessed by the authors.

To examine differences in bite force between acrodont and pleurodont taxa, analyses of covariance (ANCOVA) were performed using both size variables (SVL and HD) as covariates.

To further compare bite force across taxa of significantly different body masses, we calculated normalized bite force (NBF) as the residuals of a linear regression fit to (1) bite force and SVL or (2) bite force and HD. We refer to these values as SVL-NBF and HD-NBF, respectively. Differences in NBF between tooth implantation groups were then assessed using one-sided Kolmogorov–Smirnov (KS) and Mann-Whitney U (MWU) tests. Given unequal sample sizes, we also tested jackknife variants of the two tests (1000 replicates) which generated the same results.

Results

Bite force is higher in acrodont taxa than in pleurodont taxa when size standardized (Fig. 2). Raw bite force values ranged from 0.3 to 409.3 Newtons. SVL ranged 13.0-389.0 mm, and HD ranged 1.2-55.5 mm. SVL NBF ranged -2.14 to 1.76, whereas HD NBF ranged -2.85 to 3.93 (Table 1). ANCOVAs indicate significant differences between tooth implantation type groups after accounting for SVL and HD (Table 2). According to both KS and MWU tests acrodont SVL-NBF and HD-NBF values were significantly greater than pleurodonts (Table 2).

Linear regressions of bite force, SVL, and HD, indicate that the three variables are significantly and positively correlated (p-value < 0.05). Given strong, linear log-log relationships amongst the three values, data were log-transformed for all analyses. This relationship was stronger between bite force and SVL (p-value $<< 0.05$, Adj R-square = 0.729), compared to bite force and HD (p-value $<< 0.05$, Adj R-square = 0.337). Given this, we focus on the relationship between SVL and bite force for the remainder of this paper.

To evaluate the proportion of the lepidosaurian tree that has been examined in terms of bite force, we tallied all known publications to the best of our knowledge that record lepidosaurian bite force (Fig. 3; Supplementary Files). This includes those publications that were not included in the initial analyses that compare bite force between acrodont and pleurodont taxa. Species of seventeen lepidosaurian families were found to be represented, including four acrodont families and 13 pleurodont families. Dactyloidae was represented by the most species (n = 49), while the families of Sphenodontidae, Varanidae, and Trogonophidae were only represented by one species each (n = 1).

Discussion

Thus far, anatomical research related to biteforce in lepidosaurian reptiles has focused primarily on cranial musculature and skeletal dimensions, namely head depth, length, and width. However, teeth are more intimately associated with biting and oral processing than the aforementioned elements. Dental morphology is often adapted for diet, with generalists possessing a more generalized dentition and specialists possessing more unique tooth morphologies. For example, large bulbous molariform teeth are seen in some durophagous lizards (Estes and Williams, 1984). This is a stray from most iguanian and gekkotan lizards that possess simple columnar teeth with one to three small cusps. It should come as no surprise that tooth implantation and attachment is also shaped by oral processing capabilities. However, there is still the question of whether (1) AVSA developed due to strong bite force, or if (2) strong bite force evolved in response to AVSA.

In the first scenario, AVSA is a response to increased bite force. This concept must take into account the morphology of a typical pleurodont tooth versus a tooth that is influenced by AVSA. A typical pleurodont tooth, like that of geckos and non-acrodontan iguanians, is roughly cylindrical, and possesses a tooth base that is much less wide than it is tall. Unworn teeth in acrodontans and *Sphenodon punctatus* are comparatively much shorter and possess a wide tooth base that is strongly adhered to the jaw. Under higher bite forces and larger amounts of oral processing, a pleurodont tooth would be more susceptible to breakage. While pleurodont teeth are regularly replaced, high rates of breakage would still be detrimental to the animal's feeding capability. An acrodont tooth with a wide base and firm attachment is better suited to withstand higher bite forces without breakage. However that is not to say that breakage could not occur in taxa possessing AVSA. The extremely strong adherence of teeth can result in the occasional breakage of both tooth and bone in those taxa (Dosedělová et al., 2016).

In the second scenario, strong bite force is a response to AVSA. Lepidosaurs possessing AVSA are monophyodont and exhibit severe wear, particularly in the anterior dentition as seen in older individuals. Although those individuals have extremely worn teeth, they still manage to capture and consume prey. This is particularly the case for *Sphenodon punctatus*, which is known to capture and saw small birds with their teeth using propalinal jaw movement (Cartland-Shaw et al., 1998). If dentition is severely worn due to a lack of replacement, increased bite force would be crucial in allowing the jaws to clamp tightly onto prey. Thus, older individuals with few functional teeth can still forage and consume as needed. If strong bite force in *S. punctatus* and Acrodonta evolved as a mechanism to aid in territory defense or increased mating success, an older animal may still be successful even though it possesses severely worn teeth. At this time, we cannot favor one hypothesis over another. It is also possible that different lineages acquired AVSA under either scenario.

Of the taxa that were examined in previous publications, fewer species of lepidosaurs with acrodont tooth implantation have been studied in regard to bite force in comparison to those with pleurodont implantation (Fig. 3). Of the pleurodont taxa, 49 species of *Anolis* lizards (Dactyloidae) were the subjects of 20 publications that record bite force alone. Those taxa make up the largest proportion of pleurodont taxa analyzed here. The large number of *Anolis*-based studies is partly because they are speciose and represent a particularly important model taxon for ecological studies in the Americas. Conversely, only 16 unique species of acrodont lepidosaurs belonging to four separate families are the subject of 17 publications that record bite force. A larger sampling of acrodont taxa need to be examined in order to lend further support to the hypothesis that acrodont taxa possess a stronger bite force than pleurodont taxa. While this is impossible for *Sphenodon punctatus*, which is the only living representative of Sphenodontidae, a larger sampling of different species of acrodontan lizards and trogonophid amphisbaenians may be subjected to bite force analyses. Representatives of 16 families of squamate lizards have been subjected to bite force analyses, which leaves a large portion of the squamate line understudied. This is particularly the case for particularly snakes, for which we could find no bite-force research

Can AVSA be reversed?

The transition from pleurodont to acrodont tooth implantation occurred independently several times within Lepidosauria, but only in Acrodonta and Rhynchocephalia is the ankylosing so extreme that the tooth-bone boundary is difficult to detect upon initial inspection. Stem Acrodonta do not possess the extensive ankylosis and apical tooth implantation that is seen in the crown group, although the roots of the teeth are much shorter than most other iguanians (Simões et al., 2015). All crown acrodontans possess some degree of acrodont tooth implantation accompanied by severe ankylosis. Within that clade, AVSA may be a fixed trait that lacks the plasticity to explore other forms of tooth implantation and attachment. It is also possible that there has been no selective pressure acted upon tooth implantation and attachment within Acrodonta that would drive members of the clade away from AVSA since it initially evolved.

While this may imply a potentially adaptive circumstance to the initial evolution of this trait, it cannot be excluded that this trait may not longer act as an adaptation in extant Acrodonta.

AVSA is persistent within Rhynchocephalia, but several transitions in tooth implantation and attachment occurred from an initially acrodont state (Jenkins et al., 2017). *Ankylosphenodon pachyostosus* possesses 'ankylothecodont' dentition, in which the tooth has deeply implanted roots, but is nonetheless ankylosed to the surrounding bone (Reynoso, 2000). One genus, *Sapheosaurus*, potentially lacks marginal dentition, although it is unknown if this is due to extensive wear or if this taxon was truly edentulous (Cocude-Michel, 1963). The tooth plates seen in *Oenosaurus muelheimensis* also represent an interesting derivation from the typical tooth seen within Rhynchocephalia (Rauhut et al, 2012). Nonetheless, the tooth implantation seen in *O. muelheimensis* is acrodont, and tooth attachment is extensive. Although acrodonty is widespread within the clade, tooth implantation seems to be a more plastic trait within Rhynchocephalia than it is within Acrodonta.

Acrodonty in Amphisbaenia

Trogonophidae do not possess the severe ankylosing associated with AVSA, as seen in Gans (1960) and Gans and Montero (2008). The relatively lower bite force seen in *T. wiegmanni* compared to other acrodont taxa seen in our results was also likely impacted by the fact that *T. wiegmanni* is an elongate, serpentine-like form. Because of that, using SVL to standardize our results may not be meaningful in the case of this taxon. However, the other taxa examined in this study are not impacted by extremely elongate body plans. When bite-force is standardized by head depth, the same trend of greater acrodont bite force is more apparent for *T. wiegmanni*.

Trogonophidae is the only clade within Amphisbaenia to evolve acrodont tooth implantation. However, other amphisbaenians possess teeth with roots of varying lengths.

Overall, amphisbaenians possess shorter roots than seen in most iguanians and geckos. Tooth implantation in amphisbaenians is often described as 'subacrodont' or 'subpleurodont' to denote the stray from the 'typical' pleurodont tooth implantation seen in most other squamates (Estes, 1975; Yatkola, 1976; Sullivan, 1985; Charig and Gans, 1990; Kearney, Maisano & Rowe, 2004; Gans and Montero, 2008; Longrich et al., 2015; Čerňanský, Klembara & Müller., 2016). The evolution of tooth implantation and attachment in Amphisbaenia has not been explored further, but the trend towards dentition with shorter roots is intriguing. Bite-force experiments conducted on amphisbaenians could address the evolution of acrodonty within the clade. Further research on this, and on the dental tissues of amphisbaenians, is certainly warranted to address the evolution of tooth implantation and attachment in Amphisbaenia.

Conclusions

Acrodonty via severe ankylosis seen in *Sphenodon punctatus* and acrodontan squamates is likely an adaptation shaped by strong bite forces. The appearance of AVSA within those lineages, as well as extinct lineages, has implications for the early evolution of this trait. This may be informative of the early evolution of rhynchocephalian and acrodontan behavior~~al shifts~~, such as increased territoriality or dietary shifts. Within Amphisbaenia, a range of tooth implantation states exist, grading from pleurodonty to acrodonty. Further research on the dental changes taking place within this clade may suggest a new hypothesis for the evolution of acrodonty or lend support to the hypothesis presented here. While large portions of the squamate line have been subjected to bite force analyses, a much larger portion of the lineage has not, particularly snakes. Greater variation in bite force may exist among the clade, with subsequent implications for dental evolution in terms of tooth implantation, attachment, and morphology. A greater understanding of the evolution of dentition, particularly tooth implantation and attachment, will inform us of changes in behavior in ancient reptiles lineages.

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Figure Legend

Figure 1: Acrodont tooth implantation via severe ankylosis as seen in two acrodontan lizards (A & B) and a rhynchocephalian (C). A) the chameleon *Fercifer oustaleti* YPM R 1214, B) the agamid *Agama agama* YPM R 17936, and C) the rhynchocephalian *Sphenodon punctatus* YPM R 10647. D) Pleurodont tooth implantation as seen in *Ctenosaura* sp. YPM R 11060.

Figure 2: Acrodont vs. Pleurodont bite force. [Left panel] Log-transformed SVL and HD (mm) versus log bite force (N). Grey line represents a linear regression. [Right panel] SVL- and HD-normalized bite force distributions.

Figure 3: Number of species analyzed for bite force by family, colored by tooth implantation.

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Acrodont tooth implantation via severe ankylosis as seen in two acrodontan lizards (A & B) and a rhynchocephalian (C).

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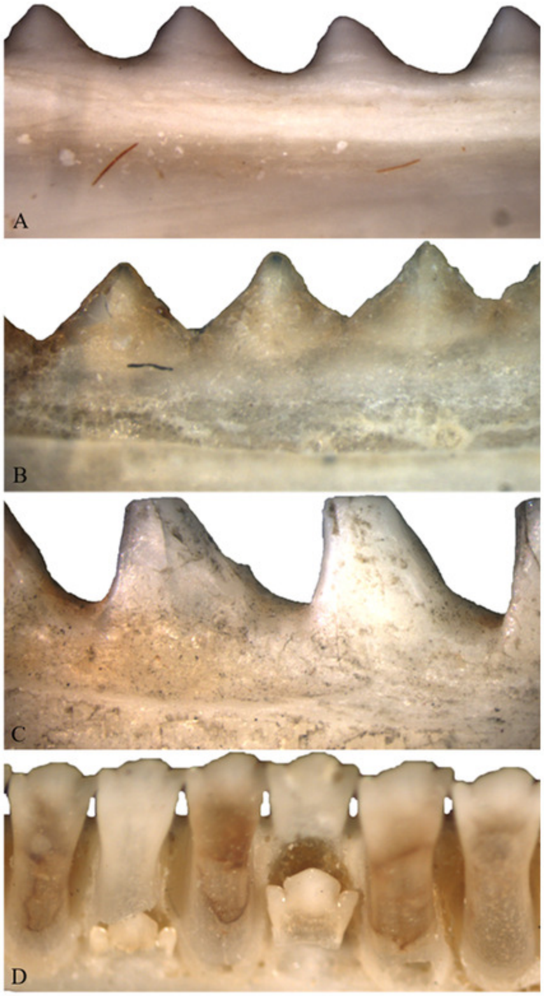
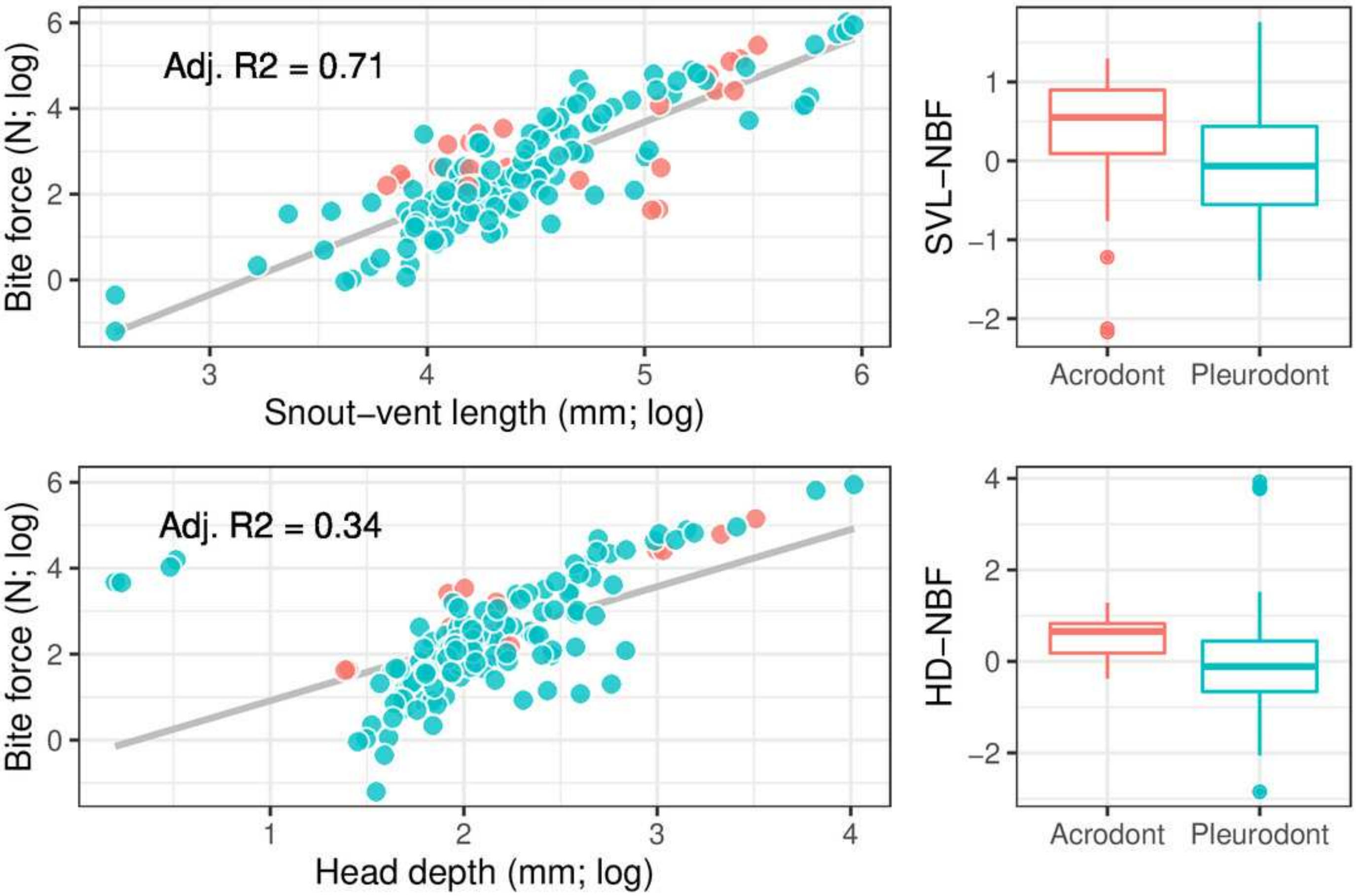


Figure 2

Acrodont vs. Pleurodont bite force.

[Left panel] Log-transformed SVL and HD (mm) versus log bite force (N). Grey line represents a linear regression. [Right panel] SVL- and HD-normalized bite force distributions.



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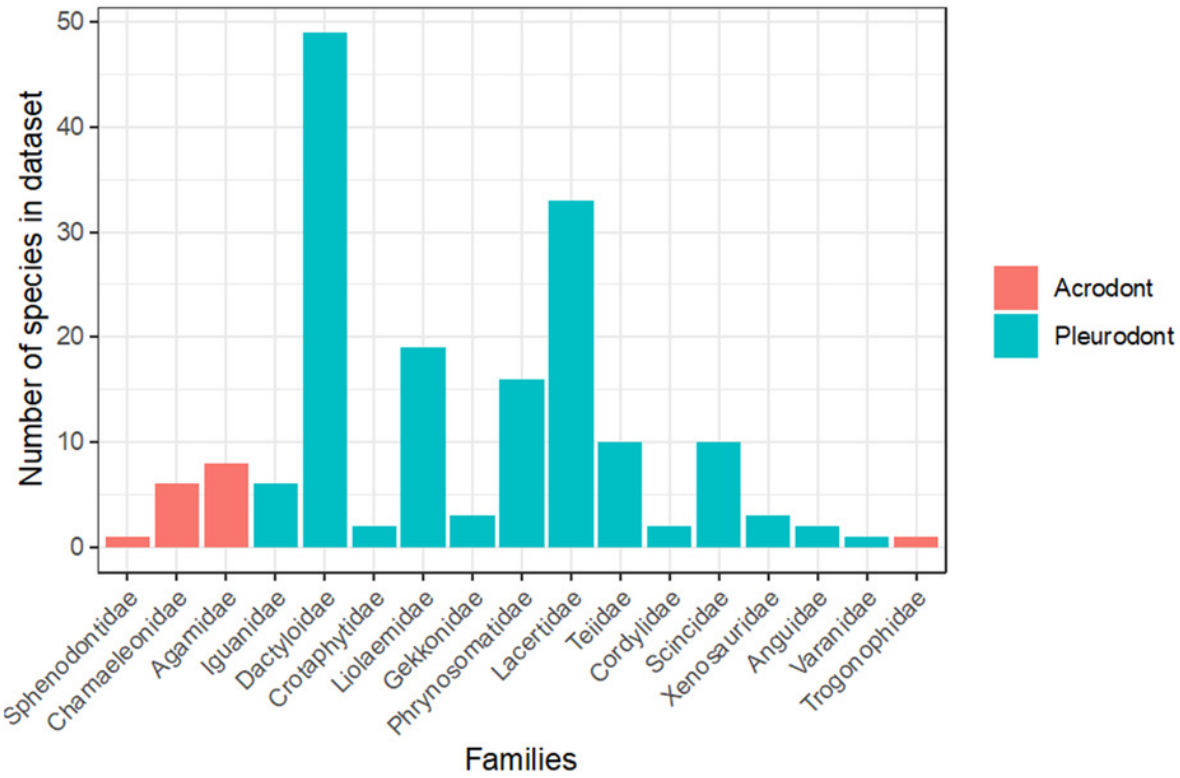

Table 1(on next page)

Summary statistics. SVL = snout-vent length. HD = head depth. NBF = normalized bite force

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	SVL (mm)				HD (mm)				Raw bite force (N)				SVL NBF				HD NBF			
	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
All	13.00	389.00	100.91	71.15	1.22	55.50	9.93	7.12	0.30	409.35	34.46	65.21	-2.17	1.76	0.00	0.72	-2.85	3.93	0.00	1.03
Acrodont	45.34	250.00	125.22	71.33	4.00	33.40	12.19	8.96	5.08	238.30	52.20	65.40	-2.17	1.30	0.26	1.00	-0.38	1.28	0.51	0.51
Pleurodont	13.00	389.00	97.27	70.65	1.22	55.50	9.67	6.87	0.30	409.35	31.81	64.99	-1.52	1.76	-0.04	0.67	-2.85	3.93	-0.06	1.06

7

Table 2(on next page)

Summary of statistical test results describing differences between bite force of taxa with different tooth implantation.

ANCOVAs tested covariation and raw bite force values. KS and MWU tests compared distributions of NBF values.

Table 2: Summary of statistical test results describing differences between bite force of taxa with different tooth implantation. ANCOVAs tested covariation and raw bite force values. KS and MWU tests compared distributions of NBF values.

Variable	Test	Test statistic	P-value	Jackknife mean p-value (10000 replicates)
SVL (logged)	ANCOVA	4.32	0.041	
	KS	0.38258	0.003748	0.0483
	MWU	2160	0.003064	0.0313
Head depth (logged)	ANCOVA	4.21	0.042	
	KS	0.4803	0.002	0.0344
	MWU	1461	0.001303	0.0246