A study of the Mio-Pliocene marine palaeoenvironment on South Africa’s west coast revealed aspects of the biology and behaviour of fossil marine mammals. Close examination showed that seals from Langebaanweg suffered from pathologies and bore marks of marine carnivore activity. This study adds to our knowledge of shark feeding behaviour in the geological past and is one of a few studies of sharks feeding on seals in the fossil record. Two incomplete seal humeri with shark tooth marks are the first documented evidence from South Africa’s Mio-Pliocene of such behaviour. These injuries show no healing, which suggests that the animals were most likely scavenged.

**Significance:**
- Fossil rich deposits at Langebaanweg contribute to the knowledge of South African Mio-Pliocene fossils by placing them in a global context.
- This study is one of five globally that have documented marine carnivores feeding on seals.
- This is the first description of white sharks feeding on seals from South Africa’s geological past.
- This study shows this behaviour was in place on South Africa’s coast as early as 5 million years ago.
- The injuries show no signs of healing, suggesting the most parsimonious explanation is that white sharks were scavenging seal carcasses.

**Introduction**
Along South Africa’s south and west coasts today, there are offshore breeding colonies of South African fur seals (*Arctocephalus pusillus pusillus*), white shark (*Carcharodon carcharias*) predation on these colonies is well documented. It therefore follows that there should be evidence of similar behaviour in the geological past. Diedrich et al. showed that the correlation between the presence of seal fossils and abundance of shark teeth in the Proto North Sea may indicate the earliest specialisation for seal hunting in the fossil record in the northern hemisphere. This indicates that a specialisation by white sharks to hunt seals was already in place 50 Ma. Collareta et al. described bites from a megatooth shark (*Carcharocles megalodon*) on the acapula of a large seal from Peru’s late Miocene, while Squalus (dogfish shark) tooth marks were identified on an *Alloodesmus* skull (a large extinct seal-like pinniped known from the Northern Pacific Ocean) from the early Late Miocene of southwestern Washington State. Purdy et al. described a long unserrated bite mark on the distal humerus of *Callorhinchus obscura* (an extinct earless seal) left by *Isurus xiphodon* (an extinct mako shark), eliciting the question as to whether this shark preferred warm-water seals.

Part of this study was to understand the interactions occurring between animals living on or visiting the west coast. An analysis of the marine mammal fossils has produced evidence of white and mako sharks feeding on cetaceans off the coast 5 Ma, like they do today. It was therefore expected to find similar evidence of sharks feeding on seals as they do today off South Africa’s south and west coasts. This study documents the first evidence of sharks feeding on seals from South Africa’s Mio-Pliocene west coast.

**Geological setting**
Langebaanweg is located on the stable platform of South Africa’s west coast; 13 km inland from the current coastline and less than 2° north of the southern tip of Africa (Figure 1a). The Varwater Formation at ‘E’ Quarry spans the middle Miocene (Langhian) to the early Pliocene (Zanclean) and is associated with a number of changes in sea level. The bonetbed is at the base of the Muishond Fontein Pelletite Phosphorite Member (MPPM) within a channel fill in the Langeberg Quartzose Sand Member (LQSM) (Figure 1b). The Langebaanweg fossils were deposited during the 30-m high sea level when ‘E’ Quarry was less than a kilometre from the river mouth. During the earliest Pliocene, the ambient and sea surface temperatures cooled, and the Benguela Upwelling System intensified, providing a rich feeding ground.

‘E’ Quarry sedimentary facies include a river channel deposit near the river mouth, shallow marine, estuarine, marsh and fluvial systems. At Langebaanweg during the earliest Pliocene (Zanclean) there was a protected lagoon open to the ocean as well as an estuary. Marine mammal skeletal elements were deposited by storm surges flooding the neighbouring land surface and by terrestrial carnivore activity. Areas of high relief formed islands off the west coast during the early Pliocene (Zanclean) and provided ideal conditions for seals to breed.

**Materials and methods**
There is a total of 3131 complete, incomplete, and fragmentary cranial and postcranial elements in the phocid seal (*Homiphoca*) assemblage from Langebaanweg. Two isolated right humeri (SAM-POL-34631 and SAM-POL-60698) have shark tooth marks and root etching on the distal two-thirds (Table 1; Figures 2 and 3).
Bone fragments are embedded in the bone cortex due to the force of a bite or the pressure causing the fracture (Figure 2a). The bites are preserved on the shaft and distal part of the bone. These specimens were collected in 1976 from MPPM as part of an excavation. The bites described below follow Govender and Chinsamy:

1. CF1 damage can be subdivided into two types (herein designated serrated Types CF1a and CF1b): CF1a is a simple, superficial groove with dotted markings left by serrations, whereas CF1b is a deeper groove with ridges and grooves caused by tooth serrations.
2. CF2 is a simple groove with tapered end and no trace of serrations.
3. CF3 damage has subparallel ridges and grooves corresponding with the tooth’s serrated edge. There is no cut groove.
4. CF4 damage suggests cutting and/or scraping action with rotating movement. This action leaves curvilinear markings caused by the rotation of the tooth.

Table 1: List of seal specimens with the number and type of bites identified

| Element                  | Specimen number | Locality                  | Number of bites | CF1 | CF2 | CF3 | CF4 |
|--------------------------|-----------------|----------------------------|-----------------|-----|-----|-----|-----|
| Incomplete right humerus | SAM-PQL-34631   | MPPM (BCWW T2 area RS)    | 2               | –   | –   | x   | –   |
| Incomplete right humerus | SAM-PQL-60688   | MPPM (W Wall IWRP 1976/2) | 19              | x   | x   | –   | –   |
Figure 2: Right humerus SAM-PQL-34631. (a) Anterior view showing the proximal break. (b) Lateral view showing the periosteal reaction indicated by the arrow. (c) Arrow 1 showing the undulating CF3 and arrow 2 showing the CF3.

Figure 3: Right humerus SAM-PQL-60698. (a) CF2 on the lateral surface showing the tooth moving over the surface a few times. (b) Posterior view showing laterally placed CF2. (c) CF1a and CF1b medially located on the posterior surface. (d) Close-up of CF1a and CF1b. (e) Fossil white shark tooth [SAM-POSS-225 (SAM-POY-24A)] from Saldanha Steel – a similar aged site west of Langebaanweg.
Description of bite marks
SAM-PQL-34631 shows periosteal reaction like that seen in SAM-PQL-30080\(^1\), suggesting that this seal was suffering from an infection (Figure 2b arrow). The shark tooth marks are on the lateral surface of the bone; one is directed at an angle down the long axis of the bone and is proximally incomplete while the other is directed across the bone towards the lateral margin. There are groups of subparallel ridges and grooves with a wavy appearance (Figure 2c arrow 1). Another set of ridges and grooves (Figure 2c arrow 2) run to the lateral margin just above the distal articulation. This damage suggests that the serrated edge of the tooth scraped across the surface of the bone (CF3).

SAM-PQL-60698 has at least four bites along the lateral margin. The shark’s tooth moved across the bone and left behind a simple groove with tapered ends (CF2; Figure 3a); the tooth moved over the same area a few times. Laterally, on the posterior surface, there are four CF2 bites, two bites leading to a bite on the lateral surface. From the middle of the bone to the medial border below the broken edge of the shaft, there are six bites caused by the shark biting down but not penetrating the bone causing only surface damage (CF1a; Figure 3b). Two bites – one towards the lateral surface and the other towards the medial surface – show evidence of the shark biting down and leaving grooves with ridges and grooves inside (CF1b, Figure 3c, d). The damage suggests that the tooth moved across the bite area multiple times (see Govender and Chinsamy’s fig. 4E).

Discussion
Extant sharks, including white (Carcharodon carcharias), tiger (Galeocerdo cuvier), Zambezi (bull) (Carcharhinus leucas), whale (Rhincodon typus), ragged tooth (sandtiger, Carcharias taurus) and shortfin mako (Isurus oxyrinchas) sharks, inhabit varying habitats along South Africa’s coast.\(^8\) Sharks from ‘E’ Quarry include Carcharias taurus, Carcharodon carcharias and Isurus sp.\(^8\). A re-examination of the shark teeth identified probable Carcharinus cf. leucas from Langebaanweg (personal observation 2013). Today, studies document extant adult white shark (Carcharodon carcharias) predation on South African fur seals on islands off the coast.\(^1-3\) In the vicinity of Langebaanweg, ‘E’ Quarry, offshore islands and a protected lagoon that was open to the ocean were present 5 Ma.\(^11,18\) The islands were surrounded by shallow water\(^2\), making this ideal for haul out and rookeries. Shark tooth marks have been identified on two fragmentary humeri, which limits the discussion to hypothetical scenarios extrapolated from the damage to the bones.

Two potential scenarios are hypothesised from the damage and the lack of healing around the bites: an active hunted seal or a scavenged seal carcass. The islands and the lagoon supplied an environment that was ideal for carcasses to beach and refloat or float in quiet waters. It is also interesting that of the 3131 seal specimens, only 2 have any evidence of shark tooth marks (0.06%). This low incidence could be related to the fact that the coast was also frequented by cetaceans which were more likely the focus of shark feeding\(^13\) or that there are still specimens to be found in the collection and through excavation.

The environment in the Langebaanweg area allowed carcasses to remain afloat and when beached may have been refloated by wave action\(^1\); these carcasses leaching fluid would have attracted sharks into the area to feed, as evidenced by the presence of white shark and mako shark damage on the cetacean bones.\(^6-10\) This put the sharks in contact with the seals living on the islands. The lagoon and surrounding islands were linked like ‘Shark Alley’ today\(^4\) where seal carcasses may have remained afloat. It could also be interpreted that sharks did not frequent the area until there was a cetacean carcass to feed on and were opportunistically scavenging seal carcasses when excluded from the cetacean carcasses.

White sharks ambush seals off Seal Island, biting prey obliquely using their anterolateral teeth in a lateral snap\(^4\), and attack seals at the water surface using a steep vertical attack\(^4\). The bites on the humeri vary from superficial scrapes to deep bites penetrating the bone, suggesting that the shark and seal (carcass) were in motion. The presence of scrapes on SAM-PQL-34631 suggests that the shark tooth/teeth slid across the bone as the shark was biting. This type of damage could have resulted from the carcass or shark or both being in motion and it not being able to get a firm grip on the bone. There is evidence that this animal was also suffering from an infection which would potentially affect its ability to evade a predator or it may have succumbed to its illness.

SAM-PQL-60698 shows the presence of CF1a, CF1b and CF2 bites. The shark’s teeth slid across the surface of the bone without penetrating the periosteum (CF1a) while it fed, as a result of the shark or the carcass or both being in motion.\(^4\) This could be a result of the shark propelling itself forward to bite and then straight reverse.\(^27\) The bites on SAM-PQL-60698 suggest that the shark bite was from the right side behind the seal’s front flipper. The bite went through the muscles of the humerus, leaving evidence on the bone itself, or the carcass was partially skeletonised.

Sharks with serrated teeth left the bites seen on these seal bones (Figure 3e), which resembles the damage described in Govender and Chinsamy\(^9\) on cetaceans from Langebaanweg caused by the white shark (Carcharodon carcharias). The bite marks on the bone suggests that some skeletogenesis had occurred, further supporting the hypothesis that white sharks were scavenging seal carcasses. Deposition at ‘E’ Quarry occurred as a result of terrestrial carnivore activity or storm surges.

Conclusion
This study is the first description of sharks interacting with seals in South Africa’s geological past. At least one individual was suffering from an infection at the time of death. These carcasses remained afloat in the channels connecting the surrounding islands with the lagoon at Langebaanweg, making them available for sharks to feed on while they were also feeding on nearby whale carcasses. Based on the bone damage, the seals were carcasses that were scavenged by white sharks. Shark tooth marks are preserved on only two seal humeri. Simulations/impact models and statistical analyses are currently beyond the scope of this study but may prove beneficial in future if more specimens are collected during future excavations and/or identified from the collection.

Acknowledgements
I thank the Cenozoic collections staff, Sarena Govender (Assistant Collections Manager; Cenozoic Palaeontology), Angus Rayners (Technical Assistant; Cenozoic Palaeontology) and Mark de Benedictis (Technical Assistant; Cenozoic Palaeontology) at Iziko South African Museum, Cape Town, for their assistance. I also thank Dr Graham Avery for his encouragement, and the two anonymous reviewers whose comments greatly enhanced the manuscript. This research was funded by an NRF/African Origins Platform grant (grant numbers UID 98834 and UID117782).

Competing interests
There are no competing interests to declare.

References
1. De Vos A, O’Rain M, Meyer MA, Kotze PG, Kock AA. Behavior of Cape fur seals (Arctocephalus pusillus pusillus) in relation to temporal variation in predation risk by white sharks (Carcharodon carcharias) around a seal rookery in False Bay, South Africa. Mar Mamm Sci. 2015;31(3):1118–1131. https://doi.org/10.1111/mms.12028
2. Johnson RL, Keswick T, Bester MN, Oosthuizen WH. Encounters between white sharks and Cape fur seals in a shallow channel. Mar Biodiv Rec. 2009;2:1–5. https://doi.org/10.1017/s1755672000000682
3. Hammerschlag N, Martin RA, Fellows C. Effects of environmental conditions on predator–prey interactions between white sharks (Carcharodon carcharias) and Cape fur seals (Arctocephalus pusillus pusillus) at Seal Island, South Africa. Environ Biol Fish. 2006;76:341–35. https://doi.org/10.1007/s10641-006-0038-2
4. Diedrich CG. Evolution of white and megatooth sharks, and evidence for early predation on seals, sirenians, and whales. Natural Sci. 2013;5(11):1203–1218. http://dx.doi.org/10.4236/ns.2013.511148
5. Collareta A, Lambert O, Landini W, Di Celma C, Malinverno E, Varas-Malca R, et al. Did the giant extinct shark Carcharocles megalodon target small prey? Bite marks on marine mammal remains from the late Miocene of Peru. Palaeogeogr Palaeoclimatol Palaeoecol. 2017;469:84–91. https://dx.doi.org/10.1016/j.palaeo.2017.01.001

6. Bigelow PK. Occurrence of a squalloid shark (Chondrichthyes: Squaliformes) with the pinipod Allodus from the Upper Miocene of Washington. J Paleont. 1994;68(3):680–684. https://dx.doi.org/10.1016/0022-3360(94)90026-0

7. Purdy RS, Schneider VP, Applegate SP, McLellan JH, Meyer RL, Slaughter BH. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In: Ray CE, Bohaska DJ, editors. Geology and paleontology of the Lee Creek Mine, North Carolina. Vol. III. Smithsonian Contribution toPaleobiology 90. Washington DC: Smithsonian Institution Press; 2001. p. 71–202.

8. Govender R, Chinsamy A. Early Pliocene (5 Ma) shark–cetacean trophic interaction from Langebaanweg, western coast of South Africa. Palaeo. 2013;28(5):270–277. http://dx.doi.org/10.2110/palo.2012.p12-058r

9. Govender R. Shark-cetacean trophic interaction, Duinefontein, Koeberg. (5 Ma), South Africa. S Afr J Sci. 2015;111(11–12), Art. #2014-0453. http://dx.doi.org/10.17159/sajs.2015/20140453

10. Govender R. Early Pliocene fossil cetaceans from Hondeklip Bay, Namaqualand, South Africa. Hist Biol. 2019;15:1–20. https://dx.doi.org/10.1080/08912963.2019.1650273

11. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in ‘E’ Quarry. Langebaanweg, South Africa, and a reinterpretation of their geological context. Ann S Afr Mus. 1981;84(1):1–104.

12. Smith RMH, Haarhoff P. Sedimentology and taphonomy of an early Pliocene Sivathere bonebed at Langebaanweg, Western Cape Province, South Africa. Afr Nat Hist. 2006;2:197.

13. Roberts DL, Matthews T, Herries AI, Boulter C, Scott L, Dondo C, et al. Regional and global context of the Late Cenozoic Langebaanweg (LBW) palaeontological site: West Coast of South Africa. Earth-Sci Rev. 2011;106(3–4):191–214. https://dx.doi.org/10.1016/j.earscirev.2011.02.002

14. Hendey QB. Langebaanweg: A record of past life. Cape Town: South African Museum; 1989.

15. Tankard AJ, Rogers J. Late Cenozoic palaeoenvironments on the west coast of southern Africa. J Biogeogr. 1978;1:319–337. https://dx.doi.org/10.2307/3038026

16. Siesser WG, Dingle RV. Tertiary sea-level movements around Southern Africa. J Geol. 1981;89(4):523–536.

17. Siesser WG. Late Miocene origin of the Benguela upwelling system off Northern Namibia. Science. 1980;208(4441):283–285. https://dx.doi.org/10.1126/science.208.4441.283

18. Kenseley BF. Pliocene marine invertebrates from Langebaanweg, Cape Province. Ann S Afr Mus. 1972:173–190.

19. Erasmus L. Virtual reconstruction of stratigraphy and past landscapes in the West Coast Fossil Park Region [MSc thesis]. Stellenbosch: Stellenbosch University; 2005.

20. Hendey QB, Dingle RV. Onshore sedimentary phosphate deposits in south-western Africa. In: Notholt AJG, Sheldon RP, Davidson DF, editors. Phosphate deposits of the world. Vol. 2: Phosphate rock resources. Cambridge: Cambridge University Press; 1989. p. 200–206.

21. Govender R, Avery G, Chinsamy A. Pathologies in the early Pliocene phocid seals from Langebaanweg, South Africa. S Afr J Sci. 2011;107:72–77. https://dx.doi.org/10.4102/sajs.v107i1/2.230

22. Tulu Y, Chinsamy-Turan A. Langebaanweg Quarry, Western Cape, South Africa: The Elasmobranch fauna and comparisons to faunas of PCS (Lee Creek) phosphate mine and Sharktooth Hill. J Vert Paleontol. 2011;31:217.

23. Rogers J. First report on the Cenozoic sediments between Cape Town and Elands Bay. Geological Survey of South Africa. 165:1–64.

24. Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, Kaschka T, et al. Sex-specific and individual preferences for hunting strategies in white sharks. Funct Ecol. 2016;30(8):1397–1407. https://dx.doi.org/10.1111/1365-2435.12613

25. Martin RA, Hammerschlag N, Ralph OP, Collier S, Fallsows C. Predatory behaviour of white sharks (Carcharodon carcharias) at Seal Island, South Africa. J Mar Biol Ass UK. 2005;85:1121–1135. https://dx.doi.org/10.1017/s002531540501216x

26. Martin RA, Rossmo DK, Hammerschlag N. Hunting patterns and geographic profiling of white shark predation. J Zool. 2009;279:111–118. https://dx.doi.org/10.1111/j.1469-9970.2009.0558.x

27. Tricas TC. Feeding ethology of the white shark, Carcharodon carcharias. Mem Calif Acad Sci. 1985;9:81–91.

28. Govender R, Bisconti M, Chinsamy A. Late Miocene–early Pliocene baleen whale assemblage from Langebaanweg, west coast of South Africa (Mammalia, Cetacea, Mysticeti). Alcheringa. 2018;40(4):542–555.