Independent Acquisition of Carnassial Teeth in Fishes and Mammals

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Abstract

Vertebrates evolved tooth replacement over 400 million years ago. Over 200 million years later, the combination of vertical tooth replacement with thecodont implantation (teeth in bone sockets) has been considered a key morphological innovation in mammal evolution. We discovered that an extinct fish taxon, Serrasalmimus secans, that shows this same innovation in a lineage (Serrasalmimidae) that survived the end Cretaceous mass extinction. Carnassial teeth are known in both mammals and pycnodont fish, but these teeth do not share the same tissues nor developmental processes. Therefore, a serrasalmimid pycnodont fish independently acquired mammal-like tooth replacement and implantation, thus showing that fishes and mammals evolved convergent carnassial dental morphologies at about the same time, around 60 Ma, in separate ecosystems.

Introduction

Vertebrates first acquired a tooth replacement mechanism in the latest Silurian, 424-million-year ago [1], which has enhanced prey-predator relationships through time. Since the Silurian, vertebrates have evolved many other patterns of tooth replacement and attachment mechanisms (e.g., [2]). In general, fishes, amphibians, and reptiles replace teeth over many generations in their lifetime, whereas mammals are shed one time or less in their lifetime (e.g., [3]). Teeth are implanted on the lingual side (i.e., pleurodonty) or on the margin (i.e., acrodonty) of the mandible in fishes, amphibians, and squamates, whereas mammals and archosaur reptiles have ankylothecodonty, in which tooth roots are enclosed in alveoli [2].

Pycnodont fishes, Pycnodontiformes, are an extinct clade of Actinopterygii, ranging from Late Triassic to late Eocene [4] in age. Within this clade, the family Serrasalmimidae is characterized by the reduction of tooth rows in their ankylothecodont-like dentitions (i.e., absence of true socket, but root-like structure firmly fused to the bone as in other pycnodonts). The geologically youngest taxon, *Serrasalmimus secans* Vullo et al. [5], known from the Paleocene of Morocco, possesses a cutting dentition, retaining only a paired set of a single tooth row on both sides of the tooth-bearing bones (vomer for upper and prearticular for lower dentition) to enhance a shear force with labiolingually compressed bicuspid teeth [5]. The compressed mammary-form teeth of *S. secans* show vertical wear facets by shearing on the labial side of the vomerine dentition and the lingual side of the prearticular dentition, which resembles carnassial teeth of mammals (though, in a reverse contact). Here, we characterize a combination of a tooth replacement pattern and implantation in *S. secans* based on 3D reconstructions of tooth germs between tubular root structure of the functional teeth, and we propose that serrasalmimids independently acquired a vertical replacement and thecodont, which usually characterize tooth replacement of mammals.

Results And Discussion

Our analyses focused on a specimen of *S. secans* (NMNS-PV20561, Figure 1A), collected from the Phosphorite Bed II (Thanetian age, Paleocene) in the Ouled Abdoun Basin, Morocco. We scanned the specimen by using X-ray micro-Computed Tomography scanning and segmented internal structures. The three-dimensional reconstruction of internal structures of NMNS-PV20561 shows the thecodont-like implantation in ankylosis attachment to the vomer bone (Figure 1C as already observed in a cross-section by Ref. [5]). Furthermore, this study visualized the internal structure of the vomer with dental implantations and teeth replacement system (Figure 1B, C). There is a pulp cavity containing a tooth germ in the center of each functional tooth, in contrast to common fishes, in which their tooth germs are formed on the lingual side of the functional teeth (e.g., Ref. [6]). NMNS-PV20561 lacks any trace of bone resorption, i.e., the replacement pore (see [7] for terminology), on the buccal nor lingual side of the bone, unlike other fishes with several teeth row (e.g., wolf fishes and blue fishes; see Ref. [8]). In archosaurians (e.g., crocodiles and dinosaurs), their replacement teeth are formed on the lingual side of their functional teeth, and then dissolved the wall of their functional teeth roots and move to a cavity below the functional teeth (see Figure 1 and Ref. [9]). In mammals, replacement teeth and tooth germs of mammals are formed directly below functional teeth (Figure 1). We interpret that, in *S. secans*, replacement teeth would have developed between tubular root structures of the functional teeth and erupted from its position directly below the teeth rather than the side of functional teeth, which closely resemble the vertical mode of tooth development in mammals. In addition, NMNS-PV20561 possesses only one generation of tooth germs under their functional teeth and no buds or caps, indicating that NMNS-PV20561 shed only one time in its life.

The concurrent combination of dental traits, carnassial teeth with one shed replacement and the thecodont implantation, is also seen in all carnivorans and some marsupials (*Thylacoleo* spp., and *Sarcophilus harrisii*). The latter carnivorous marsupials appeared in Pliocene, whereas the basal Carnivora first appeared around 60 Ma in the Paleocene. The latter is contemporaneous to the appearance of *S. secans* (Supplementary 3 and 4; Figure 2), meaning that carnassial teeth were coincidently acquired by predators in both marine and terrestrial realms.

The end Cretaceous (i.e., K-Pg) mass extinction event was a turning point for both terrestrial and marine ecosystems [10−13]. In marine ecosystems, top predators, such as ammonites, large predatory fish, and mosasaurs, went extinct, as did top predators in terrestrial ecosystems as well. It has been proposed that the absence of these top trophic predators left ecological niches that remained empty or unoccupied until the later Paleogene[14]. The appearance of both *S. secans* and the earliest carnivorans around 60 Ma, 6−7 My after the K-Pg event, may not have been coincidental: their ages are broadly coincident with a global warming event, the Early Late Paleocene Event (ELPE) [15, 16] and ELPE, which triggered faunal turnover [15]·[17]. Estimates of ecosystem recovery from K-Pg event required 100 years to 10 My both terrestrial and marine ecosystems[18−22]. These suggest that the acquisition of carnassial teeth must be closely related to filling the vacant ecological niche of top predators caused by the Cretaceous/Paleogene mass extinction and adjust with rapid global warming and faunal changes.

Although *S. secans*, carnivorans, and some marsupials have carnassial teeth, the teeth of fish and mammals do not share the same dental tissues or developmental processes. For example, the teeth of fishes consist of enameloid and dentin, while mammal teeth consist of enamel and dentin. Enameloid contains collagen and is made by odontoblasts and dental epithelial cells take place between a well-defined dental papilla (mesenchyme) and a dental organ (epithelium) [23], [24], while enamel is an inorganic material and made by epithelial cells interact with underlying mesenchymal cells in the underlying dental pulp [23, 25]. Therefore, carnassial teeth of *S. secans* are homoplastic convergence evolution because its origin and developmental process are distinctly different from that of mammals. In the evolutionary history of vertebrates, morphological homoplastic convergence appears in the appendicular skeletons (e.g., control or propulsion surfaces of limbs in volant tetrapods[26]) but this is the first such evidence for convergence in the dentition between fish and mammals. This finding suggests that there may be more homoplastic convergence evolution between phylogenetically distant vertebrate groups, fishes and mammals, than the previously known.

There are some fishes that have functional teeth with the thecodont attachment type teeth. However, these fishes do not show the vertical mode of the replacement. For example, barracudas and parrotfishes adopt the replacement system that their legions of teeth fuse together and teeth constantly bursting from the soft tissue to replace old ones (e.g., [27]). As far as we know, *S. secans* is the only fish with vertical replacement mode in ankylothecodont teeth.

In this study, we not only provided the first evidence of tooth replacement in pycnodont fishes but also showed that flesh-eating specialist *Serrasalmimus secans* had a vertical mode of tooth replacement, which is previously characteristic exclusively in mammals. Both lineages with carnassial teeth first appeared less than eight million years after the K-Pg mass extinction event and likely reflects concurrent filling of empty top trophic niches in both the marine and terrestrial realms. Their materials and developmental process are clearly different, but they share same characteristics and functions. This is the first case of homoplastic convergence evolution between fish and mammals and shares aspects of gene expression and regulation like fins and limbs [28].

Conclusions

We discovered that an extinct fish taxon, *Serrasalmimus secans*, shows the combination of vertical tooth replacement with thecodont implantation, a key morphological innovation in mammal evolution, in a lineage (Serrasalmimidae) that survived the end-Cretaceous mass extinction. A serrasalmimid pycnodont fish independently acquired mammal-like tooth replacement and implantation, thus showing that fishes and mammals evolved convergent carnassial dental morphologies at about the same time, around 60 Ma, in separate ecosystems.

Abbreviations

NMNS, National Museum of Natural History, Ibaraki, Japan.

Method

Computed tomography imaging—We scanned NMNS-PV20561 using X-ray micro-CT scanning by SkyScan 1275 Micro-CT (Bruker) with a beam energy of 100 kV and a flux of 100 μA at a resolution of 0.011 mm. This machine is at the Primate Research Institute, Kyoto University. The resulting scanned data were imported into Avizo Lite 9.3 and Amira 2020.2 (Thermo Fisher Scientific Inc.) for digital segmentation, rendering, and reconstruction.

Declarations

Ethics approval and consent to participate

The specimen we used in this study was legally collected and imported from Morocco, and there are no ethical issues in NMNS-PV20561.

Consent for publication

We got permission to use NMNS-PV20561 for our study and publish it in a journal from the curator in charge. Both authors agreed to publish this study in a journal.

Availability of data and material

NMNS-PV20561 is at National Museum of Natural History, Tsukuba, Ibaraki, Japan. All other data is listed in figures and tables.

Competing interests

There are no competing interests.

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Authors' contributions

Y.K. corrected the identification of NSM-PV20561 and conceived a research design. K.M. rendered CT scan data of the specimen and analyzed it. Both authors mutually discussed and equally wrote the paper.

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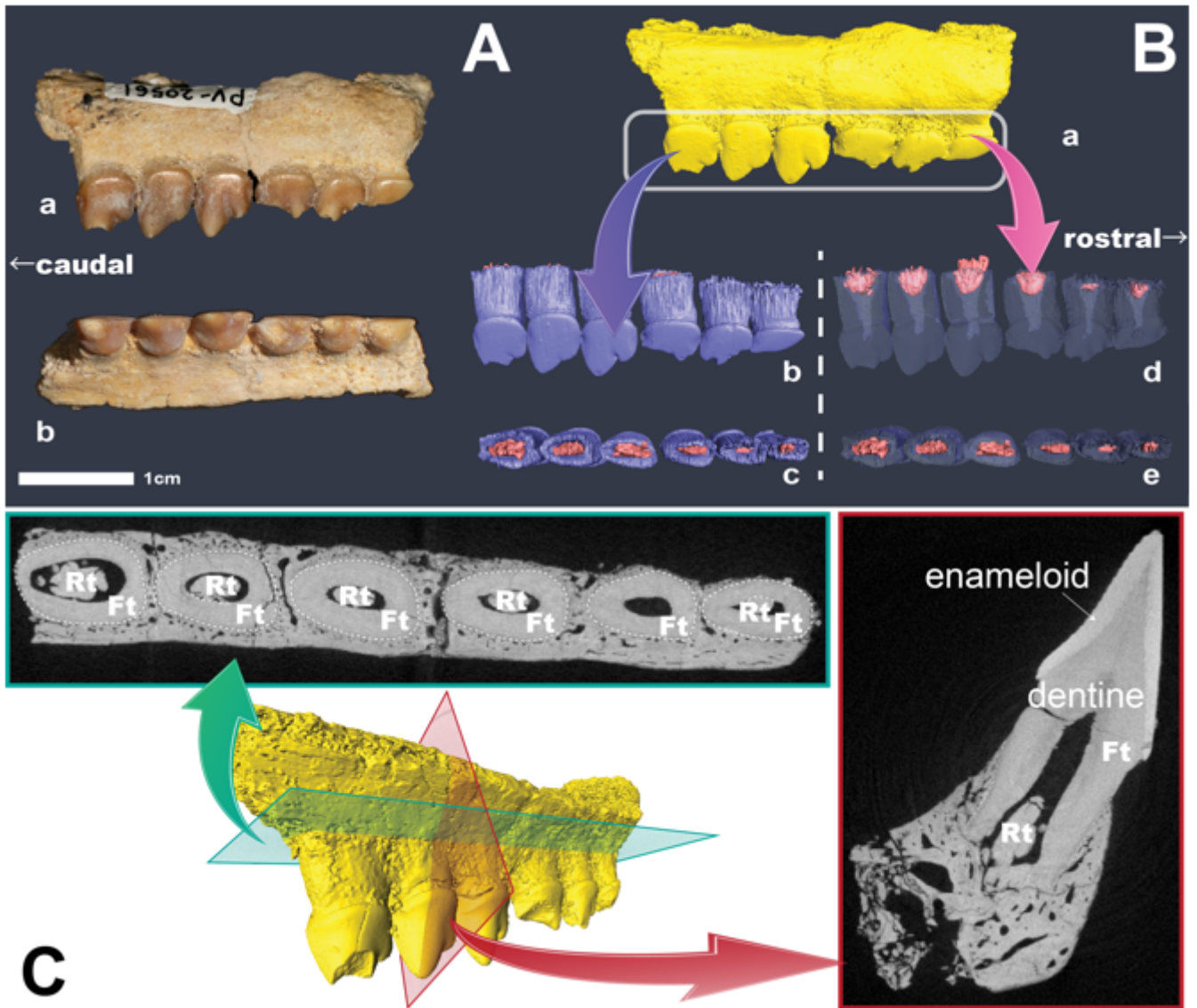
Figures

Figure 1

A right vomer of Serrasalmimus secans from Phosphorite Bed II (Thanetian age, Paleocene) in the Ouled Abdoun Basin, Morocco. (A) A right vomer of S. secans, NSM-PV20561. (a) lateral view. (b) ventral view. (B) CT-based 3D models of NSM-PV20561. (a) lateral view of NSM-PV20561 (yellow). (b) lateral view of functional teeth (blue) with replacement teeth (pink). (c) dorsal view of functional teeth with replacement teeth. (d) lateral view of translucent functional teeth with replacement teeth. (e) dorsal view of translucent functional teeth with replacement teeth. (C) horizontal and longitudinal section of NSM-PV20561. Rt: replacement teeth. Ft: functional teeth.
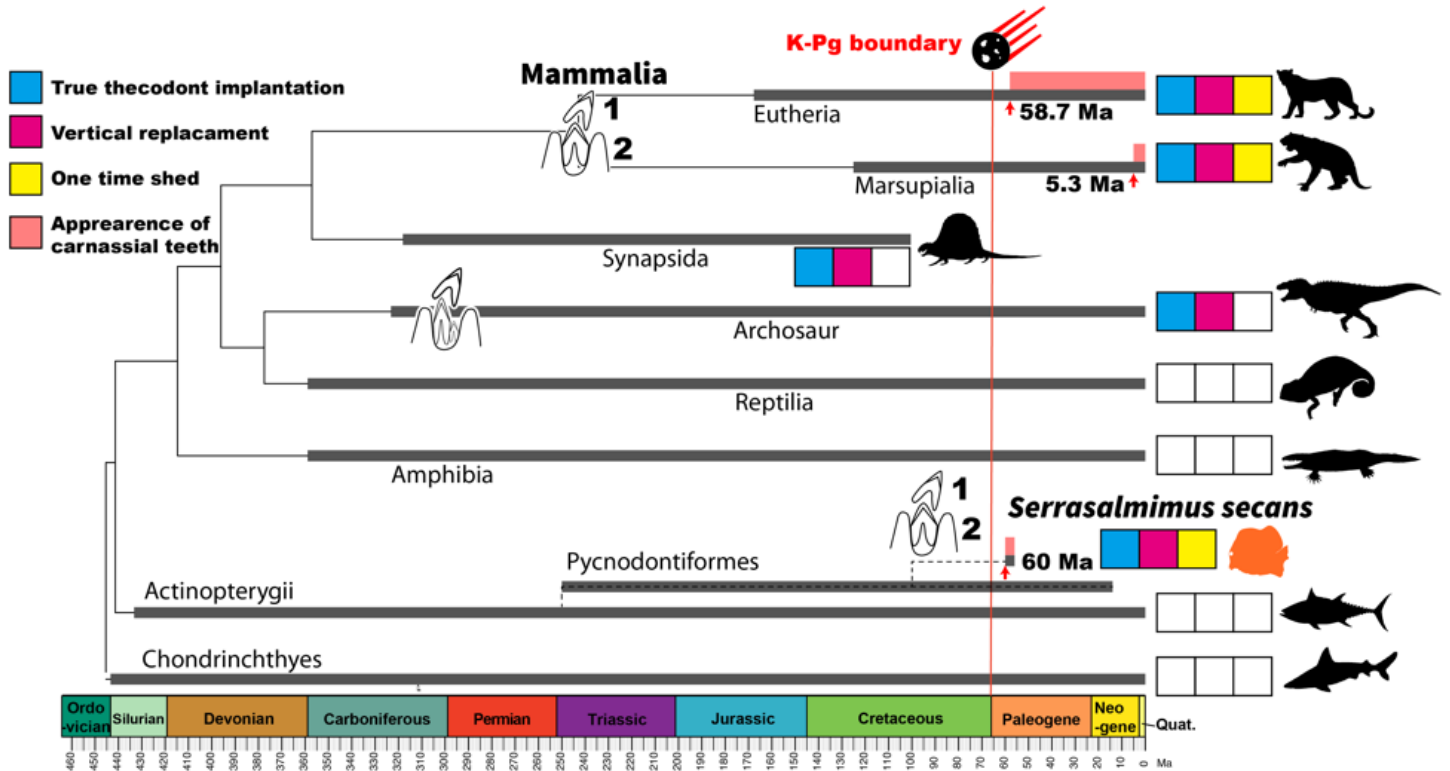
Figure 2

Dental features among vertebrates. A cladogram is a conceptual tree showing relationships of major vertebrates. Schematic teeth feature hypothetical ancestral states of the replacement mode in major lineage. blue: presence of true-thecodont implantation; magenta: vertical replacement system; yellow: one replacement in their life is one; orange: appearance of carnassial teeth. All white boxes mean absence of these characters. 1, 2: generation of a tooth. Images from phylopic.org: Eutheria by Margot Michaud (Panthera: http://phylopic.org/image/78dbe564-bcba-4dc3-8bdc-fb95fc288580/, Marsupilla by Steven Traver (Thylacoleo: http://phylopic.org/image/21dde05e-dcb4-416c-bb2a-0faec8bf4d9c/), Synapsida by Dmitry Bogdanov (Dimetrodon: http://phylopic.org/image/1f3e74df-30e6-422b-9ce2-db7df199f11d/), Archosaur by Maija Karala (Tyrannosaurus rex: http://phylopic.org/image/eb78548d-4f61-43c7-a087-a69074bc8bea/), Reptilia by Beth Reinke (Kinyongia: http://phylopic.org/image/9206cb73-a2eb-43da-bcce-ff7d8b305683/), Amphibia by Scott Hartman (Ichthyostega: http://phylopic.org/image/f002b543-ff02-4f15-8fb5-49d150c287e7/), Actinopterygii by Robbie N. Cada (Thunnus: http://phylopic.org/image/be13bcdf-ebef-4288-bdc6-114751cdb550/), Chondrichthyes by An Ignorant Atheist (Lamniformes: http://phylopic.org/image/42135d61-3549-45d2-841c-4147548b0fad/)

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