The First Healed Bite Mark and Embedded Tooth in the Snout of a Middle Permian Gorgonopsian (Synapsida: Therapsida)

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Despite their significance for paleobiological interpretations, bite marks have been rarely reported in non-mammalian therapsids (NMT). Here we describe, for the first time, the occurrence of a tooth embedded in the snout of a gorgonopsian. The tooth is surrounded by a bony callus, which demonstrates that the animal was still alive after the attack and healed. The identity of the attacker is unknown. Two hypotheses are discussed to account for this healed bite: failed predation (most likely by a biarmosuchian, therocephalian, or another gorgonopsian) and intraspecific social biting. Though predation cannot be ruled out, it has been hypothesized that gorgonopsians used their saber-like teeth for social signaling, which suggests that social biting may be the most likely scenario. The practice of social biting has long been hypothesized in NMT, but this is the first fossilized evidence of the behavior to be described.

Keywords: Gorgonopsia, bite mark, social biting, callus, paleopathology, saber-toothed

INTRODUCTION

The paleopathological study of extinct species is the gateway to many, otherwise inaccessible, paleobiological traits such as intraspecific behavior (Farke et al., 2009; Peterson and Vittore, 2012; Peterson et al., 2013), diet and food acquisition (DePalma et al., 2013), etiology and healing capabilities (Wolff et al., 2009; Kato et al., 2020), soft tissue reconstruction (Rega et al., 2012), thermophysiology (Benoit et al., 2015), interspecific interactions (Aureliano et al., 2021), biting force (Erickson et al., 1996; Gignac et al., 2010), and even key transitional events in the evolutionary history of vertebrates such as the onset of arboreality in hominins and terrestriality in early tetrapods (Bishop et al., 2015; Kappelman et al., 2016).

Published paleopathology literature on non-mammalian therapsids (NMT) is surprisingly scarce (Jinnah and Rubidge, 2007; Fröbisch and Reisz, 2008; Budziszewska-Karwowska et al., 2010; Fordyce et al., 2012; Vega and Maisch, 2014; Benoit et al., 2015; Whitney et al., 2017, 2019; Kato et al., 2020) despite the demonstrated species richness, abundance, and extensive spatial distribution of these animals in the fossil record (Ivakhnenko, 2008; Nicolas and Rubidge, 2010; Angielczyk and Kammerer, 2018). In contrast, osteopathologies are well documented in dinosaurs, crocodilians, mosasaurs, non-therapsid pelycosaurs, etc. (Buffetaut, 1983; Boucot, 1990; Rothschild and Martin, 1993; Mackness and Sutton, 2000; Tanke and Rothschild, 2002; Katsura, 2004; Lingham-Soliar, 2004; Reisz and Tsuji, 2006; Boucrot and Poinar, 2011; Zammit and Kear, 2011; Rega et al., 2012; Bakker et al., 2015; Bastiaans et al., 2020), and the existence of paleopathologies...
in contemporaneous species is attested (Fernandez et al., 2013). Bite marks, in particular, have been documented in countless fossil mammals (e.g., Scott and Jepsen, 1936; Tanke and Currie, 1998; Chimento et al., 2019), pelycosaurs (Reisz and Tsuji, 2006; Bakker et al., 2015), and outside synapsids in, e.g., dinosaurs, crocodilians, mosasaurs, ichthyosaurs (Buffetaut, 1983; Boucot, 1990; Rothschild and Martin, 1993; Tanke and Currie, 1998; Mackness and Sutton, 2000; Tanke and Rothschild, 2002; Avilla et al., 2004; Katsura, 2004; Lingham-Soliar, 2004; Zammit and Kear, 2011; Bastiaans et al., 2020), but remain rarely reported in NMT. So far, bite marks have been described on the surface of the bones of two dicynodonts (Budziszewska-Karwowska et al., 2010; Fordyce et al., 2012) and one titanosuchid dinocephalian (Shelton et al., 2019). These bites have been attributed to a gorgonopsian (Fordyce et al., 2012), an anteosaur (Shelton et al., 2019), and unknown carnivores (Budziszewska-Karwowska et al., 2010). To find a tooth still embedded in bone is even rarer and extremely significant for paleobiological interpretations (Buffetaut et al., 2004; Bell and Currie, 2010; DePalma et al., 2013; Drumheller et al., 2014; Konishi and Brinkman, 2016), but such an occurrence has never been reported in NMT.

Here we report, for the first time, the preservation of a tooth found embedded in a callus within the bone of the snout of a gorgonopsian from South Africa, and discuss its paleobiological implications.

MATERIALS AND METHODS

The embedded tooth was found in specimen SAM-PK-11490 (Figure 1). The specimen is an isolated and mostly unprepared snout of a gorgonopsian found on farm Mynhardskraal (Beaufort West District) by Dr. Lieuve D. Boonstra in 1940. Biostratigraphically, it is from the Tapinocephalus Assemblage Zone of the Beaufort Group of the Karoo Supergroup (South Africa), which correlates with the Guadalupian epoch of the Permian period (Day and Rubidge, 2020). The snout was attributed to Arctognathus cf. curvimola by Sigogneau (1970) but was then re-identified as Gorgonopsia indet. by Kammerer et al. (2015). We maintain the identification of this specimen as Gorgonopsia indet. given: (i) the specimen preserves a fragment of the snout only, (ii) the unprepared state of the specimen, and (iii) the currently unclear number of postcanine teeth [four according to Kammerer et al. (2015), but five according to Sigogneau (1970)], although ongoing preparation of the specimen appears to support that four is the correct number, see Figure 1, this last character being important for taxonomic identification. The presence of an embedded tooth in this specimen was not reported during these previous taxonomic assessments.

Institutional Abbreviations

MCA, Museo “Carlos Ameghino,” Mercedes, Buenos Aires province, Argentina; SAM, Iziko South African Museum, Cape Town, South Africa; SDSM, South Dakota School of Mines and Technology, Museum of Geology, Rapid City, SD, United States.

DESCRIPTION

The embedded tooth is located on the dorsal half of the left side of the snout, above the maxillary canine and approximately at the same height as the naris (Figure 2). The visible cross-section of the tooth is circular except for the presence of a carina (but this feature may be exaggerated due to the displacement of a portion of the tooth as it is heavily fractured). The tooth section measures 2.1 mm across, and the pulp cavity is exposed. The embedded tooth is surrounded by a porous, raised, and dorsoventrally oblong callus of bone (Figure 2), which conforms to the cicatricial osseous tissue described in most tetrapods (Boucot, 1990; Rothschild and Martin, 1993; Tanke and Rothschild, 2002; Bishop et al., 2015) including gorgonopians and other NMT (Fordyce et al., 2012; Kato et al., 2020). The callus measures 6.5 mm long and 8.5 mm wide. Its surface is porous, but no drainage canal for pus is visible. This feature is thus interpreted as a callus resulting from the healing of the bone around the tooth after it broke during a bite and remained embedded in the bone. Noticeably, the callus is not limited to the immediate surrounding of the tooth but is expanded laterally, which indicates that the bone in this area was damaged too (Figure 2). This suggests that the axis of the tooth row that inflicted the damage was oriented obliquely, almost perpendicular to the snout (Figure 3), so that the rest of the tooth row produced more superficial bone damages next to the embedded tooth. This is consistent with the position and orientation of the carina on the embedded tooth (assuming that the carina was pointing distally as in most carnivorous species). No exostosis indicative of bone infection is visible.

DISCUSSION

The presence of a callus around the embedded tooth clearly distinguishes SAM-PK-11490 from cases of post-mortem bites (e.g., Bell and Currie, 2010; Fordyce et al., 2012) as it unmistakably indicates that healing of the periosseous tissue took place after the tooth broke-off. The raised rim around the tooth provides direct evidence for the growth of a callus (assuming the gorgonopsian was alive when it was bitten 2–9 weeks before it died based on mammalian healing capabilities (Lovell, 1997; Lingham-Soliar, 2004). The absence of a drainage channel for pus or any other trace of infection suggests that an infection resulting from the bite was likely not the cause of death.
In living animals, bites can be inflicted either during an act of predation or for social signaling (Poole, 1985; Tanke and Currie, 1998). Therefore, the two hypotheses that may account for the circumstances that led to the condition in SAM-PK-11490 are attempted predation or social signaling. Regarding the predation hypothesis, specimen SAM-PK-11490 is a small to medium sized gorgonopsian. The snout is only 54 mm wide at the canines, making it similar in size to the contemporaneous *Eriphostoma microdon*, which is generally recognized as a small gorgonopsian (Kammerer et al., 2015). A wide variety of possible predators large enough to attack such a species populated the *Tapinocephalus* Assemblage Zone fauna of the South African Karoo, including large biarmosuchians, therocephalians (scylacosaurid and lycosuchid), anteosaurs, and rhinesuchid amphibians (Day and Rubidge, 2020). Attempted cannibalism or attack by another gorgonopsian are not excluded.

A rhinesuchid attacker can be excluded as the embedded tooth does not display the typical labyrinthodont pattern of plicidentine (Fortuny and Steyer, 2019) encountered in the sectioned teeth of these amphibians (Figure 2). The tooth being carinated, the bite of a prey (such as an anamodont) defending itself appears unlikely. Biarmosuchians, gorgonopsians, and therocephalians would be more likely compared to anteosaurs as the latter would have had large teeth and a crushing bite (Kammerer, 2011), not compatible with the small size of the embedded tooth and light damage observed in SAM-PK-11490. The cross-section of the anterior-most incisors is generally circular in biarmosuchians, gorgonopsians, and therocephalians (Sigogneau, 1970; Mendrez, 1975), which suggests the embedded tooth is either a lateral incisor, a canine, or a postcanine tooth. The very small size of the tooth would exclude a canine, although it could be the very tip of a canine; but this too is unlikely, given that the pulp cavity is visible (Figure 2). The lateral incisors and postcanine teeth can bear serrations on their posterior face and appear carinated in cross-section in biarmosuchians, gorgonopsians, and therocephalians (Sigogneau, 1970; Mendrez, 1975; Rubidge and Kitching, 2003; Abdala et al., 2008). It is thus likely that the embedded tooth is a lateral incisor or postcanine that belongs to a biarmosuchian, gorgonopsian, or a therocephalian (scylacosaurid or lycosuchid).

The second hypothesis is intraspecific social biting. Social biting occurs in many modern species (reptiles and mammals, particularly carnivores) to assert dominance, stimulate copulation and ovulation, compete for mates, territory and breeding rights, or simply as juvenile play biting (Poole, 1985; Tanke and Currie, 1998; Cabrera and Stankovich, 2018; Chimento et al., 2019; although, play biting can be safely excluded as this behavior is limited to juvenile individuals and the dimensions of SAM-PK-11490 corresponds to an adult-sized middle Permian gorgonopsian).

Social biting has been suggested in many extinct species, including theropod dinosaurs, aquatic reptiles, and saber-toothed cats (Scott and Jepsen, 1936; Buffetaut, 1983; Tanke and Currie, 1998; Avilla et al., 2004; Katsura, 2004; Everhart, 2008; Peterson et al., 2009; Wolff et al., 2009; Bell and Currie, 2010; Zammit and Kear, 2011; Chimento et al., 2019), and has also long been hypothesized in NMT (Geist, 1972; Barghusen, 1975; Benoit et al., 2016, 2021), but evidence was lacking. As stated above, the embedded tooth is likely a lateral incisor or postcanine of another carnivorous NMT. Its diameter is consistent with the size of the incisors and postcanines of specimen SAM-PK-11490, making a conspecific individual a possible candidate as the attacker (Figure 3).

The possibility that the embedded tooth belongs to a biarmosuchian, a therocephalian, or another species of gorgonopsian cannot be ruled out; however, intraspecific social biting is here preferred over predation to account for the condition in SAM-PK-11490 for three reasons. Firstly, the position of the embedded tooth is consistent with face biting. Face biting is a particular kind of social biting during which modern amphibians (e.g., *Ceratophrys*), reptiles (e.g., *Varanus*), and mammals (e.g., *Panthera*) bite each others' head during more or less ritualized intraspecific combat to assert dominance and secure mates, territory, or breeding rights (Tanke and Currie, 1998; Chimento et al., 2019). Secondly, the non-lethality of the bite is an expected outcome of social biting (Geist, 1966). Lethal intraspecific combat would reduce population size and attract predators and scavengers (Geist, 1966; Lorenz, 1966; Cabrera and Stankovich, 2018), and as such, social biting is meant to signal dominance and power, or stimulate breeding.

![Figure 1](image-url) Specimen SAM-PK-11490 in left lateral with a simplified diagram showing the position of the embedded tooth and surrounding callus.
rather than to injure or kill a member of the same species. Accordingly, social biting often targets the dorsal part of the neck or the snout because injuries there would neither be lethal nor disabling (Poole, 1985; Tanke and Currie, 1998; Bell and Currie, 2010; Zammit and Kear, 2011). In SAM-PK-11490, the embedded tooth is located on the maxilla, in an area of the snout generally targeted during intraspecific face-biting [e.g., in crocodilians, Peterson et al. (2009)] as this region is not susceptible to intense bleeding and has no vital organs. In contrast, a predatory action (interspecific or cannibalism) is expected to be lethal if successful, which was not the case with SAM-PK-11490. Thirdly, gorgonopsians are noticeable for their saber-like canines (Sigogneau, 1970) and one of the functions of such enlarged canines in modern species is social signaling, including sexual display and intraspecific combat (Poole, 1985; Miller, 2011; Cabrera and Stankowich, 2018). Evidence of social biting has been found in saber-toothed cats, such as specimens MCA 2046 of Smilodon populator and SDSM 348 of Nimravus brachyops, which bear distinctive healed bite marks made by their conspecifics’ enlarged canines (Scott and Jepsen, 1936; Chimento et al., 2019). The almost ubiquitous presence of enlarged canines among NMT strongly supports that social signaling using teeth (including social biting) was an important driver of their evolution (Geist, 1972; Benoit et al., 2016). Noticeably, the rare NMT with reduced or no canines (e.g., tapinocephalids, endothiodontids, cistecephalids, or bauriid therocephalians) generally have bosses, horns, or enlarged incisors to compensate (Nasterlack et al., 2012; Abdala et al., 2014; Benoit et al., 2016, 2021).

It may be argued that the embedded tooth cannot belong to a gorgonopsian because their bite force was too weak to puncture bone. To achieve a bone-crushing bite on long bones, it is generally accepted that a carnivorous species would have to develop a bite force of at least 1,000–3000 N (Tanner et al., 2008;
Bell and Currie, 2010; Snively et al., 2015), whereas the estimated bite force of Eriphostoma and Gorgonops (the two taxa that most closely resemble SAM-PK-11490) is only 25 N and 116 N, respectively (Lautenschlager et al., 2020). Even the largest gorgonopsians, such as Rubidgea atrox, would have had an estimated bite force of 715 N, insufficient for long bone-crushing (Lautenschlager et al., 2020). However, a bone-crushing bite is not a necessary condition to puncture bone, especially the rather thin bone of the snout, as demonstrated by the Komodo dragons (Varanus komodoensis), which can leave distinct bite marks on bones (D’Amore and Blumensehine, 2009) despite their weak bite force of less than 20 N (Moreno et al., 2008). Additionally, a distinctly large and deep puncture was found on the femur of an Oudenodon specimen (SAM-PK-K06446) and was attributed to the gorgonopsian Aelurognathus based on a broken tooth found close to the bone (Fordyce et al., 2012). According to Lautenschlager et al. (2020), the bite force of Aelurognathus was also very weak (61 N), but in the case of SAM-PK-K06446, it appears that the bite force of Aelurognathus was arguably strong enough to puncture the thigh bone of this large dicynodont. This shows that even a small gorgonopsian like SAM-PK-11490 could have been capable of puncturing bone and that its inability to crush bone does not disqualify social biting to account for the embedded tooth in its snout.

CONCLUSION

Social biting, and more particularly face biting, was advocated by (Geist, 1972; Barghusen, 1975; Benoit et al., 2016, 2021) to account for the evolution of oversized canines in NMT, but the absence of bite marks in the abundant fossil record of these taxa was puzzling. This is the first time a healed bite mark is documented in NMT, and its position on the snout, in line with other evidence, suggests that it was made during a face biting contest or some other type of social biting behavior (though, attempted predation by a therocephalian, biarmosuchian, or another gorgonopsian cannot be completely ruled out). Evidence of possible social behavior in NMT already supported parental care/brooding in cynodonts and the dicynodont Diictodon (Jasinoski and Abdala, 2017; Hoffman and Rowe, 2018; Smith et al., 2021 but see Sues, 2018 and Benoit, 2019 for different interpretations), gregariousness in dicynodonts (Fiorelli et al., 2013; Viglietti et al., 2013; Franciscini et al., 2018), and head butting mostly in tapinocephalid dinocephalians (Barghusen, 1975; Benoit et al., 2017, 2021). In the synapsid lineage, these behaviors are traditionally considered as complex and more typical of mammals because they imply some level of social intelligence and usually correlate well with the presence of a large brain (Pérez-Barbería and Gordon, 2005; Sues, 2018; Benoit et al., 2021). The current work suggests social biting may be added to this list of advanced behaviors already present in NMT. The discovery of such significant evidence of ancient behavior on a specimen that was collected some 80 years ago and studied for at least five published and unpublished works (Sigogneau, 1970; Sigogneau-Russell, 1989; Gebauer, 2007; Kammerer, 2015; Kammerer et al., 2015) suggests that bite marks have been overlooked in NMT. This may account for the apparent paucity of recorded bite marks and other paleopathologies in NMT despite their rich fossil record. The systematic search for bite marks in the extensive collections of Permo-Triassic specimens will likely unravel a hitherto unknown diversity of bite marks and their associated behavior.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material; further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JB designed the study. JB and CB provided and analyzed the data. CB made the microscope photographs. JB drafted the manuscript. CB and LN provided critical comments. All authors gave final approval for publication.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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