Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps* (#28010)

First submission

Editor guidance

Please submit by **9 Sep 2018** for the benefit of the authors (and your $200 publishing discount).

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Raw data check
Review the raw data. Download from the materials page.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files
Download and review all files from the materials page.

8 Figure file(s)
1 Table file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- Original primary research within Scope of the journal.
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- Data is robust, statistically sound, & controlled.
- Speculation is welcome, but should be identified as such.
- Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	***Example***
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps*

Yara Haridy Corresp. [1, 2]

[1] Department of Biology, University of Toronto Mississauga, mississauga, Ontario, Canada
[2] Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt Universität zu Berlin, Museum für Naturkunde, Berlin, Germany

Corresponding Author: Yara Haridy
Email address: yara.haridy@mfn.berlin

Teeth have been a focus of research in both extinct and extant taxa alike; a significant portion of dental literature is concerned with dental patterning and replacement. Most non-mammalian vertebrates continuously replace their dentition but an anomalous group of squamates has forgone this process in only having one tooth generation; these squamates all have apically implanted teeth, a condition known as acrodonty. Acrodont dentition and various characteristics attributed to it, including a lack of replacement, have often been defined ambiguously. This study explores this type of implantation through histology in the ontogeny of the acrodont agamid *Pogona vitticeps.* The non-replacing teeth of this squamate provides an opportunity to study wear adaptations, maintenance of occlusion in a non-mammalian system, and most importantly post-eruption changes in the tooth bone interface. In this study the post-eruption changes combined with dental wear likely gives the appearance of acrodont implantation.

Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps*

Yara Haridy[1,2]

[1] Department of Biology, University of Toronto Mississauga, 3359 Mississauga Road,
Mississauga, Ontario, L5L 1C6, Canada

[2] Museum für Naturkunde, Leibniz-Institut für Evolutions und Biodiversitätsforschung an der
Humboldt Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany

Corresponding Author:

Yara Haridy[1]

Email address: yara.haridy@mfn.berlin

Abstract. Teeth have been a focus of research in both extinct and extant taxa alike; a significant portion of dental literature is concerned with dental patterning and replacement. Most non-mammalian vertebrates continuously replace their dentition but an anomalous group of squamates has forgone this process in only having one tooth generation; these squamates all have apically implanted teeth, a condition known as acrodonty. Acrodont dentition and various characteristics attributed to it, including a lack of replacement, have often been defined ambiguously. This study explores this type of implantation through histology in the ontogeny of the acrodont agamid *Pogona vitticeps.* The non-replacing teeth of this squamate provides an opportunity to study wear adaptations, maintenance of occlusion in a non-mammalian system, and most importantly post-eruption changes in the tooth bone interface. In this study the post-eruption changes combined with dental wear likely gives the appearance of acrodont implantation.

Introduction

Reptilian dentition has been extensively studied in both extinct and extant taxa, and for the vast majority of these taxa, there is constant replacement of teeth, a condition known as polyphyodonty. However, in a subset of reptiles, there has been an evolutionary cessation of replacement, a condition known as monophyodonty. Among lepidosaurian reptiles, this suppression of replacement is limited to Sphenodontidae (Rhynchocephalia), Chamaeleonidae, and Agamidae, with the latter two being grouped within the clade Acrodonta (Squamata) (Pyron et al., 2013). This squamate group is aptly named for the acrodont style implantation of the dentition, and all acrodontians have apically implanted teeth making up the majority of their dentulous surface (Jenkins et al., 2017). This is in contrast to the condition found in most squamates and other reptiles (e.g., Zaher and Rippel, 1999; Delgado et al., 2003a; LeBlanc and Reisz, 2015) in which the tooth is implanted to the lingual surface of the jaw bone, a condition known as pleurodonty that is exemplified in taxa like *Iguana iguana* (Throckmorton, 1976; Montanucci, 2008; Kline and Cullum, 2017). The most studied form of implantation among tetrapods is thecodonty, where the tooth is implanted in a deep socket; this form of implantation is found in all mammals and also occurs within crocodilians and in many extinct archosaurs (e.g., Brown et al., 2015; García and Zurriaguz, 2016). Tooth implantation should not be conflated with tooth attachment, which refers to the tissue that attaches the tooth to the dentulous bone; this study is primarily concerned with implantation, and how ontogenetic change can influence the appearance of implantation categories.

Acrodonty in Reptilia is largely associated with a lack of tooth replacement (e.g., Zaher and Rippel, 1999; Smirina and Ananjeva, 2007), an association that often alludes to causality but that is never stated outright. At first glance it seems understandable that acrodont implantation and monophyodonty be associated as most acrodont squamates have both acrodont and pleurodont dentition. In individuals with both pleurodont and acrodont dentition, the pleurodont teeth are replaced by a new generation of teeth, yet the acrodont teeth are not (Cooper et al. 1970), which seems to have cemented the idea that acrodonty somehow inherently disrupts or inhibits replacement. While extant acrodont squamates are monophyodont, it is important to note that acrodonty is also found in some extinct reptiles (Simões et al., 2015; Haridy et al., 2018) and in non-reptile vertebrates such as piranhas (Shellis and Berkovitz, 1976), all of which replace their dentition. The supposed function of constant replacement is to avoid excessive wear (Throckmorton, 1979; Benton, 1984; Erickson, 1996); accordingly, higher rates of replacement are often seen in herbivorous taxa, as their fibrous diet and frequency of mastication requires a constant renewal of their dentition. In extreme instances, there are examples of starvation in herbivorous mammals that lack continuous replacement and that have worn their dentition to such a degree such that it is no longer functional (Spencer, 2005). Therefor the lack of replacement in acrodont squamates raises the question: if acrodontians that lack tooth replacement are relatively long-lived (Zari, 1999; Smirina and Ananjeva, 2017), how are they able to maintain a viable occlusal surface during later stages of life? Monophyodonty also poses two mechanical dilemmas: (1) how do acrodontians adapt to dental wear at a tissue level, and (2) how do the mandibular and maxillary teeth stay in occlusion through ontogeny without replacement or a ligamentous attachment? The former of the two questions has been partially addressed through histology of the acrodontians *Uromastyx aegyptia* (Throckmorton, 1979) and *Chamaeleo calyptratus* (Buchtová et al., 2013; Dosedělová et al., 2016a), and members of acrodontan Uromastycinae and Chamaeleoninae (Pyron et al., 2013). These studies found that these acrodontians have a peculiar way to combat wear – they secondarily infill the teeth with bone and/or dentine and remodel the underlying jaw bone into more compact bone. There are six other groups within Acrodonta that presumably also lack replacement and have undocumented wear adaptations (Pyron et al., 2013). This study tests if the agamid *Pogona vitticeps* (the central bearded dragon), conforms at a tissue lever to the wear adaptation patterns of other acrodontians previously documented in literature.

To better understand the relationship between acrodonty, monophyodonty, and wear adaptations, the implantation mode itself should be more thoroughly examined, particularly when it comes to acrodonty as it is the least studied form of implantation. Acrodont implantation has been ambiguously defined at best, with various authors describing the mode of implantation as: (1) apically placed teeth (Edmund, 1960) (2) teeth ankylosed to the margin of the jaw (Motani, 1997) (3) teeth fused to the edge of the jaw bone via undefined tissues (Peyer,1968). Most definitions used acrodontian squamates or rhynchocephalians as representative groups for acrodont implantation, with acrodonty used as a phylogenetic character (e.g., Zaher and Rieppel, 1999), to ground truth the use of acrodontians as acrodont representatives the natural question becomes: are the acrodont teeth of acrodontians really acrodont? It has been previously proposed that ichthyosaurs and alligators can change implantation types through ontogeny by growth in the jaw ramus and additional ossification on the lingual side (Motani, 1997), the alligators go from pleurodont to thecodont, and the ichthyosaurs become subthecodont from their juvenile state of pleurodonty.

This study explores the ontogenetic change in the teeth of *Pogona vitticeps,* with a focus on comparisons of wear adaptations of this member of Agamidinae to those previously described in Uromastycinae and Chamaeleoninae. This study aims to explain: (1) Do tissue level wear adaptations documented in other acrodontians extend to *P. vitticeps*? (2) How do monophyodont reptiles that lack a ligamentous attachment maintain occlusion through ontogeny? (3) Are the teeth of these reptiles truly acrodont, and does acrodonty limit tooth replacement as indicated by literature? This is the first study to document the change in implantation types through ontogeny due to osteological remodeling of the dentary and the tooth body, with evidence of a change from pleurodont implantation to acrodont implantation in a modern squamate. This has implications on how we view implantation categories as they are likely to be more ontogenetically variable than previously thought.

Materials and Methods

In this study, the genus *Pogona* was represented by the central bearded dragon (*P. vitticeps*). Thirty-seven specimens (S. Figure1) of *P. vitticeps* from the Royal Ontario Museum (ROM) recent osteology collection were externally examined, and all measurements were taken by K. Seymour prior to skeletonizing. All the *Pogona vitticeps* specimens were photographed using a Canon EOS40D prior to sectioning. To access normally inaccessible anatomical features of the lower jaw and its dentition, 5 specimens were sectioned in both coronal and longitudinal planes. *Pogona vitticeps* was sectioned at two ontogenetic stages, a juvenile stage (ROM R8234, ROM R8510), and an adult stage (ROM R8507, ROM R8189, ROM R9422). The illustrations and diagrams found in the figures were made using Adobe Photoshop CS6 and Adobe Illustrator CS6.

Histology

All thin sections were made following the ROM histology protocol and were executed in the ROM vertebrate paleontology thin sectioning facility. Specimens were embedded in AP Castolite acrylic resin, vacuumed, and left to cure for a minimum of 24 hours. All specimens were cut using a Buhler Isomet 1000 wafer saw at a low speed of 275rpm. The specimens were mounted on plexiglass slides using Scotch-Weld SF-100 cyanoacrylate. The slides were then mounted on the Hillquist grinding cup and ground down using the grinding cup until optical clarity was achieved; subsequently the specimen was manually ground using progressively finer grit suspensions on glass plates, beginning with a 600-grit silicon carbide powder and working down to a 1-micron aluminum oxide powder. All slides were imaged using a Nikon DS-Fi1 camera mounted to a Nikon AZ 100 microscope fitted with crossed-polarizing and lambda filters and an oblique illumination slider and NIS-Elements software registered to R. R. Reisz of the University of Toronto Mississauga.

Results

External anatomy

The external morphology of both the mandible and dentition is noticeably different between the juvenile and adult specimens of *Pogona vitticeps* (Figs. 1A, B). Several specimens that represented a relatively complete ontogenetic sequence were examined; for the sake of brevity, two representative specimens, an adult (ROM R8507) and a juvenile (ROM R8234), were chosen for external description. The juvenile specimen (ROM R8234) has fewer tooth positions (16 tooth positions) on the dentary; however, some smaller individuals were found to have as few as 10 teeth (S1. Fig.). There are external mandibular features of ROM R8234 that identify it as juvenile: (1) the symphysis is poorly ossified, (2) the mandible is less robust in bone density, which is externally apparent as a character of bone opacity, and in dorsoventral width, and (3) the mandible is relatively short, with the dentulous region making up more than half the total length. The wear facets on the labial surface of the dentary are not as well developed in the juvenile specimen as those seen in the adults. This specimen of *P. vitticeps* is found to have two teeth implanted in a pleurodont fashion; these occupy the first two tooth positions on the rostral end of the mandible (Fig. 1B). The pleurodont teeth are conical and taper to a point; this represents the most common condition among many, but not all agamids (Cooper et al. 1970). Posterior to the pleurodont dentition, the remaining tooth row has been described in literature to be acrodont and is the focus of this study(Cooper et al., 1970). The acrodont teeth in *P. vitticeps* are triangular and mediolaterally compressed and lack the multi-cuspid morphology that other acrodontians (S.Figure 1), like chameleons and *Uromastyx* display. Compared to the older anterior teeth, the teeth are larger in size posteriorly correlating with age, with the youngest teeth added posteriorly being largest. It appears that the newest tooth is not ankylosed to the jaw bone prior to the development of the next tooth in the series. Instead, the newest tooth appears be attached to the jaw only by soft tissue, a desiccated fibrous tissue separates it from the bone in skeletonized material, (Fig. 2); this is readily recognizable by external observation, as the last two teeth are not oriented at an angle that is congruent with the rest of the dentition (Fig. 1A). This was also observed in several other juvenile specimens in which it is observed only in the posteriormost teeth. Lastly, the newest and last tooth position is growing directly against, and partially resorbing (Fig. 1A), the coronoid process, which does not allow sufficient space for the next more posterior tooth position.

As with the juveniles, several adult individuals were examined, and a representative specimen chosen. Several changes correlated with size and thus presumably with ontogeny can be recognized in the adult specimen of *Pogona vitticeps* (ROM R8507) including an increase in the number of tooth positions. The specimen chosen for sectioning has 17 tooth positions, although other specimens have been found to have as many as 19 tooth positions; in most specimens a definite tooth count was difficult to ascertain via examination of the external morphology due to extensive wear but was later verified in thin section. Wear on the adult mandible is evident on both the acrodont dentition and the jaw bone. Interestingly, the anterior pleurodont dentition was mostly unworn in the adult specimen or worn to a minimal degree on other adult specimens examined; this is similar to the condition seen in *Agama agama*, which has been documented to replace its anterior pleurodont dentition (Cooper et al. 1970). However, the anterior acrodont teeth are all but worn away, making it difficult to differentiate it from the jaw bone; to circumvent this problem, tooth counts were made under a microscope and later confirmed in thin section when possible. The wear observed on the anterior acrodont dentition was extensive – often there were only traces of the tooth left – which is similar to the dental wear seen in *Uromastyx*, a taxon can become functionally edentulous in adulthood (Throckmorton, 1979).

The evidence of extensive wear is not only seen on the teeth but is also found on the mandible itself in the form of wear facets, which are only present on the labial side of the dentary where the maxillary dentition occludes, interdigitating between dentary tooth positions. Wear facets have been characteristically found in acrodont squamates as far back as the Cretaceous (Simões et al., 2015), which are formed due to the maxillary dentition wearing down on the dentary bone during mastication and passive occlusion. These wear facets are present along the posterior two-thirds of the tooth row but are most developed in the posterior region of the dentary of adult specimens of *P. vitticeps.* However, in adult individuals of other acrodontians, like chameleons (Dosedělová et al., 2016a), the wear facets are found along the entire tooth row. Lastly, it is important to mention that the jaw ontogenetically increases posteriorly in length and dorsoventrally in width, with the articular increasing in robustness, and the coronoid process moving posteriorly relative to the tooth row. This ontogenetic change effectively creates more space for the posterior addition of teeth to the dentary, a feature that is frequently seen in lepidosaurs (Berkovitz and Shellis, 2017).

Histology

Juvenile tissue histology

Longitudinal and coronal sections of the mandible of the juvenile specimen (ROM R8234) were examined (Fig. 2&3). The mandibular ramus in the juvenile specimen is not as well ossified as in the adult (ROM R8507) and has a medial curvature anteriorly; this made obtaining sections of the anterior and posterior dentition within the same sectioning plane difficult. Furthermore, the focus of this study is the non-replacing acrodont dentition, and therefor, the anterior pleurodont dentition were not included in this study. In longitudinal section, only the dentine is exposed with no other dental tissues (e.g., cementum, enamel) being visible. In longitudinal section, the implantation relationship of the teeth to the jawbone is not easily discernable. However, this plane of section allows for visualization of the incremental maturation of dentition. The most anterior teeth are the oldest, a characterization based on the thickness of dentine, whilst the most posterior teeth are the youngest and have the least amount of dentine infilling. In longitudinal section, the interaction between the individual tooth and its neighboring teeth can be seen in this plane (Fig. 2B-D); there is distinct tissue that attaches the teeth to each other as well as to the jaw bone. This tissue is tentatively identified as alveolar bone (*sensu* LeBlanc and Reisz, 2015) based on the position and presumed function of the tissue rather than on its histological appearance, which does not completely conform to alveolar bone description in literature. The alveolar bone in this specimen has a woven appearance that is less organized than the bone that makes up the dentary. However, it lacks the extensive trabecular or ‘spongy’ appearance that is found in other squamates, such as snakes (Budney, 2004; Budney et al., 2006). This tissue attaches the teeth to each other, as well as to the jaw bone proper, a function that has been attributed to ‘bone of attachment’ (Ananjeva and Smirina, 2007), better known as alveolar bone (Budney et al., 2006; Caldwell, 2007; LeBlanc and Reisz, 2013, 2015; LeBlanc et al., 2016a). The alveolar bone in *P. vitticeps* is also not distinguished from the jaw bone by a reversal line; this is possibly an effect of the plane of section or due to a lack of resorption prior to attachment (Fig. 2). It is important to note that not all the teeth in the juvenile specimen are fully ankylosed to the dentary (Fig. 3); however, each tooth seems to ossify to the adjacent dentition, which occurs prior to full ankylosis and which mirrors what has been documented in *Chamaeleo calyptratus* (Buchtová et al., 2013; Dosedělová et al., 2016a). This observation is based on the youngest tooth (Fig.3), which has yet to ankylose to the dentary, which is attached to the neighboring teeth.

In coronal section, all of the common dental tissues are identifiable, with dentine comprising the bulk of the tooth identified by its characteristic radiating dentinal tubules. The enamel is best visualized in cross-polarized light and is unworn in the youngest teeth (Fig.3B). Because of the mediolateral compression of the tooth, the coronal plane of section is the best plane in which to examine the enamel as it transects the labial and lingual surfaces of the tooth this. The enamel is fairly thick, which has also been reported in *Uromastyx* (Throckmorton, 1979). Due to the lack of wear in the juvenile specimen, the enamel is of equal thickness on the lingual and labial sides of the tooth crown (Fig.3B). On the lingual side of the tooth, the tapering edge of the enamel leads down to a layer of acellular cementum, meeting at the cementoenamel junction, which defines the boundary between the anatomical crown and root of the tooth. It is likely that the cementum cannot be visualized on the labial side because the alveolar bone has grown to meet the cementum, effectively ankylosing the tooth while obstructing the cementum, or possibly because of resorption of the cementum in this process, although the latter has not been previously documented.

In the coronal section of the juvenile specimen of *P. vitticeps*, it is evident that both the shape of the dentition and the manner in which the tooth is implanted are more congruent with the pleurodont condition, as the lingual side of the tooth is markedly greater in length than that of the labial side (Fig. 3A, C). Although both ends of the tooth are ankylosed to the jaw, it is clear that there is more contact with the jaw bone and more attachment tissues on the labial side, a character of pleurodont implantation. Apart from the obvious labial bias of attachment, alveolar bone can be seen at the base of the tooth, being more woven than the rest of the jaw bone yet apparently lacking the more porous structure that is usually associated with alveolar bone. In coronal section (Fig. 3B), the reversal line defining the boundary between the new alveolar bone and the preexisting jaw bone is visible in cross-polarized light. The labial side of the tooth (Fig. 3C) is shorter and is attached to the jaw bone with more attachment tissue than that present at lingual side; furthermore, the labial side appears to be actively remodeled by osteoblasts and osteoclasts (Fig. 3D). The osteoclast on the labial side of the tooth is identified on the basis of its large size, general shape and the resorption bay that is created in the dentine (Witten and Huysseune, 2009). The high density of bone cell lacunae directly posterior to the osteoclast are identified as osteocytes, which were osteoblasts, indicating that the labial side of the tooth is being resorbed and that bone is being deposited in its place. It is also important to note that the strut like structure of the cancellous bone likely give the mandible form and function prior to full ossification and maturity.

Lastly, a coronal section through the coronoid process (Fig. 3E), shows the presence of a developing tooth. Its identification as a developing tooth is based on its general shape, as well as the presence of thick enamel relative to the amount of dentine. The presence of more enamel than dentine denotes an early stage of tooth development, as dentine is deposited by odontoblasts later in development (Erickson, 1996; LeBlanc et al., 2016b). The presence of this developing tooth was serendipitously discovered by sectioning the specimen since there were no external indicators that this tooth was buried within the bone of the coronoid process. This new tooth is developing within the coronoid process and is visibly resorbing the bone tissues of both the coronoid and the dentary, effectively making space for itself prior to attachment.

Adult tissue histology

In the longitudinal and coronal sections of the mandible of the adult specimen (ROM R8057), lamellar bone makes up the main body of the dentary (Fig. 3). In coronal section, it can be seen that the large trabeculae seen in the juvenile have been incrementally infilled by lamellar bone, giving the mandible an osteological density that was not present in early ontogeny (Fig 3). As previously reported in agamids(Ananjeva and Smirina, 2007), the bone tissue is not highly vascularized nor actively remodeled, particularly in dentary bone. This is in line with the findings in the adult jaw, where no reversal lines or large areas of remodeling are found. No primary or secondary osteons can be identified in the longitudinal sections. However, in one of the coronal sections, a single osteon could be identified ventral to the tooth implantation site (Fig. 5A). In longitudinal section (Fig. 4C), posterior to the most worn dentition, the wear facets become a marked feature of the dentary's labial surface. The pervasiveness and the depth of the wear facets should not be considered informative in thin section, as the variation of depth is a false impression, and is due to the sectioning plane in combination with the curvature of the dentary. The wear facets form pseudo-pedicels for the tooth remnants; these should not be confused for the 'bony pedicles' that have been identified developmentally in chameleons (Buchtová et al., 2013). These pseudo-pedicels are formed by the wear facets, as the maxillary teeth wear away lamellar bone between the functional dentition on the jaw, leaving the remaining tooth caps on secondarily formed pedicels of lamellar bone (Fig. 4C-D). This gives the tooth implantation region its distinctly acrodont appearance.

acrodont The teeth in the adult specimen~~, specifically concerning the acrodont teeth~~, are markedly different than those described in the juvenile (Fig. 5). The unequal shape and implantation of the teeth reported in the juvenile is not recognized in the adult, which has acrodont implantation with no lingual bias (Fig 5B). The anterior pleurodont dentition is shown to maintain its vasculature, which is associated with an open pulp cavity; this is typical of pleurodont dentition among squamates. Perhaps the most interesting feature of the longitudinal sections is seen in the worn acrodont teeth directly posterior to the pleurodont pair (Fig. 4). The teeth are worn to such an extent that often no dentine or enamel is detectable (Fig. 4B), even in thin section. However, the vasculature is maintained and denotes tooth positions, and the pulp cavity remains open and vascularized throughout the functional life of the tooth. Thus, the teeth appear to remain viable into adulthood (Fig. 4E), which is in contrast to the condition reported in *Chameleo* (Dosedělová et al., 2016a) and in *Uromastyx* (Throckmorton, 1979). ~~The vasculature is best seen in Figures 4 and 5.~~

Considering the high degree of post-ankylosis changes to the tooth-bone interface, it is important to characterize the tissues involved. In the adult specimen (Fig. 5B), the tissues are distinct between the tooth and the platform of lamellar bone ~~are particularly interesting when viewed in cross-polarized light, as they are clearly distinct from both the tooth and the lamellar bone that makes up the jaw~~. The presence of these tissues alone provides evidence of remodeling. In this case, 'remodeling' is used in the broad sense rather than to refer strictly to bone remodeling. For example, in this agamid, the dentine that was once present in the lingual side of the tooth of the juvenile has been resorbed and is no longer present, or it is present in a greatly reduced extent in the adult. In both instances, it has been replaced by woven bone. The woven bone can be seen at the base of the teeth in longitudinal section (Fig. 2). However, the true extent of remodeling and change in tooth morphology is best seen in cross-polarized light in coronal section as this plane allows for the best direct comparison to the juvenile teeth in figure 4. Positioned between the dentine and the organized lamellar bone of the jaw is a layer of bone with disorganized fibers previously referred to as woven bone. The lack of organization in this bone indicates the occurrence of relatively fast deposition and is unlikely to be the original alveolar bone that was identified in the juvenile specimen. The woven appearance under cross-polarized light identifies this as woven bone. In conjunction with its position relative to the teeth, it is tentatively identified here as a remodeling zone (*sensu* Budney, 2004) (Fig. 4C, 5B). In coronal section (Fig. 5B) the remodeling zone is clearly identifiable in cross-polarized light, and the distribution of dental tissues and bone is markedly different than that previously described in the juvenile speci. In the adult specimen, the anterior acrodont dentition was either completely worn away, or all that remained was a dentine fragment (Fig. 4). The most posterior dentition retained more comparatively more dentine and often with a lingual bias (Fig. 5A), but this was only discernable in thin section. The anterior acrodont teeth in the adult had no evidence of enamel, while the posterior most teeth were the only ones that maintained some enamel, although it is only present on the lingual side. Within the pulp cavity of the adult, there often remains evidence of vasculature (Fig. 4) although it is greatly reduced to the center of the tooth. The overall shape of the tooth is markedly different to that reported in the juvenile, and the external appearance is acrodont like that described in literature (e.g., Budney, 2004).

Discussion

Tooth replacement has been a topic of great interest in recent years in groups ranging from fish to mammals and across broad time scales. There have been several studies documenting the presence of replacement patterns in relation to dental development (e.g., Westergaard and Ferguson, 1990; Richman and Handrigan, 2011; LeBlanc and Reisz, 2015) . However, there has been relatively little work on the anomalous squamates that completely cease tooth replacement, the acrodontians. The clade Acrodonta (Cope, 1864) is aptly named for the form of tooth implantation known as acrodonty that this group possesses, namely where the teeth are attached to the apex of the jaw. Grouping based on tooth implantation has divided squamates between acrodontians and pleurodontans (Cope, 1864; Budney, 2004), the latter of which attach their dentition to the lingual margin of the jaw (pleurodont implantation). The classic categories of acrodonty, pleurodonty, and thecodonty have been used as descriptors, as well as phylogenetic characters (Zaher and Rippel, 1999), and continue to be pervasive in even the latest literature (Jenkins et al., 2017) but have been called into question by Estes et al. (1988) who suggested these categories are artificial and are not likely representative of natural groupings.

True teeth in most non-mammalian vertebrates are well known for their extensive replacement patterns through their life (Zaher and Rieppel, 1999; Delgado et al., 2003b; LeBlanc and Reisz, 2015; LeBlanc et al., 2016b); therefor any condition that deviates from polyphyodonty is unusual and worthy of study. An important example of non-polyphyodont dentition is seen in mammals, in which there are only two generations of dentition, the deciduous teeth and the permanent teeth. Some mammals such as shrews have even forgone the deciduous phase by resorbing the dentition prior to eruption, functionally giving them one tooth generation (Järvinen et al., 2009). Other than mammals, most fish (but see ratfish, e.g., Huber et al., 2008), amphibians, reptiles and non-mammalian synapsids have continuous tooth replacement through life, making acrodontian squamates an anomaly amongst toothed vertebrates. The lack of replacement comes with a set of challenges, two of which are addressed here. The first challenge is how does an organism grow the jaw whilst having permanently ankylosed dentition and whilst maintaining occlusion with the maxillary dentition? The second challenge is how to maintain a single set of functional teeth through the lifetime of an animal, which essentially is a problem of combating or adapting to wear. These two obstacles are also faced by mammals, which have one primary set of teeth throughout most of their life. In mammals, the issue of maintaining occlusion appears to be solved by maintaining a ligamentous tooth attachment, which allows for the teeth to remain mobile as the mandible grows and remodels (Lumsden and Osborn, 1977; LeBlanc and Reisz, 2013). The issue of wear is at least partially addressed by having much thicker prismatic enamel than that found in most reptiles (Dauphin and Williams, 2008; Kieser et al., 2009). However, the question remains how reptiles that permanently ankylose their dentition to the jaw and those with reptilian enamel adapt to growth and wear.

Wear adaptations

This study found that the unworn teeth on the mandible of the juvenile agamid *P. vitticeps* have a uniform layer of enamel on both the lingual and labial sides, and the enamel is relatively thick in comparison to polyphyodont reptiles such as crocodilians. The thick enamel also seems to occur in two other acrodontians, *Uromastyx* enamel has been documented as 'thickened' (Cooper and Poole, 1973; Throckmorton, 1979), and chameleons' enamel appears thick in recent studies but is not explicitly commented on (Buchtová et al., 2013; Dosedělová et al., 2016b). Furthermore, *Uromastyx*, a herbivorous acrodontian, has been reported to have thickened prismatic enamel (Throckmorton, 1979), similar to mammalian enamel. This shows that thickening of the enamel is a convergent adaption against wear in both squamates and in mammals.

Enamel thickening is not the only adaptation that acrodontians appear to have evolved in order to combat wear. Previous studies of chameleons and *Uromastyx* have shown that their pulp cavities were infilled with 'mineralized tissue' (Dosedělová et al., 2016b) or 'bone' (Throckmorton, 1979). The likely purpose of this infilling is to prevent the pulp cavity from being exposed as the external surface of the tooth is worn away; both aforementioned studies also reported the disappearance or significant restriction of vasculature that initially supplied the dentition in early ontogeny. Dosedělová et al. (2016a) also showed increased mineralization in the bone underlying the tooth-bone junction in chameleons, and Throckmorton (1979) found that in *Uromastyx*, the bone below the teeth had become more compact in appearance rather than cancellous. These findings are quite comparable with one another, even though *Uromastyx* and chameleons are on two disparate branches of Acrodonta (Pyron et al., 2013). ~~These results then beg the question: is this (?) pattern more widespread across acrodontians?~~

This study found comparable results in *Pogona vitticeps.* The pulp cavity is also greatly diminished through ontogeny (Fig. 2B) but is not completely 'obliterated,' as seen in *Uromastyx*. The infilling of the pulp cavity in *P. vitticeps* is done through a combination of dentine, and the woven bone. The progressive infilling of dentine is a normal development for teeth, as odontoblasts continue to sequentially deposit dentine post- eruption. What is abnormal is the bone growing into the pulp cavity and the resorption of the dentine root. In some of the sampled sections of *P. vitticeps*, the teeth fail to show the extent of bone infilling reported in *Uromastyx*, as the matrix that infills the pulp cavity does not seem to have any of the cellular spaces reported in *Uromastyx*. However, in other sections of the same individuals, the teeth experience a lot of remodeling and infilling, often with bone growing over the dentition. This is identified as 'bone' rather than 'mineralized material' as mentioned by (Dosedělová et al. 2016b) based on the amount of osteocyte lacunae present as well as the presence of osteons. Together the bone and dentine restrict the pulp cavity to such an extent that the tooth can then be worn away without the risk of exposing the vulnerable vasculature and nerves that are within the pulp cavity. Furthermore, the bone making up the dentary is not vascularized and sequentially also becomes more infilled with bone, making compact bone through ontogeny; this allows for the jaw to be worn in the form of distinct wear facets.

The amount of wear on the adult dentition of *Pogona vitticeps* changes the external morphology significantly. This is common in ungulate mammals (Fortelius and Solounias, 2000) and in herbivorous fossil reptiles (e.g., Reisz, 2006) but has not been reported in other squamates. The dentine and enamel on the labial side of the mandible are worn in the older specimens of *P. vitticeps*, which is compatible with the findings in *Uromastyx* (Throckmorton, 1979), where depending on the tooth position, the enamel and dentine were either completely worn away or were worn to such a degree that the lingual side of the tooth retained a much thicker layer of these two tissues. This pattern is likely caused by the combination of extensive wear from feeding and passive occlusion with the maxillary dentition, as well as the complete lack of tooth replacement. Interestingly, the vasculature that leads to the pulp cavities is still present in the adult specimens of *Pogona vitticeps* indicating that even the most worn teeth probably remained viable through the heavy wear process and likely closed the pulp cavity progressively until they were worn away. This phenomena has also been observed in hadrosaurs, which progressively infill their dentition with dentine as it nears the occlusal surface in their dental batteries and then wear away the entire tooth (LeBlanc et al., 2016b; Bramble et al., 2017).

Maintaining occlusion

Continuous growth of the mandible throughout ontogeny is concurrent with the increased size of the skull. In most polyphyodont taxa, this is not problematic, as constant tooth replacement adjusts for increase in tooth size as well as possible migration (e.g., Haridy et al. 2018); even in mammals, after the acquisition of ~~animal acquire~~ their permanent set of dentition, a maintained ligamentous attachment of teeth allows for migration and remodeling. However, for acrodont squamates that have ankylosed monophyodont dentition, this becomes problematic – the question becomes how occlusion is maintained as the jaw grows. Through examination of 37 specimens and histological sections, this study of *P. vitticeps* has shown that the growth of the jaw and the initiation of additional tooth development are decoupled processes. This is evident in the juvenile specimen in which the dentition is growing into the coronoid process (Fig. 3E, F), where the youngest un-erupted tooth is resorbing the ventral portion of the coronoid process in order to continue developing. This indicates that in the early stages of ontogeny, tooth development likely happens at a rate faster than dentary growth. This is reinforced by comparing the juvenile specimen (103mm SV length), which has 16 tooth positions, with the adult, which is more than twice as long (222 mm SV length), only has 17 tooth positions. This supports the hypothesis that attaining the maximum number of teeth occurs relatively early in ontogeny, well before attaining maximum adult size., ~~indicating that~~ T tooth development eventually slows and likely stops early in ontogeny, while the various jaw elements continue to grow. The mandible of *P. vitticeps* undergoes many changes through ontogeny, but there is little distortion of the tooth row during growth. This is likely achieved by appositional bone growth of the jaw, with deposition of parallel-fibered bone both internally and externally to achieve the increase in internal ossification, width and length that is seen in the adult and without remodeling or migration of the ankylosed dentition. Through the histological results of this study, which show little bone remodeling, and external observation of 37 specimens (S1), it is hypothesized that occlusion is maintained through the allometric growth of the various portions of the jaw elements. The dentary and its corresponding dentition are the first to reach adult size, while the other jaw elements continue to grow through ontogeny, gradually increasing in robustness but not interfering with occlusion.

Acrodont implantation as a result of ontogenetic remodeling

Acrodont implantation is defined ambiguously in literature. The mode of implantation has been defined as attachment to the ‘edge’ of a jaw (Peyer, 1968), as teeth ankylosed to the ‘apex’ of the jaw by cement (Edmund 1969), or as the fusion of dentition to the ‘margin’ of the jaw (Motani, 1997). Eventually, the lack of replacement also became a character of acrodont tooth implantation (Zaher and Rippel, 1999), as the condition is present in acrodont squamates. Implantation categories are pervasive in literature and are often used as phylogenetic characters, but these definitions are problematic and tend to imply an evolutionary progression of tooth implantation from simple to more complex (Budney et al., 2006). In reality, the traditional categories of acrodonty, pleurodonty, and thecodonty are, at best, descriptive terms (Estes and Charles, 1988) (Fig. 6A). *Pogona vitticeps* and likely other agamids change implantation categories through ontogeny, and therefor, they are a good representation as to why implantation categories should only be used descriptively. The teeth in the juvenile *P. vitticeps* are unequal in shape, with the lingual side being much longer than that of the labial side (Fig. 3), and attachment mostly occurring on the labial side, which are characteristics of pleurodont implantation. Traditionally in literature, the anatomy present in adult individuals of various taxa is described; this likely explains why acrodont squamates got their namesake since in their adult stage, the teeth do appear acrodont. This study reveals how implantation may appear to be acrodont in adulthood through a combination of factors (Fig 7); (1) the gradual infilling of teeth with dentine that allows for progressive wear (2) resorption of the dentine by odontoclasts (Fig3C,D; Fig 6-2), (3) growth on the dentary that infills part of the pulp cavity with woven bone and that reduces the trabecular structure of the dentary bone, (4) the continued remodeling of the dentary which removes traces of buried dentine and the previous pleurodont dentition. Tooth wear then further changes the ~~tooth~~ crown morphology (5-7) the maxillary dentition occludes with the mandibular dentition wearing away the labial side of the mandibular dentition and wearing away part of the dentary creating wear facets. This progression model shows how teeth that were originally pleurodont in implantation (Fig 6-1) can appear acrodont (Fig 6-7) and have an entirely different morphology due to a combination of dentine infilling, bone remodeling, and tooth wear. It is difficult without experimental testing to ascertain if these secondary remodeling steps would occur in any pleurodont squamate taxa but are suppressed by tooth replacement, or if these are secondarily acquired adaptations in monophyodont taxa to combat wear. Therefor, at least in the agamid *P. vitticeps*, the dentition changes from pleurodont to acrodont in appearance through ontogeny. This indicates that we should not use implantation categories as phylogenetic characters if the ontogenetic stage of the specimen is unknown, as is the case in many fossil taxa.

Conclusion

The dentition of acrodontians has recently been an area of interest in the context of dental development and implantation, as this group is known for its mode of implantation and monophyodonty. The latter is an anomalous occurrence among tetrapods, as intermittent to continuous replacement of teeth is the primitive condition for toothed vertebrates, including most extant fish, amphibians, and amniotes. This lack of replacement has become associated with acrodonty, resulting in monophyodonty becoming a formal characteristic of acrodont implantation in squamates, and previous authors have implied that acrodont implantation is the cause of monophyodonty. However, this study shows that at least some modern acrodont reptiles do not initially have acrodont implantation early in ontogeny, and there is a distinct ontogenetic change in the morphology and implantation of dentition of the agamid *Pogona vitticeps.* The youngest teeth in juvenile specimens are pleurodont in implantation, with a greater lingual contribution of tooth tissues and an attachment biased towards the labial side. These tissues are secondarily remodeled through a step-wise process of: (1) resorption of dentine, (2) deposition of bone and dentine, (3) wear of the tooth surface, and (4) wear of the jaw bone proper, effectively changing the morphology. These processes give *P. vitticeps* the appearance of acrodont dentition in adulthood. This is an important distinction to make as it signifies that this acrodont squamate*,* and likely other acrodont reptiles, do not develop acrodont teeth, but rather develop pleurodont teeth like the vast majority of squamates, making their teeth inherently pleurodont, and secondarily acrodont. Therefor, the wear adaptations, remodeling, and dental wear ~~all~~ come together to give the appearance of an acrodont mode of implantation. The wear adaptations documented in this study likely evolved due to the lack of replacement. ~~Essentially~~ Importantly the monophyodont condition causes the acrodont condition, rather than acrodonty causing monophyodonty, as has been implied in literature.

This raises the question as to how we should code acrodont dentition in squamate phylogenies; is it true acrodonty if this implantation mode is only achieved through secondary remodeling of the teeth and dentary? Finally, another important consideration, and a direction of future studies, is that if all acrodontians share these ontogenetic changes and wear adaptations, then what is the significance of the convergence seen between acrodontian squamates and the other rhynchocephalian *Sphenodon*, which is also reported to have acrodont dentition?

Acknowledgments

Incredible thanks go to Robert R. Reisz and Aaron H. Leblanc who brought this issue to light and encouraged the development of this study. I would like to thank Diane Scott for photographs and SEM images and beaded dragon husbandry advice. Thanks to Bryan Gee for his everlasting patience and editing of this manuscript into presentable form. I would like to thank Kevin Seymour of the Royal Ontario museum (ROM) for assistance in locating appropriate specimens for this study and to thank David Evans for allowing the use of the ROM histology laboratory and reading early versions of this manuscript. Lastly, I would like to acknowledge Osiris the bearded dragon whose presence in the lab was essential to the direction of this study.

References

Ananjeva, N., and E. Smirina. 2007. Growth layers in bones and acrodont teeth of the agamid lizard *Laudakia stoliczkana* (Blanford, 1875) (Agamidae, Sauria). Amphibia-Reptilia 28:193–204.

Berkovitz BK, Shellis RP. The teeth of non-mammalian vertebrates. Academic Press; 2016 Oct 14.

Bramble, K., A. R. H. LeBlanc, D. O. Lamoureux, M. Wosik, and P. J. Currie. 2017. Histological evidence for a dynamic dental battery in hadrosaurid dinosaurs. Scientific Reports 7:15787.

Brown, C. M., C. S. Vanburen, D. W. Larson, K. S. Brink, N. E. Campione, M. J. Vavrek, and D. C. Evans. 2015. Tooth counts through growth in diapsid reptiles: Implications for interpreting individual and size-related variation in the fossil record. Journal of Anatomy 226:322–333.

Buchtová, M., O. Zahradníček, S. Balková, and A. S. Tucker. 2013. Odontogenesis in the Veiled Chameleon (*Chamaeleo calyptratus*). Archives of Oral Biology 58:118–133.

Budney, L. 2004. A survey of tooth attatchment histology in squamata: The evaluation of tooth attatchment classiciation and characters. University of Alerta pp.

Budney, L. A., M. W. Caldwell, and A. Albino. 2006. Tooth socket histology in the Cretaceous snake *Dinilysia*, with a review of amniote dental attachment tissues. Journal of Vertebrate Paleontology 26:138–145.

Caldwell, M. W. 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). Zoological Journal of the Linnean Society 149:687–700.

Cooper JS, Poole DF. The dentition and dental tissues of the agamid lizard, Uromastyx. Journal of Zoology. 1973 Jan;169(1):85-100.

Cope, E. D. 1864. On the characters of the higher groups of Reptilia Squamata: and especially of the *Diploglossa*. Academy of Natural Sciences 16:224–231.

Dauphin, Y., and C. T. Williams. 2008. Chemical composition of enamel and dentine in modern reptile teeth. Mineral Mag 72:247–250.

Delgado, S., T. Davit-Beal, and J. Y. Sire. 2003a. Dentition and tooth replacement pattern in Chalcides (Squamata; Scincidae). Journal of Morphology 256:146–159.

Dosedělová, H., K. Štěpánková, T. Zikmund, H. Lesot, J. Kaiser, K. Novotný, J. Štembírek, Z. Knotek, O. Zahradníček, and M. Buchtová. 2016a. Age-related changes in the tooth–bone interface area of acrodont dentition in the chameleon. Journal of Anatomy 229:356–368.

Erickson, G. M. 1996. Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. Proceedings of the National Academy of Sciences of the United States of America 93:14623–14627.

Estes, R., and C. Charles. 1988. Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp, illustrate. (Gregory K. Pregill (ed.)). Stanford University Press, 631 pp.

Fortelius M, Solounias N. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. American Museum Novitates. 2000 Oct:1-36.

García, R. A., and V. Zurriaguz. 2016. Histology of teeth and tooth attachment in titanosaurs (Dinosauria; Sauropoda). Cretaceous Research 57:248–256.

Haridy, Y., A. R. H. LeBlanc, and R. R. Reisz. 2018. The Permian reptile *Opisthodontosaurus carrolli*: a model for acrodont tooth replacement and dental ontogeny. Journal of Anatomy 232:371–382.

Huber, D. R., M. N. Dean, and A. P. Summers. 2008. Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish *Hydrolagus colliei*. Journal of The Royal Society Interface 5:941–953.

Hugall, A. F., R. Foster, M. Hutchinson, and M. S. Y. Lee. 2008. Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. 343–358.

Järvinen, E., M. Tummers, and I. Thesleff. 2009. The role of the dental lamina in mammalian tooth replacement. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 312:281–291.

Jenkins, K. M., M. E. H. Jones, T. Zikmund, A. Boyde, and J. D. Daza. 2017. A review of tooth implantation among rhynchocephalians (Lepidosauria). Journal of Herpetology 51:300–306.

Kieser, J. A., T. Tkatchenko, M. C. Dean, M. E. H. Jones, W. Duncan, and N. J. Nelson. 2009.

Microstructure of dental hard tissues and bone in the tuatara dentary, *Sphenodon punctatus* (Diapsida: Lepidosauria: Rhynchocephalia). Frontiers of Oral Biology 13:80–85.

Kline, A. L. W., and D. Cullum. 2017. A long term study of the tooth replacement phenomenon in the young green iguana, *Iguana iguana*. Society for the Study of Amphibians and Reptiles 18:176–185.

LeBlanc, A. R. H., and R. R. Reisz. 2013. Periodontal ligament, cementum, and alveolar bone in the oldest herbivorous tetrapods, and their evolutionary significance. PLoS ONE 8.

LeBlanc, A. R. H., and R. R. Reisz. 2015. Patterns of tooth development and replacement in captorhinid reptiles: a comparative approach for understanding the origin of multiple tooth rows. Journal of Vertebrate Paleontology 4634:e919928.

LeBlanc, A. R. H., R. R. Reisz, D. C. Evans, and A. M. Bailleul. 2016a. Ontogeny reveals function and evolution of the hadrosaurid dinosaur dental battery. BMC Evolutionary Biology 16:152.

LeBlanc, A. R. H., R. R. Reisz, K. S. Brink, and F. Abdala. 2016b. Mineralized periodontia in extinct relatives of mammals shed light on the evolutionary history of mineral homeostasis in periodontal tissue maintenance. Journal of Clinical Periodontology 43:323–332.

Lumsden, A. G. S., and J. W. Osborn. 1977. The evolution of chewing: A dentist's view of palaeontology. Journal of Dentistry 5:269–287.

Montanucci, R. 2008. Comparative dentition in four iguanid lizards. Herpetologica 24:305–315.

Motani, R. 1997. Temporal and Spatial Distribution of Tooth Implantation in Icthyosaurs; pp. 81–103 in Ancient marine reptiles. San Diego: Academic Press.

Pyron, R., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Reisz RR. Origin of dental occlusion in tetrapods: signal for terrestrial vertebrate evolution?. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution. 2006 May 15;306(3):261-77.

Richman, J. M., and G. R. Handrigan. 2011. Reptilian tooth development. Genesis 49:247–260.

Shellis, R. P., and B. K. B. Berkovitz. 1976. Observations on the dental anatomy of piranhas (Characidae) with special reference to tooth structure. Journal of Zoology 180:69–84.

Simões, T. R., E. Wilner, M. W. Caldwell, L. C. Weinschütz, and A. W. A. Kellner. 2015. A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. Nature Communications 6:8149.

Smirina, E., and N. Ananjeva. 2017. On the longevity, growth and reproductive characteristics of Lichtenstein's Toadhead Agama, *Phrynocephalus interscapularis* Lichtenstein, 1856 (Agamidae, Sauria). Amphibia-Reptilia 38:31–39.

Smirina, E. M., and N. B. Ananjeva. 2007. Growth layers in bones and acrodont teeth of the agamid lizard *Laudakia stoliczkana* (Blanford, 1875)(Agamidae, Sauria). Amphibia-Reptilia 28:193–204.

Spencer, M. A. 2005. Dental functional morphology: How teeth work. American Journal of Human Biology 17:384–385.

Throckmorton, G. S. 1979. The effect of wear on the cheek teeth and associated dental tissues of the lizard Uromastix aegyptius (Agamidae). Journal of Morphology 160:195–207.

Throckmorton, G. Y. S. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agarnidae). Journal of Morphology 148:363–390.

Westergaard, B., and M. W. J. Ferguson. 1990. Development of the dentition in *Alligator mississippiensis*: Upper jaw dental and craniofacial development in embryos, hatchlings, and young juveniles, with a comparison to lower jaw development. American Journal of Anatomy 187:393–421.

Witten, P. E., and A. Huysseune. 2009. A comparative view on mechanisms and functions of skeletal remodelling in teleost fish, with special emphasis on osteoclasts and their function. Biological Reviews 84:315–346.

Zaher, H., and O. Rippel. 1999. Tooth implantation and replacement in Squamates, with special reference to mosasaur lizards and snakes. American Museum Novitates 3271:1–19.

Zari, T. A. 1999. On the reproductive biology of the herbivorous spiny-tailed agamid *Uromastyx philbyi* in Western Saudi Arabia. Zoology in the Middle East 19:123–130.

Zheng, Y., and J. J. Wiens. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Molecular Phylogenetics and Evolution 94:537–547.

Captions

FIGURE 1. A comparative figure showing the external morphological differences in the dentition and mandibles between juvenile and adult specimens of *Pogona vitticeps*; (A) Right mandibular ramus of juvenile specimen ROM R8234; (B) Right mandibular ramus of adult specimen ROM R8507; (C) superimposed outlines of mandibles of varying ontogenetic stages, showing that most growth occurs in the posterior end of the mandible. **Abbreviations; ad,** acrodont dentition; **cp,** coronoid process; **pd,** pleurodont dentition; **wf,** wear facets. Arrows indicating un-ankylosed teeth. Scale bar= 1 cm.

FIGURE 2. Details of external morphology of the juvenile dentition of *Pogona vitticeps.* (A) ROM R8234 in lingual view showing un-ankylosed dentition, the most posterior growing into the coronoid; (B) ROM R8418 scanning electron microscope image of incomplete juvenile mandible with; (C) closeup showing fibrous alveolar bone between the teeth; (D) closeup showing the lingual contribution of dentine to the teeth; (E) closeup showing the youngest tooth growing into and resorbing the coronoid. **Abbreviations; ab,** alveolar bone; **cr,** coronoid bone; **de,** dentine. Arrows showing un-ankylosed teeth.

FIGURE 3. Longitudinal histological sections of the juvenile mandible of *Pogona vitticeps* with a focus on the dentition. (A) External view of ROM R8234, box outlining the dentition cut; (B) a section of the posteriormost seven tooth positions. (C) a section of the posterior seven tooth positions in cross polarized light; (D) a schematic representation showing the distinct tissues as well as the progressive ankylosis of the teeth. **Abbreviations; ab,** alveolar bone; **de,** dentine; **jb,** jaw bone; **pc,** pulp cavity. Scale bar = 1000um

FIGURE 4. Coronal sections of juvenile mandible of *Pogona vitticeps* with a special focus on tooth histology. (A) Coronal section of the jaw and tooth of a juvenile specimen of *P. vitticeps* ROM R8510 showing minimal ossification of the jaw bone, and pleurodont tooth attachment; (B) close up of a juvenile specimen's (ROM R8510) dentition, showing unworn morphology; (C) coronal section of a juvenile specimen (ROM R8234) showing pleurodont implantation, and remodeling; (D) closeup of the attachment site in ROM R8234, showing the labial side of the dentition being resorbed by the osteoclast; (E) coronal section of the coronoid process in ROM R8234 showing a tooth developing lingually inside the coronoid and dentary; (F) a close up of

the tooth in the jaw bone, showing the resorption of the jawbone around newly developing tooth. **Abbreviations: ab,** alveolar bone; **ac,** acellular cementum; **cb,** cancellous bone; **cp,** coronoid process **de,** dentine; **dt,** developing tooth; **lb,** lamellar bone; **en,** enamel; **ob,** osteoblast **oc,** osteoclast; **rb,** resorption bay. All un-labeled scale bars = 1 mm.

F IGURE 5. Longitudinal sections of adult mandible of *Pogona vitticeps* with a focus on tooth histology. (A) External view of specimen ROM R8507, box outlining the dentulous area sectioned; (B) broad view showing the variation between the anterior and the posterior dentition; (C) a closeup of the worn dentition showing wear facets and remodeling zones; (D) broad view showing the variation between the anterior and the posterior dentition, showing the depth of wear facets and arrangement of vasculature; (E) a close up of the anterior dentition with open pulp cavities and associated vasculature. **Abbreviations: de,** dentine; **jb,** jaw bone; **pc,** pulp cavity; **vc,** vascular canal; **wf,** wear facet. The arrows demarcate the extensive vasculature leading to pulp cavities. Scale bar=1000um

FIGURE 6: Coronal sections of adult mandible of *Pogona vitticeps* with a focus on tooth histology. (A) Coronal section of the jaw and tooth of an adult specimen of *P. vitticeps* ROM R8507 showing the maintained vasculature and worn enamel on the labial side; (B) coronal section of the jaw and tooth of an adult specimen of *P. vitticeps* ROM R8507 showing the extensive remodeling of the tooth attachment site as well as the tooth. **Abbreviations: de,** dentine; **lb,** lamellar bone; **en,** enamel; **vc,** vascular canals; **rz,** remodeling zone. Scale bar=500um

FIGURE 7: Schematic explanation of implantation changes through ontogeny and tooth wear. (A) three basic traditional implantation categories, without attachment tissue illustrated; (B) pleurodont impanated tooth is attached via alveolar bone, yellow arrows show direction of dentine deposition; (C) purple arrows show direction of dentine resorption by odontoclasts, blue arrow shows direction of bone deposition by odontoblasts, trabecula in the dentary is reduced; (D) blue arrow shows further bone deposition; (E) the tooth appears implanted at the apex of the dentary; (F) Shows the position of maxillary tooth; (G) the enamel is worn on the labial side; (H) with advanced wear, the enamel, dentine, and dentary bone are worn on the labial side.

Supplementary

S.FIGURE 1. Ontogenetic sequence of *P. vitticeps* mandibles that were used to make the growth schematic in Figure 1C. (A) ROM R8234; (B) ROM R8150; (C) ROM R8227;(D) ROM R9422; (E) ROM R8507; (F) ROM R8189. Scale bar = 1 cm.

TABLE 1. A table of all specimens of *P. vitticeps* examined for this study. In orange are specific specimens either sectioned or figured.

Figure 1

A comparative figure showing the external morphological differences in the dentition and mandibles between juvenile and adult specimens of *Pogona vitticeps*

(A) Right mandibular ramus of juvenile specimen ROM R8234; (B) Right mandibular ramus of adult specimen ROM R8507; (C) superimposed outlines of mandibles of varying ontogenetic stages, showing that most growth occurs in the posterior end of the mandible. **Abbreviations; ad,** acrodont dentition; **cp,** coronoid process; **pd,** pleurodont dentition; **wf,** wear facets. Arrows indicating un-ankylosed teeth. Scale bar= 1 cm.Photo credit: Diane Scott

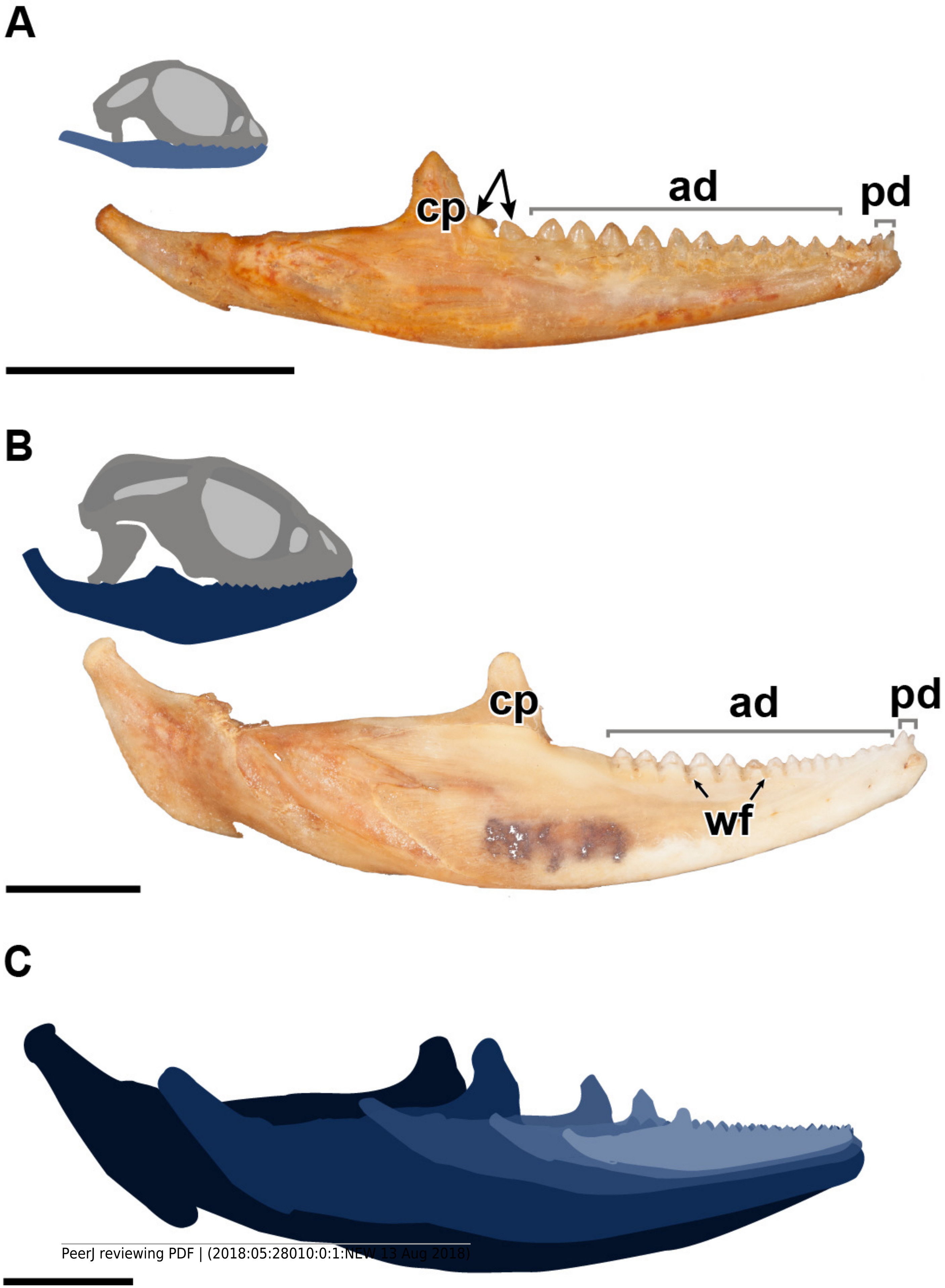

A
cp
ad
pd
B
cp
ad
pd
wf
C

Figure 2

Details of external morphology of the juvenile dentition of *Pogona vitticeps.*

(A) ROM R8234 in lingual view showing un-ankylosed dentition, the most posterior growing into the coronoid; (B) ROM R8418 scanning electron microscope image of incomplete juvenile mandible with; (C) closeup showing fibrous alveolar bone between the teeth; (D) closeup showing the lingual contribution of dentine to the teeth; (E) closeup showing the youngest tooth growing into and resorbing the coronoid. **Abbreviations; ab,** alveolar bone; **cr,** coronoid bone; **de,** dentine. Arrows showing un-ankylosed teeth. Image credit: Diane Scott

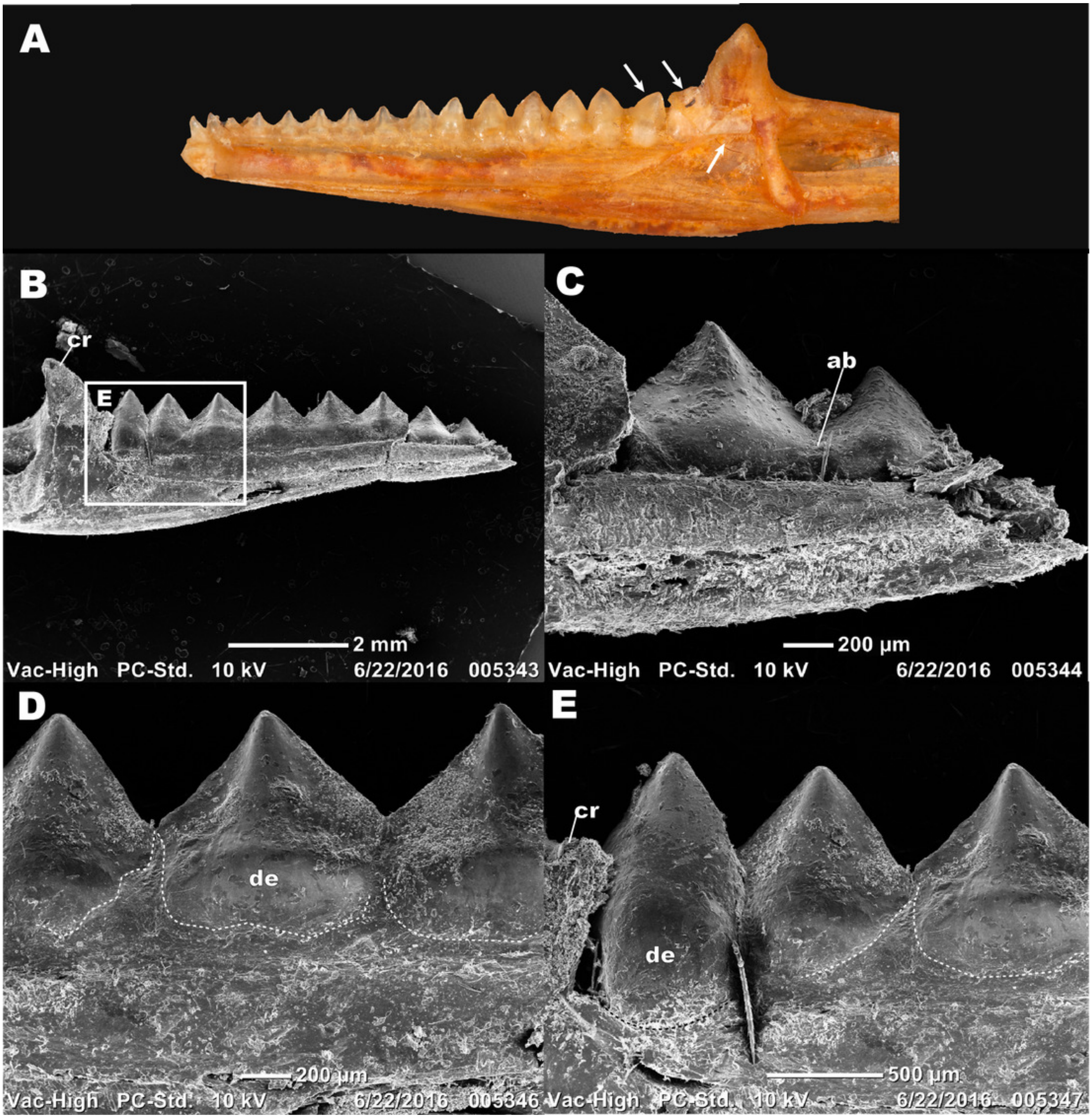

A
B
cr
E
2 mm
Vac-High PC-Std. 10 kV 6/22/2016 005343
C
ab
200 µm
Vac-High PC-Std. 10 kV 6/22/2016 005344
D
de
200 µm
Vac-High PC-Std. 10 kV 6/22/2016 005346
E
cr
de
500 µm
Vac-High PC-Std. 10 kV 6/22/2016 005347

Figure 3

Longitudinal histological sections of the juvenile mandible of *Pogona vitticeps* with a focus on the dentition.

(A) External view of ROM R8234, box outlining the dentition cut; (B) a section of the posteriormost seven tooth positions. (C) a section of the posterior seven tooth positions in cross polarized light; (D) a schematic representation showing the distinct tissues as well as the progressive ankylosis of the teeth. **Abbreviations; ab,** alveolar bone; **de,** dentine; **jb,** jaw bone; **pc,** pulp cavity. Scale bar = 1000um

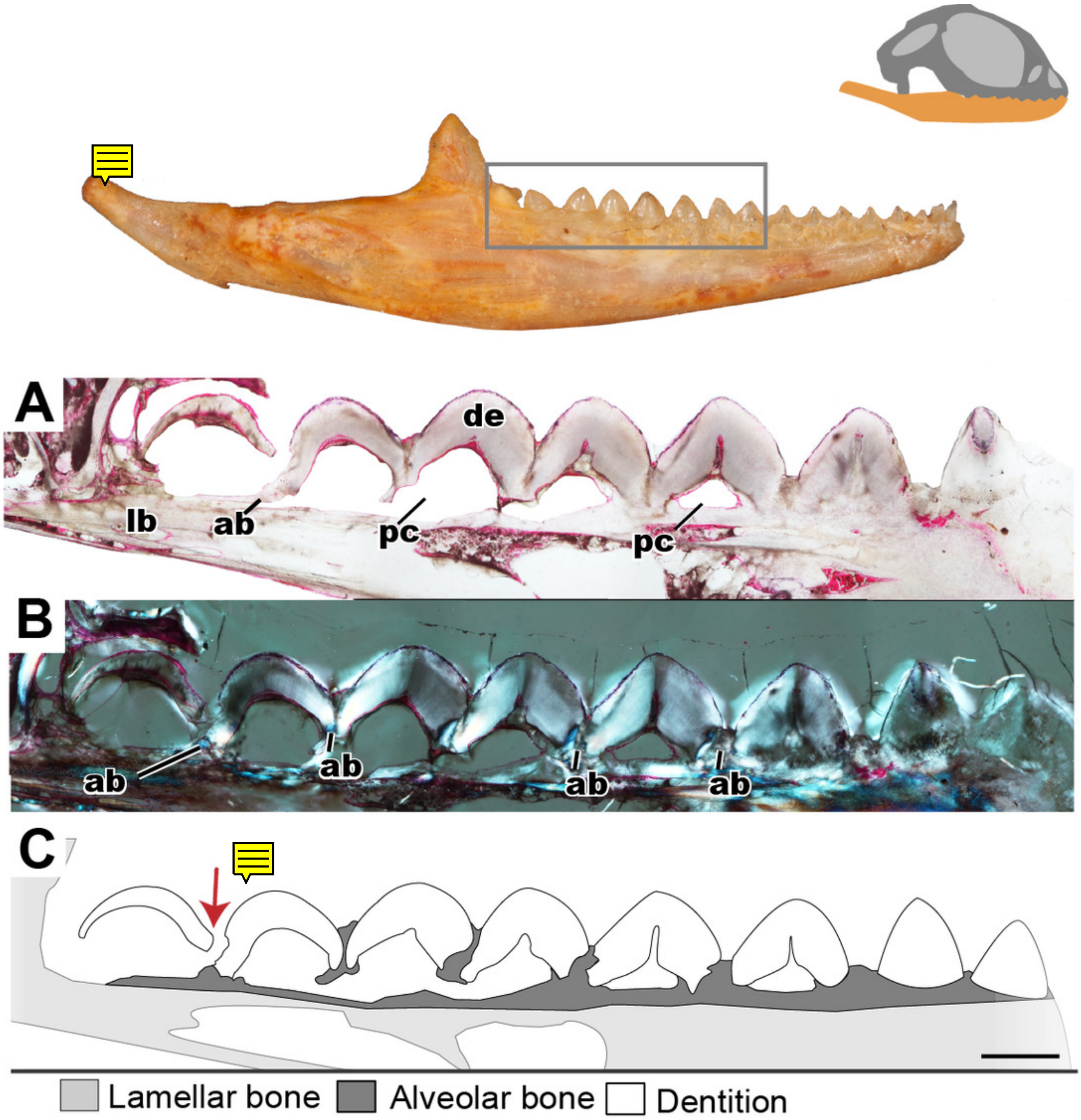

A
de
lb
ab
pc
pc
B
ab
ab
ab
ab
C
Lamellar bone
Alveolar bone
Dentition

Figure 4

Coronal sections of juvenile mandible of *Pogona vitticeps* with a special focus on tooth histology.

(A) Coronal section of the jaw and tooth of a juvenile specimen of *P. vitticeps* ROM R8510 showing minimal ossification of the jaw bone, and pleurodont tooth attachment; (B) close up of a juvenile specimen's (ROM R8510) dentition, showing unworn morphology; (C) coronal section of a juvenile specimen (ROM R8234) showing pleurodont implantation, and remodeling; (D) closeup of the attachment site in ROM R8234, showing the labial side of the dentition being resorbed by the osteoclast; (E) coronal section of the coronoid process in ROM R8234 showing a tooth developing lingually inside the coronoid and dentary; (F) a close up of the tooth in the jaw bone, showing the resorption of the jawbone around newly developing tooth. **Abbreviations: ab,** alveolar bone; **ac,** acellular cementum; **cb,** cancellous bone; **cp,** coronoid process **de,** dentine; **dt,** developing tooth; **lb,** lamellar bone; **en,** enamel; **ob,** osteoblast **oc,** osteoclast; **rb,** resorption bay. All un-labeled scale bars = 1 mm.

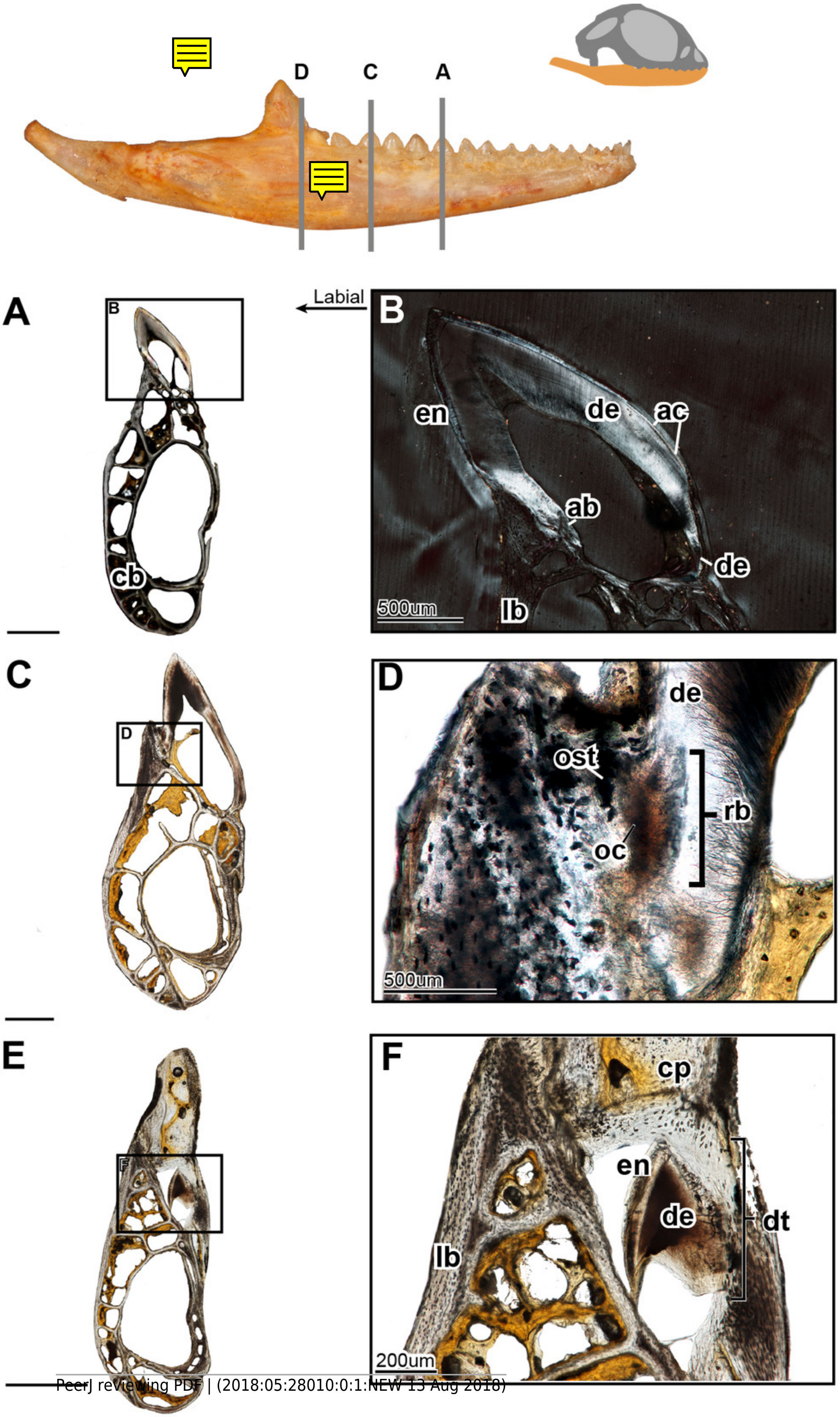

D
C
A
A
B
Labial
B
en
de
ac
ab
de
500um
lb
cb
C
D
D
de
ost
rb
oc
500um
E
F
F
cp
en
de
dt
lb
200um

Figure 5

Longitudinal sections of adult mandible of *Pogona vitticeps* with a focus on tooth histology.

(A) External view of specimen ROM R8507, box outlining the dentulous area sectioned; (B) broad view showing the variation between the anterior and the posterior dentition; (C) a closeup of the worn dentition showing wear facets and remodeling zones; (D) broad view showing the variation between the anterior and the posterior dentition, showing the depth of wear facets and arrangement of vasculature; (E) a close up of the anterior dentition with open pulp cavities and associated vasculature. **Abbreviations: de,** dentine; **jb,** jaw bone; **pc,** pulp cavity; **vc,** vascular canal; **wf,** wear facet. The arrows demarcate the extensive vasculature leading to pulp cavities. Scale bar=1000um

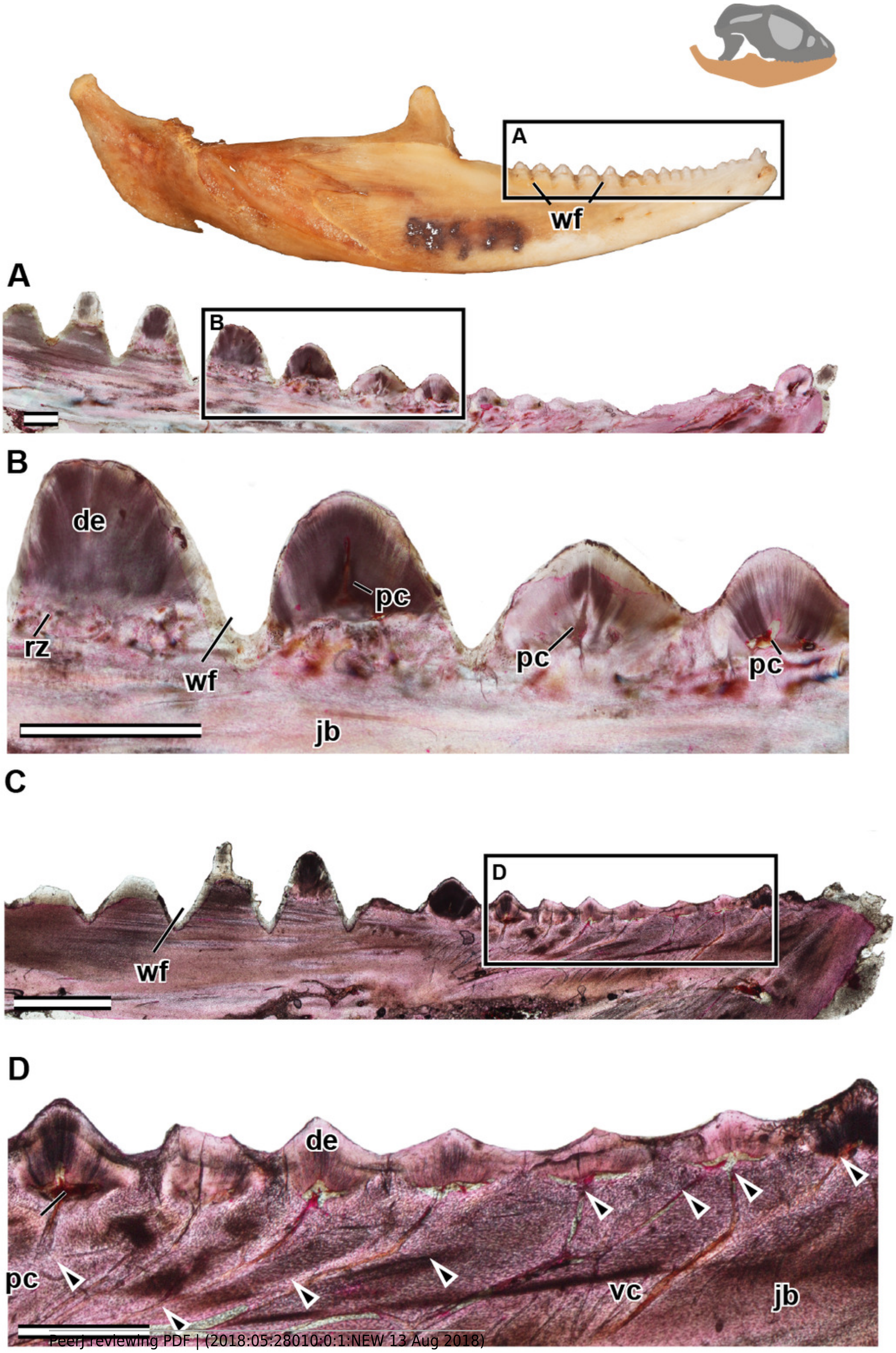

A
wf
A
B
B
de
pc
rz
wf
pc
pc
jb
C
D
wf
D
de
pc
vc
jb

Figure 6

Coronal sections of adult mandible of *Pogona vitticeps* with a focus on tooth histology.

(A) Coronal section of the jaw and tooth of an adult specimen of *P. vitticeps* ROM R8507 showing the maintained vasculature and worn enamel on the labial side; (B) coronal section of the jaw and tooth of an adult specimen of *P. vitticeps* ROM R8507 showing the extensive remodeling of the tooth attachment site as well as the tooth. **Abbreviations: de,** dentine; **lb,** lamellar bone; **en,** enamel; **vc,** vascular canals; **rz,** remodeling zone. Scale bar=500um

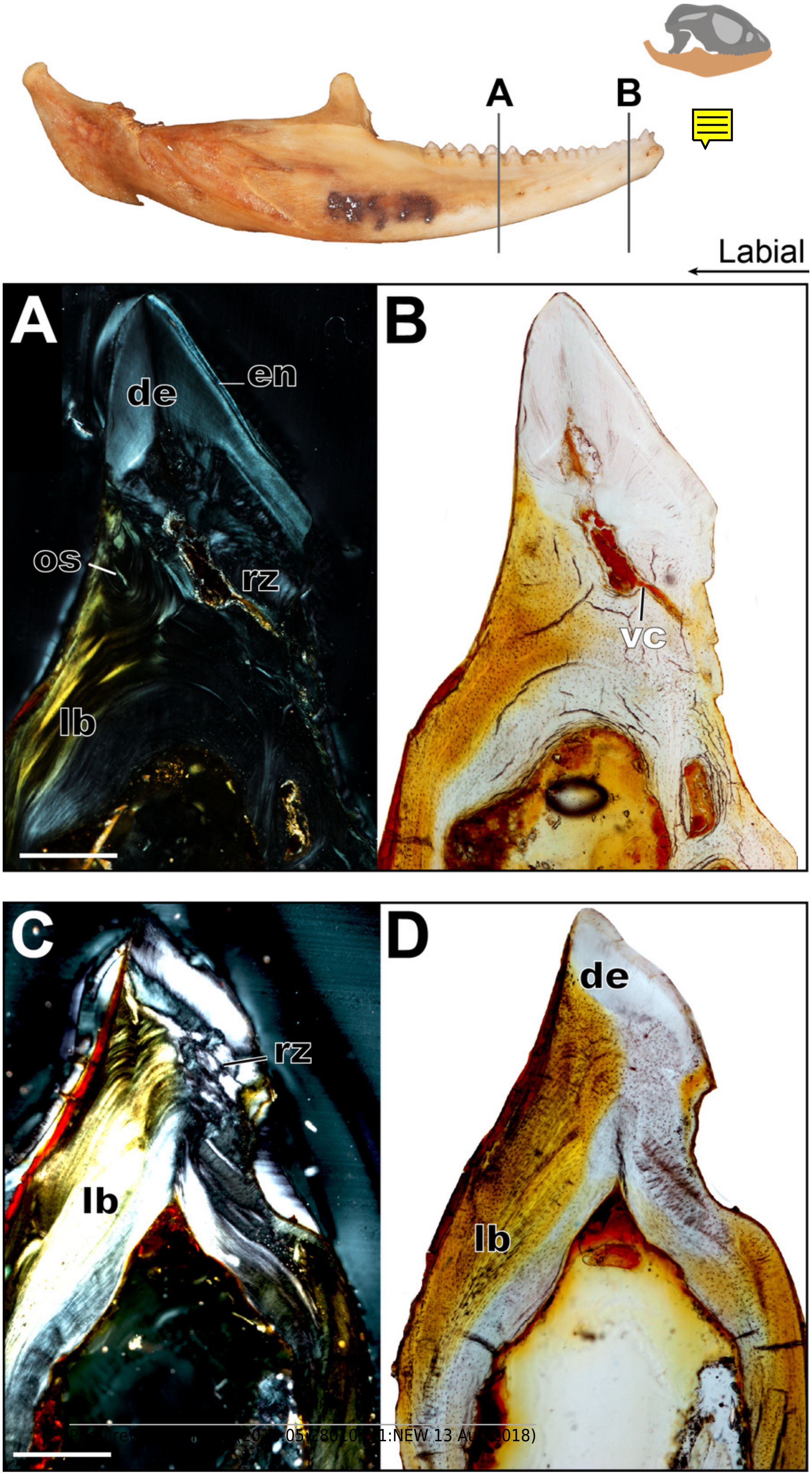
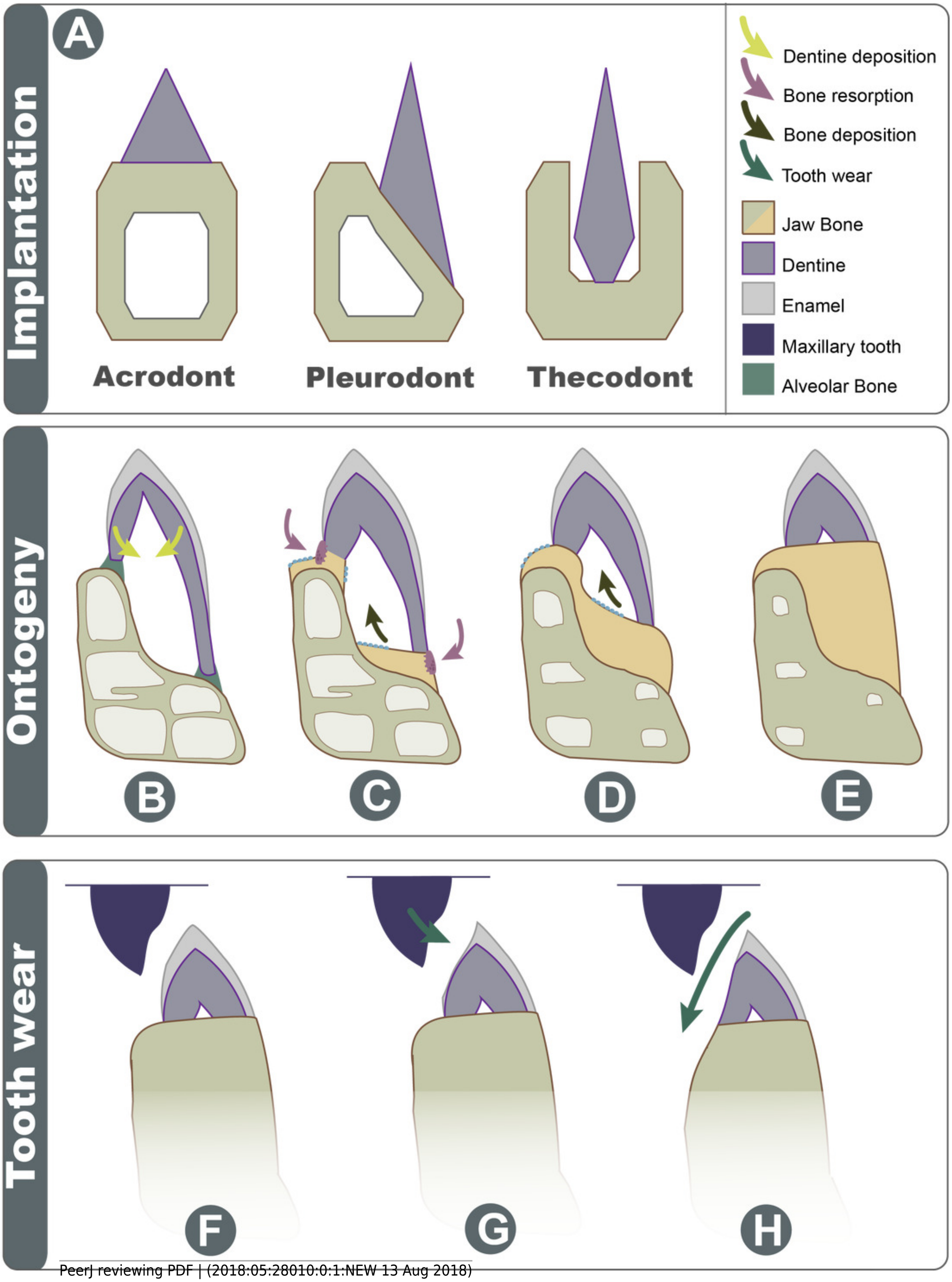

A
B
Labial
A
de
en
os
rz
lb
B
vc
C
rz
lb
D
de
lb

Figure 7

Schematic explanation of implantation changes through ontogeny and tooth wear.

(A) three basic traditional implantation categories, without attachment tissue illustrated; (B) pleurodont impanated tooth is attached via alveolar bone, yellow arrows show direction of dentine deposition; (C) purple arrows show direction of dentine resorption by odontoclasts, blue arrow shows direction of bone deposition by odontoblasts, trabecula in the dentary is reduced; (D) blue arrow shows further bone deposition; (E) the tooth appears implanted at the apex of the dentary; (F) Shows the position of maxillary tooth; (G) the enamel is worn on the labial side; (H) with advanced wear, the enamel, dentine, and dentary bone are worn on the labial side.


Implantation
A
Acrodont
Pleurodont
Thecodont
Dentine deposition
Bone resorption
Bone deposition
Tooth wear
Jaw Bone
Dentine
Enamel
Maxillary tooth
Alveolar Bone
Ontogeny
B
C
D
E
Tooth wear
F
G
H