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Supplementary information

The origin of vertebrate teeth and evolution of sensory exoskeletons

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SUPPLEMENTARY DISCUSSION

Comments on mechanisms of odontode sensation

Odontodes the precursors to teeth, are thought to evolve as a means for protection, drag reduction and also been hypothesized to have a sensory function[1–6]. However, this is fundamentally the least discussed hypothesis of the purported functions. in the existing literature. Establishing the sensory ability of external odontodes would hinge on the presence of 1) exposure to stimuli 2) sensory receptors and 3) local innervation. Considering that modern teeth in the oral cavity are a specialized homologues subset of odontodes, it is logical to look to their sensory pathways and compare them to external odontodes. In mammals, the reduction of enamel or the exposure of dentine above the gingiva causes exposure of dentine tubules to stimuli and leads to sensitivity[2]. However, even without the removal of enamel, dentine remains sensitive to small amounts of deformation through different pathways such as deformation of the periodontal ligament or minute deformation of the mineralized structure[6]. Teeth are not typically thought of as sensory organs due to their obviously prominent role in feeding, Interestingly, a large number of studies in the past half century have pointed out their integral role in nociception and even mechanosensation[15,17,18]. Mechanosensation is the ability to convert external mechanical energy to an electrical or chemical signal in a process called mechano-transduction; in teeth both the periodontal ligament[39] and odontoblasts in the pulp cavity[15] have the ability to act as sensory receptors and produce the aforementioned signals. The odontoblast is a neural crest-derived cell that is characteristically unipolar. Odontoblasts form dentine and recede into the pulp cavity where the cell body remains, a single odontoblast process extends within dentine tubules through the entire height of the dentine to the enamel dentine junction (Fig. 5a-d). The presence of odontoblasts in fossil odontodes is inferred by the presence of dentine, dentine tubules and their lacunae. Therefore, where present, it is parsimonious to accept that odontoblasts had a similar sensory receptor function[3] in extinct early vertebrates as they do in modern taxa.

There is a scarcity in the literature regarding the presence of innervated external odontodes. However, studies of the innervation of oral dentition in mammals have shown that during odontogenesis of teeth in humans a shift in expression from neurorepulsive to neuroattractive dental papilla/pulpal factors occurs. Additionally, there is evidence of cross-talk between the dental mesenchyme and the development and maintenance of innervation of the pulp cavity[35]. This shows that the tooth bud has some control of how and when it is innervated, and this continuous cross talk plays a role in maintaining the pulp cavity. If this is extrapolated to fossil odontodes, then it would lead us to infer that an open pulp cavity is likely innervated while a closed pulp cavity has no way of maintaining innervation. This further supports that the odontodes of *Eriptychius* which maintain an open pulp cavity are likely innervated, while *Astraspis* is not, as it narrows its pulp cavity. This in conjunction with the extant data showing innervation of fin odontodes in catfish, and odontode associated nerves in catsharks (Fig. 4) leads us to conclude that odontodes can transmit sensory stimuli from odontoblasts to local nerves.

The exact means as to how sensation is transduced from external stimuli to the nerves has been a matter of debate. Three theories have been proposed; the hydrostatic theory, the dental innervation theory and the odontoblast transduction theory. The hydrostatic theory proposes that a signal is produced when a change in pressure of the fluid in the dentine microtubules is directly stimulates the nerve[7,8]. The dental innervation theory proposes that the nerves directly enter the dentine tubules and are directly stimulated by external forces when the tubules are exposed[2]. And finally, the odontoblast transduction theory proposes that the odontoblast cell acts as a pain receptor or modulator and then sends a signal to the nerve which does not directly act within the dentine tubule[3,6]. All three theories have major criticisms against them as they do not provide a unifying theory that encompasses all instances of pain or stimulus transduction[10]. However most recent studies provide data which supports a combination of all three theories[9,11,12], showing that pressure change, odontoblasts and more distant innervation all play a role in in stimulating a sensation of pain or pressure. Whether these findings also apply to sensitivity in external odontodes is unknown, but our data in catshark, little skate and catfish indicate that innervation is present in close proximity or within the pulp cavity of the external odontodes which is a prerequisite that satisfies all three proposed theories.

Comments on Cow Head Formation 'Vertebrates'

The Cow Head group of western Newfoundland Canada has yielded many phosphatic remains, the majority of which are conodonts. We do not dispute the conodonts as identified in Fortey et al 1982[13], and whether conodonts are true vertebrates is not the subject of this study as their mineralized tissues are not homologues to vertebrate dentition[14,15]. However, the samples of *'Anatolepis'* and other 'unidentified fish' are of particular interest as they morphologically resemble the purported first Ordovician vertebrates published by Bockelie and Fortey's (1976)[16]. These specimens are extremely small and fragile due to acid preparation, only the most robust samples have been analyzed in this study.

We find that *Phosphannulus universalis* (GCS65596) does not have microstructure comparable to other vertebrates nor to aglaspidids, however we hypothesize it is some other invertebrate cuticle (Fig S6 a-d). Regarding 'undetermined fish B' (GCS65603) and *'Anatolepis*' (GCS65600), as mentioned by other skeptics of *Anatolepis'* vertebrate affinity [17] the tubercle shape does not conform to other Ordovician vertebrates. (Fig. S6). We also find that 'undetermined fish B' (GCS65603) and *'Anatolepis*' (GCS65600) are most parsimoniously identified as the exocuticle of an aglaspidid. This is based on similar external and internal morphology of the tubercles, internal central cavities, presence of horizontal canals and the presence of the distinctive cuticular organs found in 'undetermined fish B' (GCS65603), *Aglaspis franconensis* USNM PAL 98916, and other Aglaspid fragments (Fig 1, Extended Data Fig 1, Extended Data Fig. 2). Therefor not withstanding conodonts, the phosphatic material from the Cow Head formation is unlikely to be of vertebrate origin.

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