Bite force data suggests relationship between acrodont tooth implantation and 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 (gomphosis) or via fusion (ankylosis). Generally speaking, 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 acrodont ankylosis that is seen in several lineages of Lepidosauria, a clade that is plesiomorphically pleurodont. The convergent evolution of acrodont ankylosis in several clades of lepidosaurs suggests a selective pressure shaped the evolution of the trait. We hypothesize that acrodont ankylosis as seen in Acrodonta and *Sphenodon punctatus*, is an adaptation either resulting from or allowing for a stronger bite force. We analyzed bite force data gathered from the literature to show that those taxa possessing acrodont dentition possess a stronger bite force on average than those taxa with pleurodont dentition. Dietary specialists with pleurodont dentition may also possess relatively high bite forces, though body size may also play a role in their ability to bite hard. Furthermore, our results have implications for the evolution of acrodont ankylosis and potential behaviors related to strong bite force that influenced the evolution of acrodonty within Acrodonta and Rhynchocephalia.

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13 Abstract

14   Extant and extinct reptiles exhibit numerous combinations of tooth implantation and

15 attachment. Tooth implantation ranges from those possessing roots and lying within a socket

16 (thecodonty), to teeth lying against the lingual wall of the jawbone (pleurodonty), to teeth

17 without roots or sockets that are attached to the apex of the marginal jawbones (acrodonty).

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19 adaptative reasonings are proposed as an underlying driver for evolutionary changes in some

20 forms of tooth implantation and attachment. However, a substantiated adaptive hypothesis is

21 lacking for the state of acrodont ankylosis that is seen in several lineages of Lepidosauria, a clade

22 that is plesiomorphically pleurodont. The convergent evolution of acrodont ankylosis in several

23 clades of lepidosaurs suggests a selective pressure shaped the evolution of the trait. We

24 hypothesize that acrodont ankylosis as seen in Acrodonta and *Sphenodon punctatus*, is an

25 adaptation either resulting from or allowing for a stronger bite force. We analyzed bite force data

26 gathered from the literature to show that those taxa possessing acrodont dentition possess a

27 stronger bite force on average than those taxa with pleurodont dentition. Dietary specialists with

28 pleurodont dentition may also possess relatively high bite forces, though body size may also play

29 a role in their ability to bite hard. Furthermore, our results have implications for the evolution of

30 acrodont ankylosis and potential behaviors related to strong bite force that influenced the

31 evolution of acrodonty within Acrodonta and Rhynchocephalia.

Introduction

33 Acrodont tooth implantation, where the tooth rests at the summit of the tooth-bearing

34 bone, evolved multiple times within Lepidosauria. It appears at least twice within squamate

35 reptiles, as seen in Acrodonta (Romer, 1956) and Trogonophidae (Gans, 1960), and once within

36 Rhynchocephalia (Jenkins et al., 2017) (Fig. 1). In Acrodonta and *Sphenodon punctatus,* the only

37 living representative of Rhynchocephalia, the dentition is strongly ankylosed (i.e., fused) via the

38 adjacent bone. In those taxa, teeth and surrounding tissues have been investigated thoroughly via

39 histological studies (Cooper & Poole, 1973; Smirina & Ananjeva, 2007; Kieser et al., 2009,

40 2011; Haridy, 2018), CT data (Dosedělová et al., 2016), and *in vitro* staining (Buchtová et al.,

41 2013; Salomies et al., 2019). However, the evolution of acrodont tooth implantation is seldom

42 discussed in an adaptive context.

43 Smith (1958) suggested that acrodonty is a trait associated with anchoring a permanent

44 dentition, and possibly inhibiting tooth replacement. Presently, this remains the only functional

45 hypothesis associated with acrodont dentition. Furthermore, growing body of work shows that

46   anchoring dentition does not inhibit tooth replacement, and anchoring occurs after tooth

47   generation and replacement cease (Handrigan & Richman, 2010; Buchtová et al., 2013;

48   Dosedělová et al., 2016; Haridy, 2018; Salomies et al., 2019). Smith (1958) also suggested that

49   thecodonty, where the tooth sits within a socket, is associated with permanent dentition. While

50   that is the case in mammals, it is well known that several reptilian lineages and early synapsids

51   possess thecodont implantation and replace their teeth with some regularity (e.g., Edmund, 1960,

52   1962; Gaengler, 2000; McIntosh et al., 2002; LeBlanc et al., 2017; D'Emic et al., 2019; Snyder

53   et al., 2020). Unlike acrodont dentition, thecodonty is not necessarily associated with ankylosis

54   and may attach to the surrounding bone ligamentously, termed gomphosis (Osborn, 1984).

55   There are a suite of traits commonly associated with acrodont tooth implantation, most

56   typically reduced tooth counts and severe tooth wear (Augé, 1997; Haridy, 2018). However,

57   those characters are not necessarily associated with every taxon exhibiting acrodont tooth

58   implantation. Though some have noted a loss of the alveolar foramen in the teeth of acrodontan

59   squamates, using this trait to diagnose those taxa (Zaher & Rieppel, 1999), it was later found that

60   *Pogona vitticeps* possesses nutrient foramina supplying the pulp cavities (Haridy, 2018). A

61   slowing or lack of tooth replacement, called monophyodonty, is also commonly associated with

62   acrodont tooth implantation (Smith, 1958; Cooper et al., 1970), although exceptions do exist

63   (Gow, 1977; Haridy, LeBlanc & Reisz, 2018). Even with monophyodont dentition, additional

64   teeth are typically still added to the posterior end of the tooth row throughout ontogeny, as is the

65   plesiomorphic condition within Reptilia (Robinson, 1976; Gow, 1977; Rieppel, 1992; Reynoso,

66   2003).

67   As individuals of Acrodonta and *Sphenodon punctatus* age, the boundary between tooth

68   and bone becomes difficult to determine externally (Fig. 2). This is a result of alveolar bone

69 growing to surround the outer portion of the tooth through ontogeny (Buchtová et al., 2013;

70 Haridy, 2018). This feature has caused some to erroneously propose that *S. punctatus* lacks teeth

71 entirely, instead possessing a serrated jawbone (Mlot, 1997). Severe wear may obscure the

72 anterior dentition in older, acrodont, monophyodont lepidosaurs, and in some cases the teeth may

73 be worn to the point where the bone itself forms the occlusal surface in the anterior portion of the

74 mouth (Robinson, 1976). To resist wear as the reptile ages, the pulp cavity infills with bone and

75 secondary dentine as seen in members of Acrodonta (Throckmorton, 1979; Smirina & Ananjeva,

76 2007; Dosedělová et al., 2016; Haridy, 2018) or secondary dentine and pulp-stones as seen in *S.*

77 *punctatus* (Kieser et al., 2009).

78   The ancestral state of tooth implantation and attachment in the reptilian lineage is thought

79 to involve a tooth set in a shallow socket (i.e., subthecodonty) attached via ankylosis (Bertin et

80 al., 2018), though some of the most basal reptiles exhibit pleurodont tooth implantation (LeBlanc

81 & Reisz, 2015). Furthermore, the periodontal ligament is likely ancestrally present in all

82 amniotes (LeBlanc et al., 2016). However, reptiles have since explored many forms of tooth

83 implantation (acrodonty, pleurodonty, and thecodonty) and attachment (ankylosis and

84 gomphosis) in varying combinations. Adaptive interpretations are occasionally used to explain

85 why reptiles may stray from the ancestral state within their respective clades (Smith, 1958;

86 Noble, 1969; Osborn 1984). Other adaptations for attachment include dentine infoldings, called

87 plicidentine, which evolved independently multiple times within Reptilia, and it is interpreted to

88 be a mechanism to strengthen tooth attachment in kinetic-feeding predators by increasing the

89 surface area for attachment (Preuschoft et al., 1991; Maxwell, Caldwell & Lamoureux, 2011;

90 Brink et al., 2014; MacDougall et al., 2014). Even the loss of teeth may be associated with the

91 evolution of other adaptive structures, like a keratinous beak (Davit-Béal, Tucker & Sire, 2009).

92   The ancestral state of tooth implantation and attachment for crown lepidosaurs is likely

93   pleurodont ankylosis, seen in basal members of both Squamata and Rhynchocephalia (e.g.,

94   Evans, 1980; Whiteside, 1986; Reynoso, 1998; Simões et al., 2018). Additionally, the

95   lepidosauromorphs *Marmoretta* and *Sophineta* possess pleurodont tooth implantation (Evans,

96   1991; Evans & Borsuk-Białynicka, 2009). The evolution of acrodont ankylosis accompanied by

97   bone and secondary dentine deposition, as seen in Acrodonta and *Sphenodon punctatus,* lacks

98   any adaptive hypothesis. Here we suggest that this combination of traits is an adaptation

99   associated with strong bite force. Anecdotal evidence suggests that acrodont taxa possess a

100   strong bite: *S. punctatus* is said to possess a painful and 'vice-like' bite (Robb, 1977; Daugherty

101   and Cree, 1990), and one of the authors (KMJ) notes from personal experience that the veiled

102   chameleon, *Chamaeleo calyptratus*, also possesses a painful bite and is reluctant to release its

103   victim. Bite-force analyses also indicate agamids have a stronger bite than *S. punctatus*, relative

104   to body size (Schaerlaeken et al., 2008; Jones and Lappin, 2009).

105   The literature concerning bite force in lepidosaurs is numerous and implies a multitude of

106   benefits for increased bite force. For instance, increase bite force is thought to improve prey

107   capture and handling in lepidosaurs, particularly for the consumption of hard-bodied prey (Herrel

108   et al., 1999; Herrel et al., 2001; Verwaijen, Van Damme & Herrel, 2002; Meyers et al., 2018).

109   High bite force may also aid in territory defense and dominance (Herrel, Meyers &

110   Vanhooydonck, 2001; Lailvaux et al., 2004; Huyghe et al., 2005; Husak et al., 2006; Jones &

111   Lappin, 2009), and mating success (Lappin & Husak, 2005; Husak et al., 2009; Herrel et al.,

112   2010). Higher bite force in lizards is often accompanied by skeletal correlates in the cranium and

113   increased mass of the adductor musculature compared to those with lower bite force (Herrel,

114   McBrayer & Larson, 2007; Fabre et al., 2014). Cranial kinesis also plays a strong role in bite

115   force, with a more rigid or akinetic skull being more capable of producing a strong bite

116   (Erickson, Lappin & Vliet, 2003; Wroe, McHenry & Thomason, 2005; Tseng & Binder, 2010;

117   Cost et al., 2020). Thus, the varying degrees of kinesis in lizard and tuatara skulls can certainly

118   impact bite force within Lepidosauria (Frazzetta, 1962).

119   We suggest that acrodont tooth implantation is yet another skeletal trait associated with

120   bite force. We hypothesize that taxa possessing acrodont dentition also possess a higher bite

121   force, compared to those with pleurodont dentition, relative to body size. Furthermore, the

122   accompanied bone deposition around the base of the dentition may also assist in resisting strong

123   biting. In order to test our hypothesis, we analyzed bite force data based on a comprehensive

124   literature review among lepidosaurian taxa. We found that size-normalized bite force was

125   significantly greater in acrodont lepidosaurs than pleurodont lepidosaurs. Furthermore, we

126   discuss the evolution of acrodont ankylosis within an adaptive context in response to high bite

127   force.

Materials & Methods

129   To assess the relationship between lepidosaurian bite force and tooth implantation, we

130   analyzed previously recorded bite force data. We collected mean snout-vent length (SVL), mean

131   head depth (HD), and mean bite force (BF) measurements from thirty-nine peer-reviewed papers

132   (Supplementary Files). Though bite force can be measured via different methods (see Lappin &

133   Jones, 2014), all studies analyzed here measured the orthal bite. Following previous studies

134   (Erickson et al., 2004; Wroe, McHenry & Thomason, 2005; Sellers et al., 2017) we analyzed

135   log-transformed measurements (analyses of non-transformed data provided in supplement).

136   We focused on the relationship between SVL and BF, as SVL is the most commonly

137   reported measure of size in reptiles (Fig. 3). However, many squamate reptiles possess elongate

138   body forms that are not necessarily correlated to cranial allometry, and thus may not strongly

139   correlate with bite force. Because of this, we also standardized by head depth in separate

140   analyses (Fig. 4). Multiple studies evaluating lepidosaurian bite force suggest that head depth is a

141   good predictor of bite force because it accommodates the adductor musculature (Herrel, de

142   Grauw & Lemos-Espinal, 2001; Lappin, Hamilton & Sullivan, 2006; McBrayer & Anderson,

143   2007; Herrel et al., 2010). Tooth implantation was assessed by the authors.

144   To examine differences in bite force between acrodont and pleurodont taxa, analyses of

145   covariance (ANCOVA) were performed using both size variables (log-SVL and log-HD) as

146   covariates. To further compare bite force across taxa of significantly different body masses, we

147   calculated normalized bite force (NBF) as the residuals of a linear regression fit to (1) log-SVL

148   and log-BF or (2) log-HD and log-BF. We refer to these values as SVL-NBF and HD-NBF,

149   respectively. Differences in NBF between tooth implantation groups were then assessed using

150   Kolmogorov–Smirnov (KS) tests.

151   To evaluate the proportion of the lepidosaurian tree that has been examined in terms of

152   bite force, we tallied all known publications that record lepidosaurian bite force (Fig. 5;

153   Supplementary Files). This includes those publications that were not included in the initial

154   analyses that compare bite force between acrodont and pleurodont taxa due to a lack of raw bite

155   force data or a lack of necessary variables (i.e., SVL). Seventeen lepidosaurian families were

156   represented by bite force data, including four acrodont families and 13 pleurodont families.

157   Dactyloidae was represented by the most species (n = 49), while the families of Sphenodontidae,

158   Varanidae, and Trogonophidae were only represented by single species.

159   **Results**

160   Bite force is higher in acrodont taxa than in pleurodont taxa after accounting for size

161   differences (Fig. 3B & 4B). Raw bite force values ranged from 0.3 to 409.3 Newtons, SVL

162   ranged 13.0-389.0 mm, and HD ranged 4.0-55.5 mm. SVL-NBF ranged -2.17 to 1.76, whereas

163   HD-NBF ranged -2.35 to 1.61 (Supplementary Files). ANCOVAs of tooth implantation type and

164   SVL and of tooth implantation type and HD have low p-values (0.064 and 0.0023, respectively)

165   indicating differences in bite force between the acrodont and pleurodont taxa after accounting for

166   SVL and HD. According to one-sided KS tests, acrodont SVL-NBF and HD-NBF values were

167   significantly greater than those of pleurodonts. Linear regressions of log-SVL and log-BF, and of

168   log-HD and log-BF were statistically significant and exhibited positive slopes (p-value < 0.05).

169   Correlations were stronger between log-SVL and log-BF (Adj R-square = 0.71), compared to

170   log-HD and log-BF (Adj R-square = 0.69).

171   The only direct comparisons that could be made for both tooth implantation categories

172   and diet were for insectivory and herbivory (Fig. 3C & 4C). According to one-sided KS tests,

173   SVL-NBF and HD-NBF values were significantly greater for insectivorous acrodonts compared

174   to insectivorous pleurodonts (p-value < 0.05). Overall, pleurodont insectivores exhibited a large

175   range of NBF values (Fig. 3C). Although acrodont insectivores seemingly also exhibited a wide

176   range of SVL-NBF values, this is influenced by the elongate body plan seen in on taxon,

177   *Trogonophis wiegmanni*, in which head dimensions do not correlate strongly with SVL (Fig.

178   3C). HD-NBF values for acrodont insectivores range less than the SVL-NBF values of the same

179   group (Fig 4C). A direct comparison of herbivorous acrodonts and pleurodonts reveals a lack of

180   significant difference between the NBF vales of the two groups, according to one-sided KS tests.

181   While direct comparisons between tooth implantation types and other diets are not possible using

182   the available data, we also found that pleurodont frugivores exhibit the highest median NBF

183   values whereas durophagous pleurodonts exhibit the lowest median NBF values, although the

184   latter is based on a small number of measurements (n = 2).

185   Low SVL-NBF values in Trogonophidae indicate that the clade exhibits lower bite force

186   than expected for SVL (Fig. 3D). These values were much lower than for other acrodont taxa,

187   dramatically impacting the range and median SVL-NBF values for acrodonts. This trend is not

188   present in HD-NBF, in which Trogonophidae exhibits the highest median bite force (Fig. 4D).

189   Excluding Trogonophidae, Chamaeleonidae exhibited the highest SVL-NBF and HD-NBF

190   values among acrodonts. Among pleurodont taxa, Lacertidae exhibits the largest range of NBF

191   values for both SVL and HD. Anguidae exhibits the greatest median values for HD-NBF.

192   Iguanidae exhibits the greatest median SVL-NBF values. Both Gekkonidae and Scincidae exhibit

193   low median SVL-NBF values, but data does not exist for either clade for HD-NBF.

194   Phrynosomatidae exhibits the lowest median HD-NBF values.

195   **Discussion**

196   Thus far, anatomical research related to bite force in lepidosaurian reptiles has focused

197   primarily on cranial musculature and skeletal dimensions, namely head depth, length, and width.

198   However, teeth are more intimately associated with biting and oral processing than the

199   aforementioned elements. Dental morphology is often adapted for diet, with generalists

200   possessing a more unspecialized dentition and specialists often possessing more unique tooth

201   morphologies (e.g., Estes & Williams, 1984), though true specialists within lizards are rare and

202   diets are often quite varied (Greene, 1982; Schaerlaeken et al., 2012). It should come as no

203   surprise that tooth implantation and attachment are also shaped by oral processing capabilities.

204   For example, multiple functional hypotheses exist for the evolution of thecodonty and associated

205   periodontal ligament: a means of shock absorption and dissipation (Noble, 1969; Picton, 1989;

206 McIntosh et al., 2002; Bosshardt et al., 2008), facilitation of post-eruption tooth movement

207 (Osborn, 1984; Bosshardt et al., 2008), creation of a sensory system to allow the jaws to

208 reposition during mastication (Bosshardt et al., 2008), flexible attachment of tooth to bone

209 (Leblanc & Reisz, 2013), and for anchoring permanent dentition in mammals as mentioned

210 above (Smith, 1958). Similar hypotheses for the evolution of acrodont ankyloses in reptiles are

211 lacking. Here we show that there is a relationship between acrodont ankylosis and high bite

212 force. However, there is still the question of whether (1) acrodont ankylosis developed due to

213 strong bite force, or if (2) strong bite force evolved as a consequence of acrodont ankylosis.

214   In the first scenario, acrodont ankylosis is a response to increased bite force by further

215 securing the tooth to the bone as a means to resist failure during strong biting. Previous work

216 shows that a stouter, blunter tooth, like that of acrodont taxa, is more resistant to failure under

217 increased bite forces (Lucas & Luke, 1984; Evans & Sanson, 1998; Jones, 2006), compared to a

218 more columnar or piercing tooth seen in most pleurodont lepidosaurs which is prone to breakage

219 under increased forces (Evans & Sanson, 1998; Erickson, Lappin, & Vliet, 2003). We suggest

220 that the ankylosis and bone deposition seen in Acrodonta and *Sphenodon punctatus* that

221 accompanies the typical acrodont tooth morphology would also aid in resisting tooth failure.

222 Simply put, a fused tooth is sturdier than a tooth attached via soft tissue. The specific

223 combination of morphology, implantation, and attachment seen in Acrodonta and *S. punctatus*

224 allows for a tooth that is most resistant to failure. However, that is not to say that breakage is

225 impossible in taxa possessing acrodont ankylosis. The extremely strong adherence of teeth can

226 result in the occasional breakage of both tooth and bone (Dosedělová et al., 2016). Perhaps this is

227 due to the more brittle nature of such a strongly fused tooth, compared to a ligamentous

228 attachment in which the tooth is better cushioned during feeding (Noble, 1969; Picton, 1989;

229 McIntosh et al., 2002; Bosshardt et al., 2008). Though pleurodont dentition in other lizards is

230 also ankylosed, most lack the bone growth that adheres the tooth to the jaw that is seen in

231 Acrodonta and *S. punctatus*. However, there are a few notable squamates without acrodont

232 dentition that possess large deposits of boney tissue around the base of the teeth (e.g., Caldwell,

233 1999; Zaher & Rieppel, 1999).

234   In the second scenario, strong bite force is a response to acrodont ankylosis. Acrodonta

235 and *Sphenodon punctatus* are monophyodont and exhibit severe wear, particularly in the anterior

236 dentition as seen in older individuals. Although those individuals have extremely worn teeth,

237 they still manage to capture and consume prey. If the dentition is severely worn due to a lack of

238 replacement, increased bite force would be crucial in allowing the jaws to clamp tightly onto

239 prey. However, this could be a factor of monophyodonty instead of acrodonty alone.

240 Nonetheless, older individuals with few functional teeth can still forage and consume as needed.

241 If strong bite force in Acrodonta and *S. punctatus* evolved as a mechanism to aid in territory

242 defense or increased mating success (opposed to prey handling), an older animal may be

243 successful even though it possesses severely worn teeth. At this time, we cannot favor one

244 hypothesis over another. It is also possible that different lineages acquired acrodont ankylosis

245 under either scenario.

246   Two other hypotheses unrelated to increased bite force could explain the evolution of

247 acrodont ankylosis from an initially pleurodont state. The first is that this combination of

248 implantation and attachment evolved convergently in response to a shared diet. All extant

249 lepidosaurs possessing acrodont ankylosis fill various dietary niches ranging from insectivory to

250 herbivory (Fig. 3 & 4), calling to question the idea that the combined traits are currently acting as

251 an adaptation for similar diets. Furthermore, extant squamates eating hard-shelled organisms,

252   such as *Varanus niloticus* and *Tiliqua scincoides* (Rieppel, 1979; Estes & Williams, 1984), and

253   high-fibered fruit, such as *Gallotia galloti* (Valido, Nogales, & Medina, 2003), possess

254   pleurodont dentition, so it cannot be assumed that acrodont ankylosis evolved as a means to

255   process tough foods (or that it is the only means by which to process tough foods, see section

256   below). We also doubt that acrodont ankylosis first arose in response to a particular diet,

257   because basal rhynchocephalians possessing acrodont dentition were likely insectivorous (Evans,

258   1980; Fraser & Walkden, 1983; Whiteside, 1986). Insectivory is also widespread among extant

259   squamates, which mostly possess pleurodont dentition, so it seems unlikely that the initial

260   evolution of acrodont ankylosis would be strongly influenced by an insectivorous diet.

261   Acrodonty remained widespread as rhynchocephalians diversified to fill various dietary niches

262   (Jones 2006, 2009), so it seems unlikely that acrodont ankylosis evolved in response to any

263   particular diet. Possessing firmly ankylosed acrodont dentition in conjunction with a higher bite

264   force does allow access to harder foodstuffs, but it cannot be assumed to be the sole reason for

265   the evolution of acrodont ankylosis.

266   The second hypothesis is that shared oral mechanics shaped the evolution of acrodont

267   ankylosis, implying a mechanical constraint influenced the evolution of the trait. Previous bite

268   force measurements of *S. punctatus* only measure the orthal bite, and not the force of the

269   propalinal stroke (Schaerlaeken et al., 2008; Jones and Lappin 2009). While both squamates and

270   *Sphenodon punctatus* are capable of orthal shearing, *S. punctatus* is well-known for possessing

271   an akinetic skull and using propalinal jaw movement, where the lower jaw moves in an anterior-

272   posterior motion (Robinson, 1976; Gorniak et al, 1982; Cartland-Shaw et al., 1998; Jones, 2008).

273   This is in contrast with most squamates which possess kinetic skulls and typically favor

274   streptostyly in order to move the lower jaw in a fore and aft motion (Evans, 2008). The rigidity

275   afforded by an akinetic skull does allow for a relatively stronger orthal bite in *Sphenodon*

276   *punctatus* than most lizards, and kinesis is thought to reduce the strength of a bite though

277   allowing for improved prey capture and handling. However, the acrodont taxa examined here

278   possess some of the least kinetic skulls among squamates (Iordansky, 1990; Arnold, 1998),

279   possibly improving the capability of a strong bite. Though the acrodont taxa examined here do

280   possess more rigid skulls, allowing for stronger biting, there does not seem to be a shared oral

281   mechanism that would influence the evolution of acrodont ankylosis.

282   It is worth noting that not all acrodontan lizards possess a fully acrodont dentition.

283   Agamid lizards possesses a dentition that is anteriorly pleurodont and posteriorly acrodont

284   (Cooper et al., 1970). While the pleurodont dentition still regularly replaces, the acrodont

285   dentition does not. In those taxa, tooth morphology varies greatly along the tooth row, with the

286   anterior pleurodont teeth being more slender and sharp. Bite force decreases as gape angle

287   increases (e.g., Dumont & Herrel, 2003), thus the anterior pleurodont dentition is consistently

288   subjected to less force than the posterior acrodont dentition and need not be as 'reinforced' as the

289   posterior acrodont dentition. This combination of factors (tooth morphology, implantation,

290   attachment, and relative position) suggests that the anterior and posterior portions of the mouth

291   play differing roles in food processing. While the anterior dentition may be better suited for

292   grasping and piercing, the posterior dentition is more suited for crushing. Chameleons do not

293   possess such a marked difference in tooth morphology, implantation, and attachment as agamid

294   lizards. This could reflect a difference in diet as well as a difference in the nature of lingual prey

295   apprehension between agamids and chameleons. Though both use lingual prey apprehension to

296   capture food, chameleons can ballistically project their tongues a considerable distance in

297   comparison to agamids (Meyers & Nishikawa, 2000). This projection could certainly affect, or

298   potentially damage, the anterior dentition if it were of a more slender morphology and not

299   strongly ankylosed to the jaw bone.

300   Of the taxa that were examined in previous publications, fewer species of lepidosaurs

301   with acrodont tooth implantation have been studied in regard to bite force in comparison to those

302   with pleurodont implantation (Fig. 5). Of the pleurodont taxa, 49 species of *Anolis* lizards

303   (Dactyloidae) were the subjects of 20 publications that record bite force alone. Those taxa make

304   up the largest proportion of pleurodont taxa analyzed here. The large number of *Anolis*-based

305   studies is partly because they are speciose and represent a particularly important model taxon for

306   ecological and evolutionary studies in the Americas. Conversely, only 16 unique species of

307   acrodont lepidosaurs belonging to four separate families are the subject of 17 publications that

308   record bite force. Only 16 families of squamate lizards have been subjected to bite force

309   analyses, which leaves a large portion of the squamate line understudied (Fig. 5). Further

310   examination of bite force and diet across Lepidosauria may enforce our hypothesis while also

311   revealing other ecological and evolutionary trends.

312   **Can acrodont ankylosis be reversed?**

313   The transition from pleurodont to acrodont tooth implantation occurred independently

314   several times within Lepidosauria (Acrodonta, Trogonophidae, Rhynchocephalia) and it is even

315   seen in stem lepidosauromorphs (Sobral, Simões & Schoch, 2020), but only in Acrodonta and

316   Rhynchocephalia is the tooth-bone boundary difficult to detect upon initial inspection. Stem

317   Acrodonta do not possess the extensive bone deposition that accompanies ankylosis, nor do they

318   possess the apical tooth implantation that is seen in the crown group, although the roots of the

319   teeth are much shorter than most other iguanian lizards and possess a relatively increased degree

320   of ankylosis (Simões et al., 2015). All crown acrodontans possess some degree of acrodont tooth

321   implantation accompanied by ankylosis and bone deposition. Within that clade, acrodont

322   ankylosis may appear to be a fixed trait that lacks the plasticity to explore other forms of tooth

323   implantation and attachment. However, developmental evidence suggests that the tissues that

324   promote tooth formation and replacement in some acrodontan lizards is still present (Salomies et

325   al., 2019), thus there is potential for the reversal of monophyodonty, and by extension, strong

326   ankylosis. The more likely explanation is that there has been no selective pressure acted upon

327   tooth implantation, attachment, and replacement within Acrodonta that would drive members of

328   the clade away from acrodont ankylosis since it initially evolved. While this may imply a

329   potentially adaptive circumstance to the initial evolution of this trait, it cannot be excluded that

330   this trait may no longer act as an adaptation in extant Acrodonta.

331   Acrodont ankylosis is persistent within Rhynchocephalia, but several transitions in tooth

332   implantation occurred from an initially acrodont state (Jenkins et al., 2017). *Ankylosphenodon*

333   *pachyostosus* possesses 'ankylothecodont' dentition, in which the tooth has deeply implanted

334   roots, but is nonetheless ankylosed to the surrounding bone (Reynoso, 2000). One genus,

335   *Sapheosaurus*, potentially lacks marginal dentition, although it is unknown if this is due to

336   extensive wear or if this taxon was truly edentulous (Cocude-Michel, 1963). The teeth of

337   *Priosphenodon avelasi* possesses a more complex dentition, with teeth set within a shallow

338   socket and periodontium holding adjacent teeth together (LeBlanc et al., 2020). The tooth plates

339   seen in *Oenosaurus muelheimensis* also represent an interesting derivation from the typical tooth

340   seen within Rhynchocephalia (Rauhut et al, 2012). Nonetheless, the tooth implantation of *O.*

341   *muelheimensis* was described as acrodont. Although acrodonty is widespread within

342   Rhynchocephalia, tooth implantation seems to be a more plastic trait within this clade than it is

343   within Acrodonta. Though implantation and attachment within Rhynchocephalia may vary,

344 monophyodonty seems to be persistent in derived rhynchocephalians. However, the most basal

345 rhynchocephalian known, *Gephyrosaurus bridensis*, did replace its pleurodont teeth regularly

346 much like pleurodont lizards (Evans, 1985).

347 **More than One Way to Crush a Clam – Durophagous Pleurodonts**

348   Aside from the state of acrodont ankylosis, other forms of dentition may act in a similar

349 function. Many suggest that the molariform teeth of durophagous lizards are well equipped for

350 withstanding strong, crushing bites necessary for ingesting molluscs and other hard-shelled prey

351 (Evans & Sanson, 1998; Schaerlacken et al., 2012). *Dracaena guianensis* and *Tiliqua scincoides*

352 (both pleurodont) are the only durophagous taxa for which SVL-NBF data could be analyzed

353 within the present study. *D. guianensis* is the only durophagous representative for HD-NBF.

354 Though sample size is limited, those durophagous taxa showed the lowest median NBF values

355 (Fig 3 & 4). However, raw data reports a bite force of 383.3 N for *D. guianensis*, which is among

356 the higher raw bite force values recorded. Given the general increase in bite force with size, the

357 larger overall size of *D. guianensis* compared to most taxa within the dataset (Supplementary

358 Files) is likely the primary driver of its high bite force, although other morphological,

359 evolutionary, and ecological factors may play supporting roles. Nonetheless, even under higher

360 bite forces, their teeth are pleurodont, suggesting that not all dentition need evolve into acrodont

361 ankylosis in order to withstand high bite forces.

362   *Varanus niloticus* has been subjected to several studies concerning its dental morphology

363 and cranial kinematics (Rieppel, 1979; Rieppel & Labhardt, 1979; Condon, 1987; D'Amore,

364 2015). *V. niloticus* undergoes an ontogenetic change in dentition, with juveniles possessing more

365 slender teeth that later transition to more bulbous molariform dentition (Rieppel & Labhardt,

366 1979; D'Amore, 2015). This ontogenetic shift in tooth morphology is often attributed to an

367 ontogenetic shift in diet, with adults consuming larger proportions of molluscs and crabs

368 (Rieppel & Labhardt, 1979; Luiselli, Akani & Capizzi, 1999; Lenz, 2004). However, some

369 suggest there is no evidence for a dietary shift within this species (Bennett, 2002), while others

370 show that certain populations consume snails and crabs while other populations do not consume

371 hard-bodied prey (Losos & Greene, 1988). Other species of *Varanus* without specialized

372 dentition are also known to eat hard-bodied prey, such as turtles and crabs (Losos & Green,

373 1988). We might presume *V. niloticus* has a relatively high raw bite force, allowing for the

374 consumption of hard-bodied prey, but how that relates to body size and how it compares to the

375 bite forces of other varanids is unknown.

376 **Acrodonty in Amphisbaenia**

377   We know little about tooth attachment in Trogonophidae, though the clade is thought to

378 be acrodont and the teeth are likely ankylosed (Gans, 1960; Gans & Montero, 2008). The

379 relatively lower bite force seen in *T. wiegmanni* compared to other acrodont taxa seen in our

380 results was likely impacted by the fact that *T. wiegmanni* is an elongate, serpentine-like form.

381 Because of that, using SVL to standardize our results may not be meaningful in the case of this

382 taxon. However, the other taxa examined in this study are not impacted by extremely elongate

383 body plans. When bite-force is standardized by head depth, the same trend of greater acrodont

384 bite force is more apparent for *T. wiegmanni*. Further work on the dentition of this clade would

385 clarify if it too possesses strong ankylosis or bone deposition around the base of the dentition like

386 that of Acrodonta and *Sphenodon punctatus*.

387   Trogonophidae is the only clade within Amphisbaenia to evolve acrodont tooth

388 implantation. However, other amphisbaenians possess teeth with roots of varying lengths.

389 Overall, amphisbaenians possess shorter roots than what is seen in most iguanians and geckos.

390 Tooth implantation in amphisbaenians is often described as 'subacrodont' or 'subpleurodont' to

391 denote the stray from the 'typical' pleurodont tooth implantation seen in most other squamates

392 (Estes, 1975; Yatkola, 1976; Sullivan, 1985; Charig and Gans, 1990; Kearney, Maisano & Rowe,

393 2004; Gans and Montero, 2008; Longrich et al., 2015; Čerňanský, Klembara & Müller., 2016).

394 The evolution of tooth implantation and attachment in Amphisbaenia has not been explored

395 further, but the trend towards dentition with shorter roots is intriguing. Bite-force experiments

396 conducted on amphisbaenians could address if the evolution of acrodonty within the clade is

397 related to high bite force and diet. However, we cannot exclude the evolution of acrodont tooth

398 implantation within Amphisbaenia may have arose for other reasons, such as limited jaw space.

Conclusions

400   Acrodont ankylosis accompanied by increased bone deposition seen in Acrodonta and

401 *Sphenodon punctatus* is likely an adaptation related to strong bite force. We do not know if this

402 form of tooth implantation and attachment evolved in response to high bite force, or *vice versa*.

403 Nonetheless, there are behavioral implications for the early evolution of this trait. Changes in

404 tooth implantation and attachment are often associated with diet-related hypotheses. However, it

405 cannot be presumed that increased bite force or changes in tooth implantation and attachment are

406 only associated with diet. When discussing the evolution of such traits, we must take into

407 account other possible behavioral influences, such as territory defense, intraspecific combat, and

408 mating success, which are also associated with increased bite force. Testing such hypotheses in

409 the fossil record may prove impossible, but it is still necessary to speculate all scenarios.

410 Furthermore, these dental traits may have evolved convergently in response to different selective

411 pressures depending on the clade. Acrodont ankylosis accompanied by bone deposition may be

412 fixed traits in Acrodonta, which has not explored other forms of tooth implantation and

413   attachment. However, rhynchocephalians were able to explore other forms of tooth implantation

414   throughout their evolutionary history, though are largely monophyodont.

415   Acrodont ankylosis is not the only form of tooth implantation and attachment potentially

416   associated with higher bite forces. Durophagous squamates, though pleurodont, often possess

417   molariform tooth morphologies that are also able to withstand increased bite force. In the present

418   study, it appears that higher bite force is likely related to larger body size for these specialists.

419   However, bite force and its relationships with tooth morphology requires further study in

420   durophagous squamates as well as other dietary specialists. Most of the taxa analyzed were

421   insectivorous generalists, though carnivorous acrodonts, herbivorous acrodonts and pleurodonts,

422   and durophagous, frugivorous, and omnivorous pleurodonts were also included. The array of

423   diets seen in extant acrodont taxa suggests that *if* acrodont ankylosis evolved as an adaptation to

424   a particular diet, it may no longer act in an adaptive capacity for a specific diet. We encourage

425   further study on dietary specialists, for greater variation in bite force may exist among Squamata,

426   with subsequent implications for dental evolution in terms of tooth implantation, attachment,

427   replacement, and morphology.

428

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750

751 **Figure Legend**

752 **Figure 1: Simplified phylogeny of Lepidosauria from Gauthier et al. (2012).** Orange

753 branches indicate acrodont ankylosis. Phylogeny is based on a morphological dataset and

754 parsimony analysis.

755 **Figure 2: Acrodont ankylosis as seen in two species of Acrodonta (A & B) and a**

756 **rhynchocephalian (C) and pleurodont ankylosis (D).** A) the chameleon *Fercifer oustaleti*

757 YPM R 1214, B) the agamid *Agama agama* YPM R 17936, and C) the rhynchocephalian

758 *Sphenodon punctatus* YPM R 10647. D) Pleurodont tooth implantation as seen in *Ctenosaura* sp.

759 YPM R 11060.

760 **Figure 3: Acrodont vs. Pleurodont bite force (SVL).** A) Linear regression (grey line) of log-

761 transformed snout-vent length (SVL) and bite force. Acrodonts indicated by red datapoints and

762 pleurodonts indicated by blue datapoints. B) Boxplot of the distributions of snout-vent length

763 normalized bite force (SVL-NBF), calculated as the residual values from the linear regression in

764 (A), overlain with residual values as datapoints. C) Breakdown of SVL-NBF values show in (B)

765 by diet. D) Breakdown of SVL-NBF values shown in (B) by family and separated based on tooth

766 implantation (acrodonts in red, pleurodonts in blue).

767 **Figure 4: Acrodont vs. Pleurodont bite force (HD).** A) Linear regression (grey line) of log-

768 transformed head depth (HD) and bite force. Acrodonts indicated by red datapoints and

769 pleurodonts indicated by blue datapoints. B) Boxplot of the distributions of head depth

770 normalized bite force (HD-NBF), calculated as the residual values from the linear regression in

771 (A), overlain with residual values as datapoints. C) Breakdown of HD-NBF values show in (B)

772 by diet. D) Breakdown of HD-NBF values shown in (B) by family and separated based on tooth

773 implantation (acrodonts in red, pleurodonts in blue).

774 **Figure 5: Number of species analyzed for bite force by family, colored by tooth**

775 **implantation**.

776

Figure 1

Simplified phylogeny of Lepidosauria from Gauthier et al. (2012).

Orange branches indicate acrodont ankylosis. Phylogeny is based on a morphological dataset and parsimony analysis.
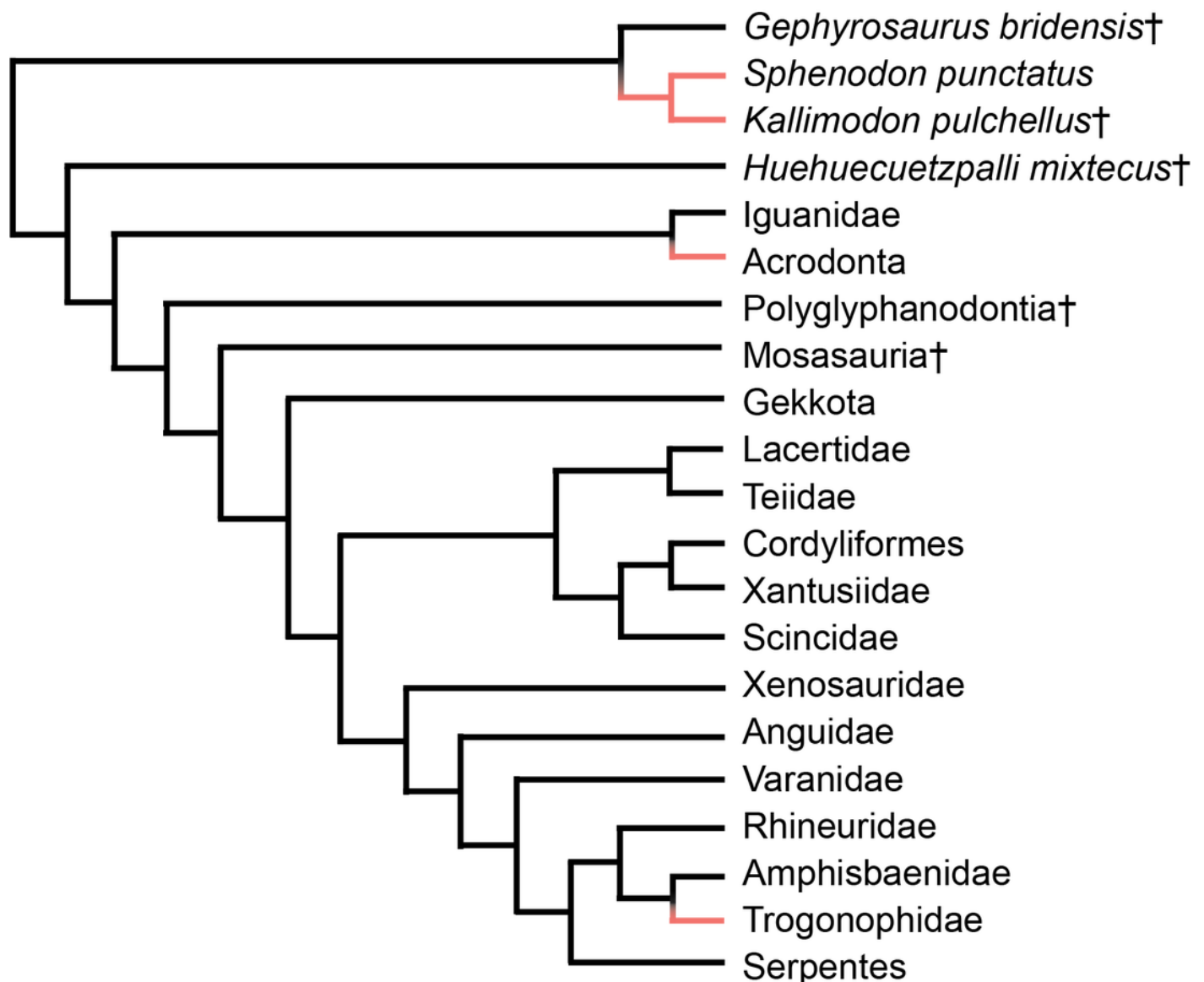
Figure 2

Acrodont ankylosis as seen in two species of Acrodonta (A & B) and a rhynchocephalian (C) and pleurodont ankylosis (D).

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.
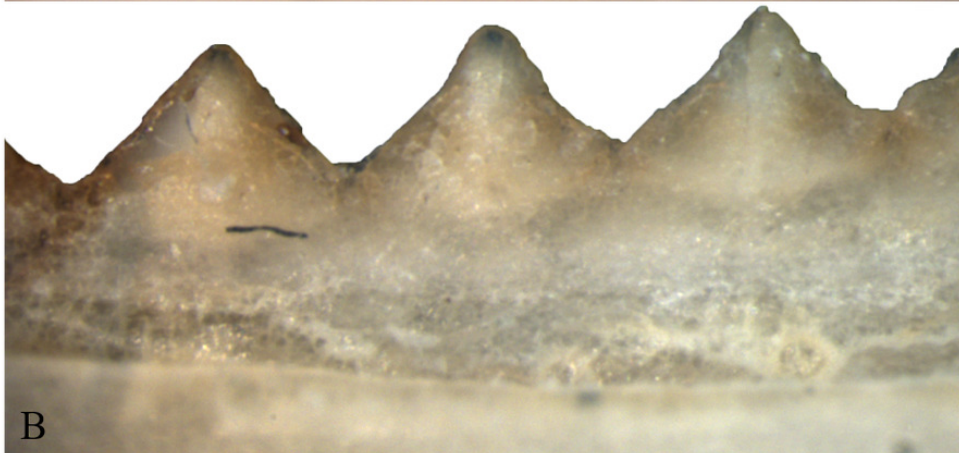
Figure 3

Acrodont vs. Pleurodont bite force (SVL).

A) Linear regression (grey line) of log-transformed snout-vent length (SVL) and bite force. Acrodonts indicated by red datapoints and pleurodonts indicated by blue datapoints. B) Boxplot of the distributions of snout-vent length normalized bite force (SVL-NBF), calculated as the residual values from the linear regression in (A), overlain with residual values as datapoints. C) Breakdown of SVL-NBF values show in (B) by diet. D) Breakdown of SVL-NBF values shown in (B) by family and separated based on tooth implantation (acrodonts in red, pleurodonts in blue).
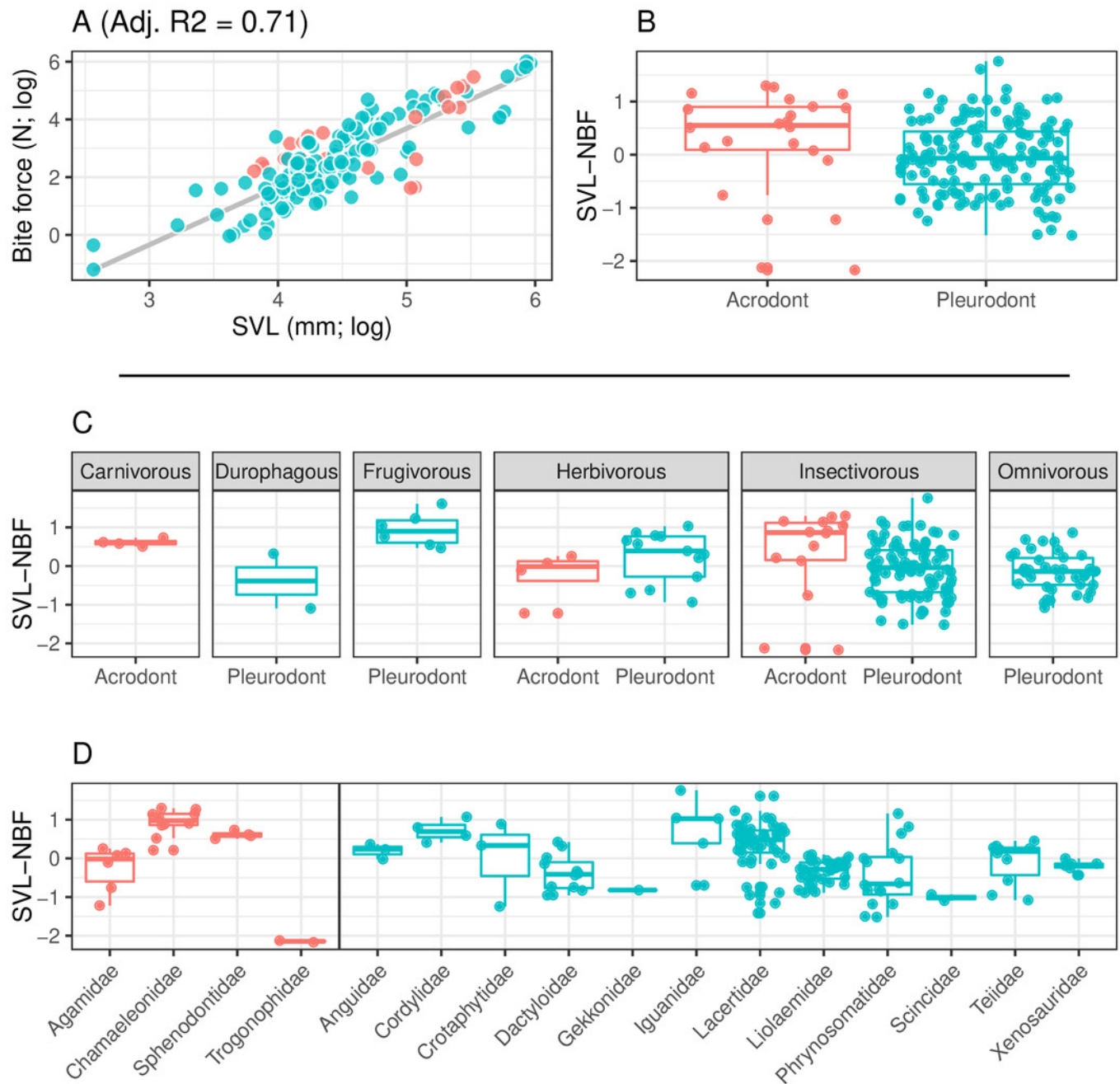
Figure 4

Acrodont vs. Pleurodont bite force (HD).

A) Linear regression (grey line) of log-transformed head depth (HD) and bite force. Acrodonts indicated by red datapoints and pleurodonts indicated by blue datapoints. B) Boxplot of the distributions of head depth normalized bite force (HD-NBF), calculated as the residual values from the linear regression in (A), overlain with residual values as datapoints. C) Breakdown of HD-NBF values show in (B) by diet. D) Breakdown of HD-NBF values shown in (B) by family and separated based on tooth implantation (acrodonts in red, pleurodonts in blue).
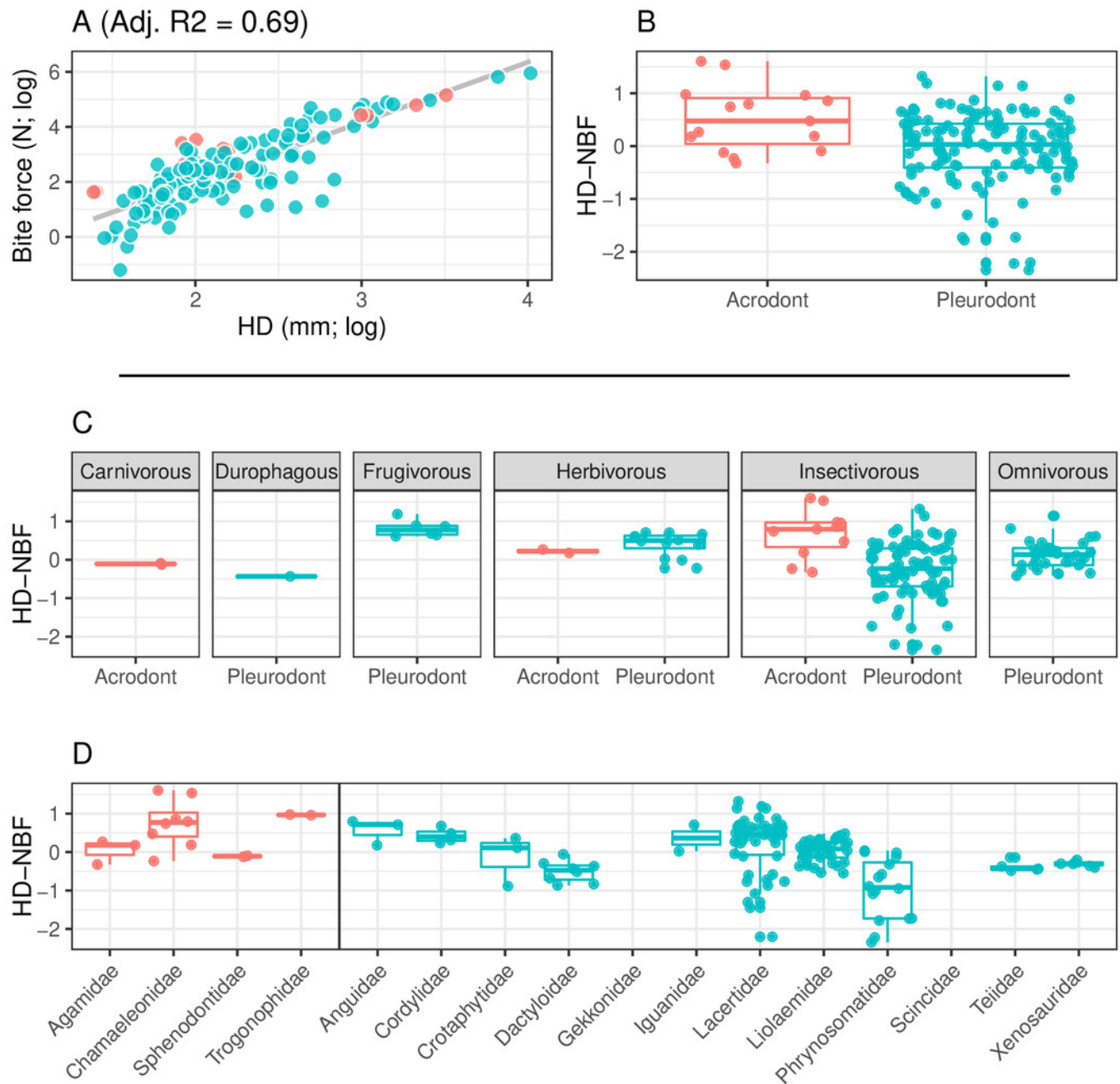
Figure 5

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