Shark–Cetacean trophic interaction, Duinefontein, Koeberg, (5 Ma), South Africa

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This study forms part of a larger project to reconstruct the Mio-Pliocene marine palaeoenvironment along South Africa's west coast. It documents the shark–cetacean trophic interaction during the Zanclean (5 Ma) at Duinefontein (Koeberg). The damage described on the fragmentary cetacean bones was compared with similar damage observed on fossils from Langebaanweg, a Mio-Pliocene site on the west coast of South Africa, and data present in the literature. This comparison showed that the damage was the result of shark bites. The state of preservation makes it difficult to determine if the shark bite marks were the cause of death or as a result of scavenging. The presence of the bite marks on the bone would, however, indicate some degree of skeletonisation. Bite marks on some cranial fragments would suggest that the cetacean's body was in an inverted position typical of a floating carcass. The preservation of the material suggests that the bones were exposed to wave action resulting in their fragmentation as well as abrasion, polishing and rolling. It also suggests that the cetacean skeletons were exposed for a long time prior to burial. The morphology of the bites suggests that the damage was inflicted by sharks with serrated and unserrated teeth. Shark teeth collected from the deposit include megalodon (*Carcharodon megalodon)*, white (*Carcharodon carcharias*) as well as mako (*Isurus* sp. and *Cosmopolitodus hastalis*) sharks, making these sharks the most likely predators/scavengers.

Introduction

Along the nearly 2000 km of southern African west coast there are few onshore deposits, but where they do occur they are rich in palaeontological and archaeological material.[1,2] During the 1970s when the foundations for the Koeberg Power Station at Duinefontein, located on the farm Duynefontyne 34[3,4] just inland of the west coast of South Africa,[5] were being dug, a subsurface locality was uncovered[3] (Figure 1a–b). This locality also contained a rich marine vertebrate faunal assemblage, for example sharks, cetaceans, seals and fish. Currently there is only one study published focusing on the fossil seal from Duinefontein (Koeberg).[6]

Previous studies show that there was a rich and diverse cetacean and seal fauna along the coast during the Mio-Pliocene.[7-9] During the current study to identify the cetacean fauna preserved at Koeberg, damage to various skeletal fragments was analysed and identified as bites. These bites were different from those identified as terrestrial carnivore damage seen at Langebaanweg (e.g. Hendey[10,11] and Govender unpublished data). There was no direct association between shark teeth collected at Koeberg and the cetacean fossils although they co-occur. When compared with the material from Langebaanweg[8] and other studies,[12-18] the most parsimonious conclusion was that the damage was produced by shark bites. This is the second study documenting the interactions between sharks and cetaceans along the south-western Cape coast during the Zanclean (early Pliocene, 5 Ma).[8] These studies will help build our knowledge of the marine mammals on the South African west coast as well as improve our understanding of the palaeoenvironment along the west coast during the Mio-Pliocene.[19,20]

Materials and methods

Geological and palaeontological setting

The fossils preserved in Duynefontyn member of the Varswater Formation are about 8.5 m below sea level and the member is divided into five beds.[3-5] The fossils that are part of the present study are preserved in the shark tooth bed (Figure 1b) which contains fossil sharks, teleost fish, marine mammals and birds; Rogers[21] interpreted this as a tsunamite deposit. The fossils provide a Zanclean age (5 Ma) for the deposit[4] which is equivalent to the Muishond Fontein Pelletal Phosphorite Member of the Varswater Formation at Langebaanweg.[5]

A barrier spit developed parallel to the coast with each successive regression and absorbed the energy from the wave action characteristic of the west coast's open ocean.[3,4] The shark tooth bed was concentrated into a placer deposit after the barrier spit was overtopped by storms or spring tides; and the retreating water scoured the intertidal flats.[3,4] The intertidal mixed flats were drained by a subtidal channel.[3] The presence of sub-Antarctic seabirds suggests that the marine temperature was colder than present,[22] while the presence of entirely pelagic, migrating and non-breeding birds indicates that the area was open to the ocean at times.[23]

Palaeontological material

The material described here was recovered during excavations of the foundations for the Koeberg Reactor site, 10–12 m below the surface.[3,5] The rich fossil material recovered from the shark tooth bed includes terrestrial mammals and reptiles[3,4] while the terrestrial pollen is too sparse to identify.[3,4] The cetacean fossil material, like that described from Langebaanweg,[8] is fragmentary; however, unlike Langebaanweg, identification of the Koeberg material is difficult; particularly those with bites.

The cetacean fossils consist of vertebral centra, tympanic bullae, periotics, isolated teeth and cranial fragments. A preliminary analysis of the cetacean fossils suggests that there are mysticetes (balaenopterids), odontocetes (e.g. sperm whale, porpoises and delphinids) present at Koeberg. These specimens form part of a separate taxonomic study (Govender unpublished data). Fossils from Duinefontein (Koeberg) show evidence of having been rolled, some have a polished surface and some are abraded (stage 2)[24] (Figure 1c–e). Most of the damage seen on the bones suggests that the breaks occurred prior to burial. The fragmentary nature of the material would also suggest that the fossils were transported prior to deposition and after the skeletons

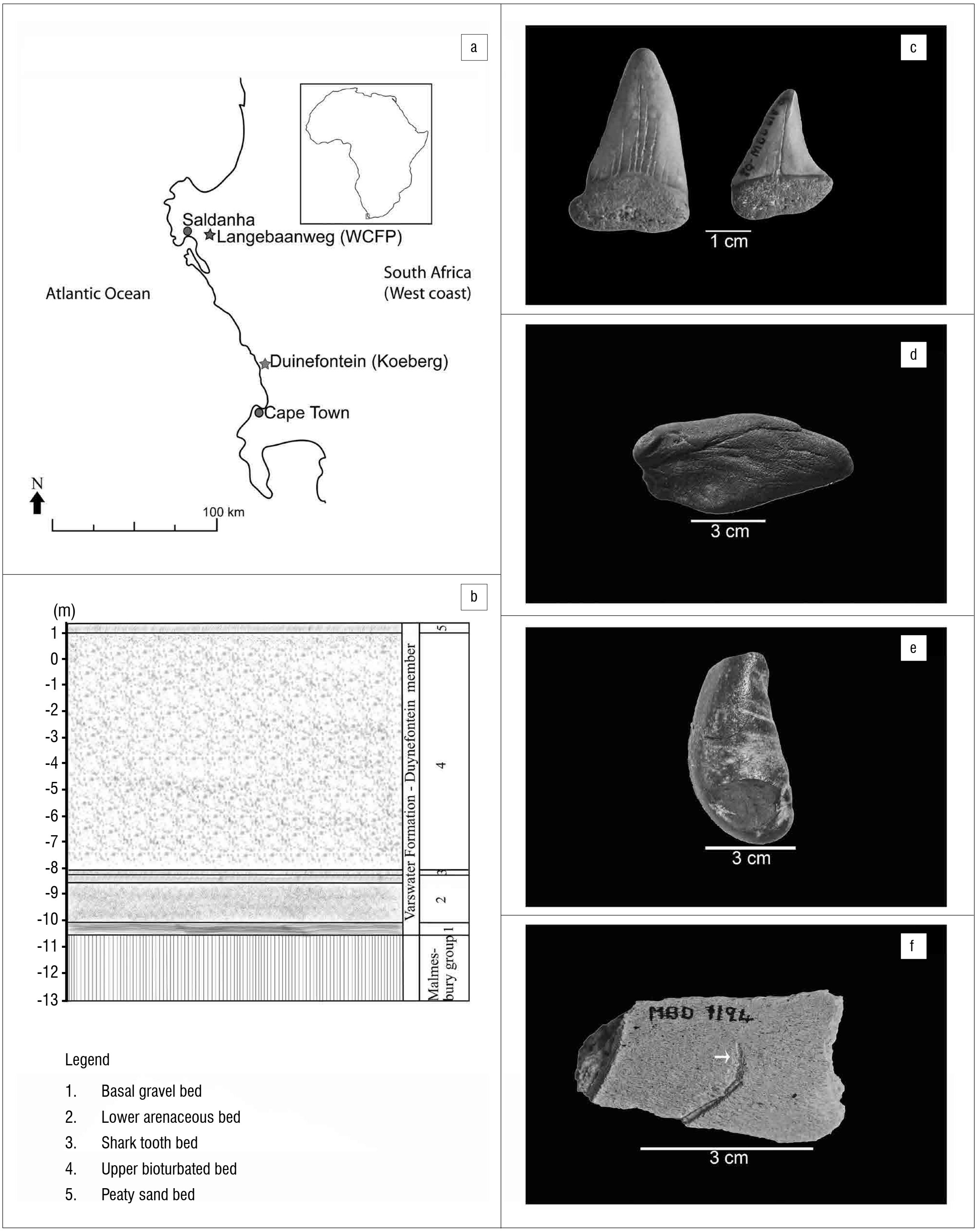

Figure 1: (a) Location of Duinefontein (Koeberg). (b) Schematic showing the stratigraphy for Koeberg – Duynefontein Member, Varswater Formation (based on Rogers[3]). (c) Shark teeth (SAMPQMB-D-618G, SAMPQMB-D-618Q) showing evidence of abrasion. (d) Rolled periotic posterior process (SAMPQMB-D-65). (e) Tympanic bulla showing a polished surface (SAMPQMB-D-1197). (f) CF1a bite mark on cranial fragment (arrow) (SAMPQMB-D-1194).

had become dissociated.[25] The rolled fossils initially came to rest on the beach where they were exposed to wave action before deposition.[25].

The terminology used follows Cigala-Fulgosi[13] and Bianucci et al.[18] Their experimental analyses of the bite action of extant sharks demonstrated four types of damage left by serrated and unserrated teeth. The designation of the type of bite follows the modification of Govender and Chinsamy[8], CF for Cigala-Fulgosi[13] and B for Bianucci et al.[18] Four types of damage were recognised as being caused by the serrated teeth of White Sharks (*Carcharodon carcharias*)[13]:

- CF1[8], damage was sub-divided into two types (designated CF1a and CF1b[8])

  CF1a is a simple, superficial groove with 'dotted' markings left by serrations

  CF1b is a deeper groove with ridges and grooves caused by tooth serrations;

- CF2[8], results in a simple groove with tapered end and no trace of serrations;
- CF3[8], damage has numerous sub-parallel ridges and grooves corresponding with the tooth's serrated edge. There is no cut groove.
- CF4[8], damage suggests cutting and/or scraping action with rotating movement. This action leaves curvilinear markings caused by the rotation of the tooth.

Unserrated shark teeth also produced four types of damage (using *Isurus oxyrinchus* and *Cosmopolitodus hastalis*)[18]:

- B1[8], produced a straight side (labial margin) and a curved side (lingual margin).
- B2[8], produced a more or less elongated incision with wide terminal extremities.

The depth of these two types depends on the tooth's position in the tooth row and the part of the crown used for the bite action that passes into the bone.[8]

- B3[8], the tooth edge had been dragged perpendicular to the dental axis, resulting in no grooves with ridges; however pseudo ridges and grooves can be created by damaged or worn teeth.
- B4[8], the tooth had also dragged perpendicular to the dental surface in a rippled or waved movement visible as parallel incisions resulting from repeated movement across the bone.

Although the tooth morphology of *Isurus oxyrinchus* and *Cosmopolitodus hastalis* is different, the experimental impressions in 'plasticine' showed that it was difficult to distinguish between the two tooth forms because of only slight variation and the number of variables involved, making it difficult to use for identifying particular sharks.[18]

Results

Description of bites on cetacean fossils

The specimens described are fragmentary and are not associated with any of the identifiable mysticete and odontocete specimens. The orientation and the depth of the bites vary amongst the specimens. The bites on the cetacean fossils were produced by serrated and unserrated teeth.

Cranial fragments

The cranial fragments, which include mandibular fragments, have superficial damage to the bone surface. This has resulted in the surface chipping off without penetrating the bone (Figure 1f, 2a-c) (and see Type 1 in Cigala-Fulgosi[13] and CF1a in Govender and Chinsamy[8] fig. 2A–B). There are instances where the teeth have shallowly penetrated the bone surface on the cranial fragment (South African Museum Quaternary Palaeontology, Melkbosstrand, Duinefontein (SAMPQMB-D)-1194; Figure 1f, arrowed) and the cranial fragment SAMPQMB-D-1341 (see Figure 2b).

There are elongated grooves with no serrations and tapered ends which represent CF2 bites caused by serrated teeth (Figure 2d–f, 3a–b) (and see Type 2[13] and fig. 3A–D in Govender and Chinsamy[8]). On SAMPQMB-D-1182, the CF2 bite mark follows the ventral surface of the mandibular fragment (Figure 2d, arrowed). On SAMPQMB-D-1194, the bite intersects the bottom of the CF1a bite (Figure 2e, arrow 1). It is possible that the fragment broke off along another CF2 bite (SAMPQMB-D-1194, Figure 2e, arrow 2). There is evidence of two different shark bites on SAMPQMB-D-1339, one having serrated teeth (Figure 2f, arrowed; CF2 bite). On the surface behind the CF1a and ventral surface of SAMPQMB-D-1342 above the CF3 bite, there is evidence of a very deep CF2 bite with bone having been removed (Figure 3a, arrow 1, 3b) and another CF2 bite above the B2 bite mark (Figure 3a, arrow 2) (and see Type 2[13] and fig. 3A-D[8]).

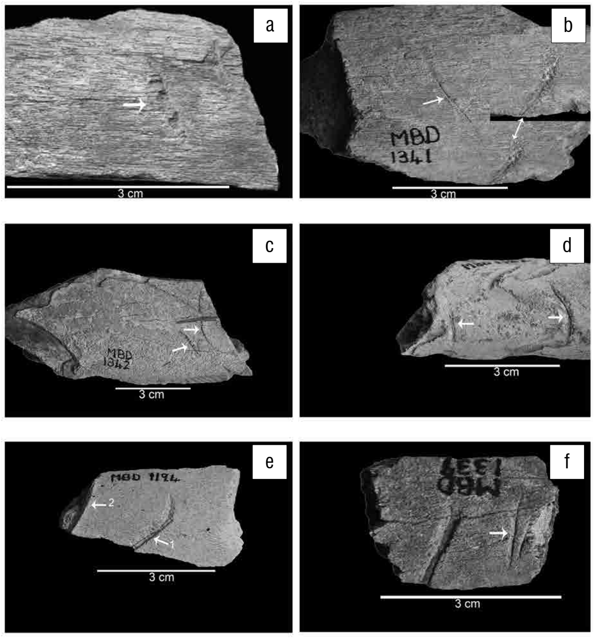

Figure 2: (a) CF1a bite mark on cranial fragment (SAMPQMB-D-1340). (b) Two CF1a bite marks on cranial fragment (SAMPQMB-D-1341) (inset close-up of second). (c) CF1a bite mark on a cranial fragment (SAMPQMB-D-1342) (arrowed). (d) CF2 bite mark on mandible fragment SAMPQMB-D-1182 (arrow). (e) CF2 bite marks on cranial fragment (SAMPQMB-D-1194) (arrow 1 and 2). (f) Two CF2 bite marks on the lateral surface of the cranial fragment (SAMPQMB-D-1339) (arrow).

On a mandibular fragment (SAMPQMB-D-1182) a bite mark tapers at one end and remains wide on the other (Figure 3c) which could be a result of the movement of the shark or the cetacean body (see Bianucci et al. fig. 3J, RR6i[18]). This bite resembles a B1 bite mark (see Type 2[18] and B1[8]). There are a number of wide grooves without ridges and grooves with wide ends (Figure 3d–f) which resemble B2 bite marks left by a shark with unserrated teeth (see Type 2[18] and fig. 3E–F[8]). On the surface of SAMPQMB-D-1342; a CF1a bite is bisected by a B2 bite mark that has damage along groove edges (see Figure 3f).

There are parallel ridges and grooves on the surface of SAMPQMB-D-1182 that are not very deep and are faint (see Figure 4a). These types of damage are similar to that caused by unserrated shark teeth scraping across the bone surface (fig. 3Hb, LR10[18] and fig. 4D[8]). The ridges and grooves could be the result of damage to the teeth and consequently it is not clear if this is a B3 or B4 bite mark (see Type 3, Type 4[18] and fig. 4D[8]). On the ventral surface of SAMPQMB-D-1342, there is a group of sub-parallel ridges and grooves (Figure 4b) which resemble a CF3 bite caused by teeth with serrated edges (Cigala-Fulgosi[13] and Govender and Chinsamy[8] fig. 4A-B).

Vertebra

SAMPQMB-D-71 is an isolated caudal vertebra with taphonomic damage to the ventral, lateral and dorsal surfaces on the left side. Ventrally on SAMPQMB-D-71, the bone surface has been damaged without penetrating the bone. This resembles a CF1a bite mark (Figure 4c) (and see Type 1 in Cigala-Fulgosi[13] and CF1a in Govender and Chinsamy[8] fig. 2A–B). Along the left lateral side of the anterior articulation, the bone surface has been removed with tapered ends which resemble CF2 caused by serrations on the shark teeth (see Figure 4d) (and see Type 2 in Cigala-Fulgosi[13] and Govender and Chinsamy[8]). Along the left lateral surface close to the posterior articulation is a deep groove that has no ridges and grooves and tapers at the ends which resembles CF2 bite marks caused by teeth with serrations (see Figure 4d) (and see Type 1 in Cigala-Fulgosi[13] and CF1a in Govender and Chinsamy[8] fig. 2A, B).

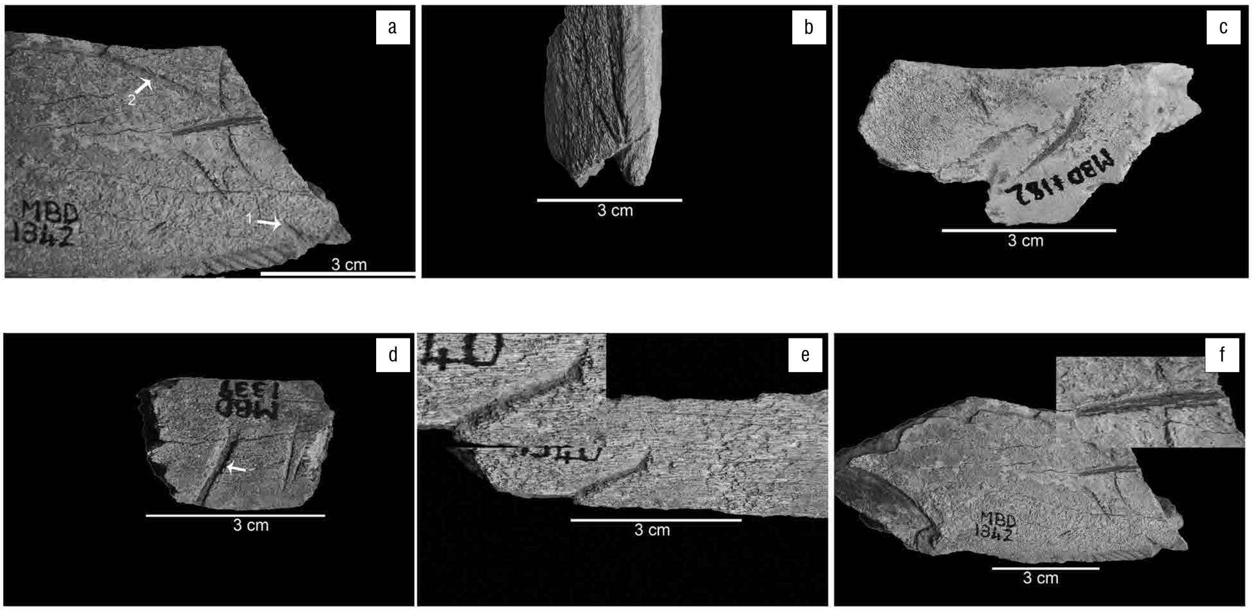

Figure 3: (a) CF2 bite marks on the lateral surface of cranial fragment (SAMPQMB-D-1342) (arrow 1, arrow 2). (b) CF2 bite mark on ventral surface of SAMPQMB-D-1342. (c) B1 bite mark on the lateral surface of a mandibular fragment (SAMPQMB-D-1182). (d) B2 bite mark on the small cranial fragment (SAMPQMB-D-1339) (arrow). (e) B2 bite mark on cranial fragment (SAMPQMB-D-1340) (inset close-up of damage). (f) B2 bite mark on the lateral surface of cranial fragment (SAMPQMB-D-1342) (inset close-up of damage).

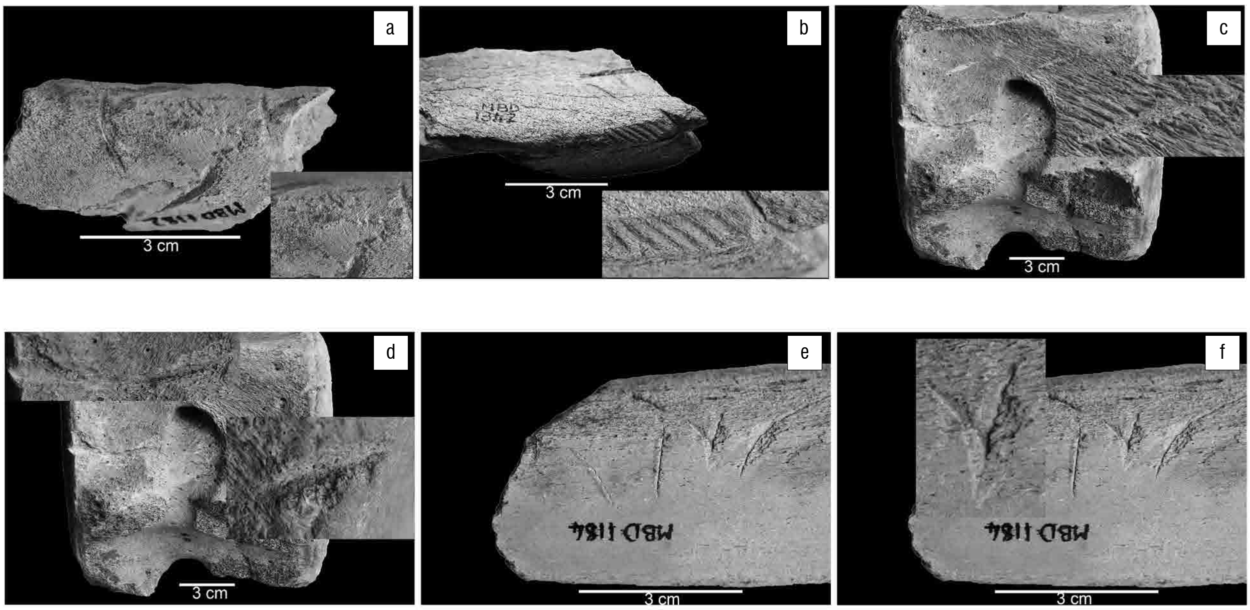

Figure 4: (a) B3/B4 bite mark caused by unserrated teeth scraping across the mandible fragment (SAMPQMB-D-1182) (inset close-up of damage). (b) CF3 bite mark on a cranial fragment (SAMPQMB-D-1342. (c) CF1a bite mark on a caudal vertebra centrum (SAMPQMB-D-71) (inset close-up). (d) CF2 bite marks on caudal vertebra centrum (SAMPQMB-D-71) (inset shows close-up of damage). (e) CF1a bite marks on a rib fragment. (f) Unusual bite mark caused by serrated teeth forming an upside down ‘V’ (SAMPQMB-D-1184) (inset close-up of damage).

Rib

On SAMPQMB-D-1184, a rib fragment (Figure 4e), there is a shallow groove that only slightly damaged the surface of the bone causing some of the surface to chip off. This type of bite mark resembles CF1a in fig 2A–B[8] (and see Type 1[13]). Other CF1a bites have shallowly penetrated the bone surface (Figure 4e). There is an unusual trace where two bite marks intersected forming an upside down 'V' (see Figure 4f).[8,13] This unusual trace may have been caused either by the shark or the cetacean being in motion which resulted in the shark losing its grip on the prey and having to bite down a second time.

Discussion

Great white (*Carcharodon carcharias*), tiger (*Galeocerdo cuvier*), Zambezi (bull) (*Carcharhinus leucas*), whale (*Rhincodon typus*), ragged tooth (sandtiger, *Carcharias tarsus*) and Shortfin Mako (*Isurus oxyrinchus*) sharks, to name a few, currently occur along the South Africa coasts and occupy various habitats. Numerous shark teeth have been collected from Duinefontein (Koeberg); however, there has been no detailed study of this material. Based on informal identifications[3-5,21] and a comparison with the Langebaanweg collection,[26] white shark (*Carcharodon carcharias*), mako shark (*Isurus* sp. and *Cosmopolitodus hastalis*), ragged tooth (sandtiger, *Carcharias tarsus*) and megalodon (*Carcharodon megalodon*) have been identified in the sample. There are also teeth that resemble lemon shark (*Negaprion brevirostris*) in the collection (author observations, 2014).

White sharks most likely had a worldwide distribution in the geological past[12,13,15-18] as they are capable of exploiting a wide range of habitats and temperatures.[27,28] At present the adults live along the cold west coast while the pups and juveniles inhabit the warmer east coast of South Africa.[27,29,30] Modern white sharks are considered to exclude other sharks while feeding,[31] however, there are documented cases where white sharks and tiger sharks have fed concurrently on a whale carcass.[32,33] These sharks were all the same size, not exceeding 3.5 m.[32] Mako are highly active, mobile sharks[27] that inhabit warm coastal and oceanic waters that range in depth from shallow coastal to 500 m.[28]

Shark diets are highly varied and include teleost fish, marine mammals and other sharks.[27,28,33-35] Some large sharks obtain most of their food by actively hunting small odontocetes and by scavenging large mysticetes.[27,28,33-35] Off South Africa's coast there are documented attacks on odontocetes.[36] Body fluids leaching from large whale carcasses are thought to attract sharks from as far as 10 km away.[30] Sharks also feed on cetacean carcasses at sea and are not always observed as carcasses may remain afloat for a number of weeks.[25,37] Large whale carcasses that have a high fat content remain afloat immediately after death and for an extended period,[25,37] while some sink and refloat from the build-up of gases resulting from decomposition.[22] Others may sink into an anaerobic environment and remain there.[22]

The nature of the preservation of the Duinefontein (Koeberg) material only allows one to extrapolate a discussion of the shark–cetacean interaction from the damage observed. Duinefontein (Koeberg) was open to the ocean during the transgression; however, during the regression a barrier spit developed along the coast.[3,4] The beach at Koeberg would have been open to wave action to varying degrees. As a result, whale carcasses could have become beached and remained long enough for gas to build up and allow the carcass to be refloated or moved during high tides or surf backwash.[25] Eventually, tensile stress would cause the stretched skin 'bag' to rupture and scatter skeletal elements already separated by decay.[25] It is also the most parsimonious reason for there being rolled and abraded fossil remains at the site; however, the flooding of the intertidal region could also be responsible for this as material was moved around by retreating water.

The cetacean fragments show evidence of superficial scrapes to penetrating bites. This variation in the depth of the bite marks is potentially as a result of the shark and cetacean both being in motion because of the currents and wave activity. There are a few CF2[8] (see Type 2[13]) bite marks. These were probably as a result of a shark propelling itself forward to bite and then reversing straight back, a behaviour seen particularly in white sharks.[38] Only the points of the teeth contact the bone surface leaving no evidence of serrations.[38] SAMPQMB-D-1182 is a mandible fragment that has bite marks on the ventral surface. The mandible probably became separated from the skull early in the decaying process.[25] In most instances, the head of the whale is the focus of feeding as the carnivores target the tongue.[30] The nature of the preservation suggests that two possible feeding scenarios could be extrapolated from the damage. The first is that the sharks were scavenging on a floating inverted whale carcass[8] prior to the mandible and skull becoming detached from the rest of the skeleton. The second would indicate a possible predatory attack on a whale as sharks also approach carcasses from below the water.[38] Other cranial fragments show bite marks on the lateral or medial surfaces. This would lend support to them being part of whale carcasses being scavenged rather than actively hunted. None of the bites show signs of healing which would suggest that the cetacean was most likely scavenged; however, the nature of the preservation does not eliminate active hunting as cause of death.

The rib fragment has bite marks on the lateral surface and an isolated caudal vertebra also shows bite marks on the ventral surface giving no context to the damage to the vertebra. The damage suggests that there are two possible scenarios; that the whale carcass was being scavenged or that the whale had been attacked by a shark. The bite marks would suggest an attack from the side as sharks do attack from the side and below.[35] The skeleton of cetaceans is protected by blubber and muscle therefore the presence of bite marks on the bones suggests that the cetacean body was in an advanced state of decomposition and becoming skeletonised, allowing the shark to penetrate the tissue and reach the bone.

A comparison with the cetacean fossils from Langebaanweg as well as other studies indicates the bite marks identified on the Koeberg cetacean fossils typically resemble bites caused by sharks with serrated teeth CF1a[8] (and see Type 1[13]), CF2[8] (and see Type 2[13]), CF3[8] (and see Type 3[13]), sharks with unserrated teeth B2[8] (and see Type 2[18]), B3/B4[8] (and see Type 3, Type 4[18]) and some unusual damage.[8,13] The damage caused by serrated teeth most closely resembles the damage caused by white sharks described by Cigala-Fulgosi[13] and Govender and Chinsamy.[8] White sharks are known to roll onto their ventral surfaces when feeding,[31,36] which can cause the shark's teeth to slip and scrape over the bone only damaging the surface (see CF3 in Figure 4b).

On SAMPQMB-D-1182 there is damage that suggests the shark with unserrated teeth first bit into the bone (B2 bite in Figure 4a) and possibly as a result of the movement of the shark and/or prey, the shark lost its hold on the prey item causing the tooth/teeth to slip across the surface of the bone leaving a scrape with very faint ridges and grooves (Figure 4a). The damage from both serrated and unserrated shark teeth documented on the fragmentary cetacean remains suggests that more than one shark taxon fed on the cetaceans.

Most of the damage inflicted on the bones from Duinefontein (Koeberg) closely resembles that described for white sharks[8,13,39] as there are no secondary serrations within the grooves like those described by Cigala-Fulgosi[13] for tiger sharks. Currently, no tiger shark teeth have been described from the Koeberg collection although they have been described from the contemporaneous site of Saldanha Steel,[40] so the most parsimonious explanation is that the whales were fed on by white sharks indicated by the numerous white shark teeth in the collections, although megalodon teeth have also been found.

There are also some B2 and B3/B4[8] bite marks on the remains. It is difficult to assign these to a specific shark as the damage on the Langebaanweg cetaceans caused by sharks with unserrated teeth retains no diagnostic information that allows exact species identification.[18] Examples of mako shark *(Isurus sp.* and *Cosmopolitodus hastalis)* are present in the collections makes them the most likely sharks to have left the traces of unserrated teeth. The unusual bites may be as a result of the shark losing traction while biting and having to grab at bone or flesh of the prey item a second or third time. The sharks may have also left evidence of their feed on partially skeletonised carcasses that eventually came to rest on the beach in the area and were later refloated and restranded on the beach resulting in the complete disarticulation of the skeleton and taphonomic damage.

Conclusion

Whale carcasses would have beached along the coast at Duinefontein (Koeberg) and refloated a number of times resulting in the breaking up of the carcasses. The wave action also resulted in some material being fragmented into small pieces, rolled, abraded and polished. Bites on a mandibular, cranial and rib fragments as well as an isolated vertebra preserve evidence of shark–cetacean interaction. The presence of the bite marks on the ventral surface of the mandibular fragment and lateral surfaces of the cranial fragments would strongly suggest that the cetaceans were in an inverted position when these bite marks were made, supporting scavenging action on floating carcasses. The fragmentary nature of the fossils, however, does not preclude the possibility of the bites being the cause of death. A comparison of the damage on the Koeberg fossil cetacean remains with other studies[8,12-18,39,41] suggested that the damage caused by serrated teeth was produced by white sharks. The grooves that do not have ridges and grooves have tapered ends and the superficial damage is similar to that described for white sharks.[8,13] There are no secondary serrations in the grooves as produced by tiger sharks.[13] Other bite marks were caused by sharks with unserrated teeth; however, definitive identification is difficult. The shark most likely to have caused the bite marks is the mako as a number of teeth are found in the collection. This second study[8] shows more evidence of shark–cetacean trophic interaction in the geological past.

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References

1. Pether J, Roberts DL, Ward JD. Deposits of the West Coast. In: Partridge TC, Maud RR, editors. The Cenozoic of southern Africa. Oxford: Oxford University Press; 2000. p. 33–54.
2. Roberts DL, Botha GA, Maud RR, Pether J. Coastal Cenozoic deposits. In: Johnson MR, Anhaeusser CR, Thomas RJ, editors. The geology of South Africa. Johannesburg/Pretoria: Geological Society of South Africa/Council for Geoscience; 2006. p. 605–628.
3. Rogers J. The sedimentary succession at the Koeberg Nuclear Power Station, Melkbosstrand. Geokongres 79: 18th Congress of the Geological Society of SA. Johannesburg: Geological Society of South Africa; 1979. p. 310–322.
4. Rogers J. First report on the Cenozoic sediments between Cape Town and Eland's Bay. Open file. Geological Survey of South Africa. 1980;165:64.
5. Rogers J. Lithostratigraphy of Cenozoic sediments between Cape Town and Eland's Bay. Palaeoecol Afr. 1982;15:121–137.
6. Avery G, Klein RG. Review of fossil phocid and otariid seals from the southern and western coasts of South Africa. T Roy Soc S Afr. 2011;66(1):14–24. http://dx.doi.org/10.1080/0035919X.2011.564490
7. Govender R, Chinsamy A, Ackermann RR. Anatomical and landmark morphometric analysis of fossil phocid seal remains from Langebaanweg, West Coast of South Africa. T Roy Soc S Afr. 2012;67(3):135–149. http://dx.doi.org/10.1080/0035919X.2012.724471
8. Govender R, Chinsamy A. Early Pliocene (5 Ma) shark–cetacean trophic interaction from Langebaanweg, western coast of South Africa. Palaios. 2013;28(5):270–277. http://dx.doi.org/10.2110/palo.2012.p12-058r
9. Govender R. Preliminary phylogenetics and biogeographic history of the Pliocene seal, *Homiphoca capensis* from Langebaanweg, South Africa. T Roy Soc S Afr. http://dx.doi.org/10.1080/0035919X.2014.984258
10. Hendey QB. The Late Cenozoic Carnivora of the south-western Cape Province. Ann S Afr Mus.1974;63:1–369.
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. Deméré TA, Cerutti R. A Pliocene shark attack on a cethotheriid whale. J Paleontol. 1982;56:1480–1482.
13. Cigala-Fulgosi F. Predation (or possible scavenging) by a great white shark on an extinct species of bottlenosed dolphin from the Pliocene of Italy. Tert Res. 1990;12:17–36.
14. Noriega JI, Cione AL, Aceñolaza F. Shark tooth marks on Miocene balaenopterid cetacean bones from Argentina. Neues Jahrb Geol Palaeontol Abh. 2007;245:185–192.
15. Aguilera OA, García L, Cozzuol MA. Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguaná Formation. Paläontol Z. 2008;82:204–208. http://dx.doi.org/10.1007/BF02988410
16. Ehret DJ, Macfadden BJ, Salas-Gismondi R. Caught in the act: Trophic interactions between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru. Palaios. 2009;24:329–333. http://dx.doi.org/10.2110/palo.2008.p08-077r
17. Esperante R, Muñiz Guinea F, Nick KE. Taphonomy of a Mysticeti whale in the Lower Pliocene Huelva Sands Formation (Southern Spain). Geol Acta. 2009;7:489–505. http://dx.doi.org/10.1344/105.000001451
18. Bianucci G, Sorce B, Storai T, Landini W. Killing in the Pliocene: Shark attack on a dolphin from Italy. Palaeontology. 2010;53:457–470. http://dx.doi.org/10.1111/j.1475-4983.2010.00945.x
19. Bianucci G, Lambert O, Post K. A high diversity in fossil beaked whales (Mammalia, Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa. Geodiversitas. 2007;29:561–618.
20. Bianucci G, Post K, Lambert O. Beaked whale mysteries revealed by seafloor fossils trawled off South Africa. S Afr J Sci. 2008;104:140–142.
21. Rogers J. Sedimentology of Late Cenozoic sediments, including the Pliocene Dynefontyn Member of the Varswater Formation, Koeberg Nuclear Power Station, Melkbosstrand, Cape Town. Afr Nat Hist. 2006;2:194–196.
22. Olson SL. Fossil seabirds and changing marine environments in the Late Tertiary of South Africa. S Afr J Sci. 1983;79(10):399–402.
23. Olson SL. An early Pliocene marine avifauna from Duinefontein, Cape Province, South Africa. Ann S Afr Mus. 1985;95(4):147–164.
24. Boessenecker RW, Perry FA, Schmitt JG. Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, Central California: Strong physical control on marine vertebrate preservation in shallow marine settings. PLoS One. 2014;9(3), e91419. http://dx.doi.org/10.1371/journal.pone.0091419
25. Schäfer W. Ecology and palaeoecology of marine environments. Chicago, IL: University of Chicago Press; 1972.
26. 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. In: 71st Annual Meeting of the Society of Vertebrate Paleontology program and abstracts book; 2011 Nov 2–5; Las Vegas, NV, USA. Bethesda, MD: Society of Vertebrate Paleontology; 2011. p. 207.
27. Compagno LJV. Sharks of the world: An annotated and illustrated catalogue of shark species known to date: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO species catalogue for fishery purposes v. 2. Rome: FAO; 2001.
28. Compagno LJV, Dando M, Fowler S. Field guide: Sharks of the world. London: HarperCollins; 2005.
29. Dewar H, Domeier M, Nasby-Lucas N. Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. Environ Biol Fish. 2004;70:133–143. http://dx.doi.org/10.1023/B:EBFI.0000029343.54027.6a
30. Dicken ML. First observations of young of the year and juvenile great white sharks (*Carcharodon carcharias*) scavenging from a whale carcass. Mar Freshwater Res. 2008;59:596–602. http://dx.doi.org/10.1071/MF07223
31. Pratt HL, Casey JG, Conklin RE. Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York. Fish Bull. 1982;80:153–156.
32. Dudley SFJ, Anderson-Reade MD, Thompson GS, McMullen PB. Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks, *Galeocerdo cuvier*. Fish Bull. 2000;98:646–649.

33. Bornatowski H, Wedekin LL, Heithaus MR, Marcondes MCC, Rossi-Santos MR. Shark scavenging and predation on cetaceans at Abrolhos Bank, eastern Brazil. J Mar Biol Assoc UK. 2012;92(08):1767–1772. http://dx.doi.org/10.1017/S0025315412001154

34. Cliff G, Dudley FJ. Sharks caught in the protective gill nets off Natal, South Africa 4: The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Mar Sci. 1991;10:253–270. http://dx.doi.org/10.2989/02577619109504636

35. Lowe CG, Wetherbee BM, Crow GL, Tester AL. Ontogenetic dietary shift and feeding behavior of the tiger shark, Galeocerdo cuvier, in Hawaiian waters. Environ Biol Fish. 2002;47:203–211. http://dx.doi.org/10.1007/BF00005044

36. Wcisel M, Chivell W, Gottfried MD. A potential predation attempt by a great white shark on an Indo-Pacific humpback whale. S Afr J Wildl Res. 2011;40(2):84–187.

37. Long DJ, Jones RE. White shark predation and scavenging on cetaceans in eastern North Pacific Ocean. In: Klimley A, Ainsley D, editors. Great white sharks: Biology of *Carcharodon carcharias*. San Diego, CA: Academic Press; 1996. p. 293–307. http://dx.doi.org/10.1016/B978-012415031-7/50028-8

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

39. Bianucci G, Bisconti M, Landini W, Storai T, Zuffa M, Giuliani S, et al. Trophic interactions between white sharks (*Carcharodon carcharias*) and cetaceans: A comparison between Pliocene and recent data. In: Vacchi M, La Mesa G, Serena F, Séret B; editors. Proceedings of the 4th Meeting of the European Elasmobranc Association; 2000 Sep 27–30; Livorno, Italy. Abbeville, France: Imprimerie F. Paillart; 2002. p. 33–48.

40. Kock A. Preliminary identification of Neogene fossil shark teeth from the Varswater Formation of the west coast of South Africa [unpublished Honours report]. Cape Town: University of Cape Town; 2002.

41. Bianucci G, Gingerich PD. *Aegyptocetus tarfa*, n. gen. et sp. (Mammalia, Cetacea), from the middle Eocene of Egypt: Clinorhynchy, olfaction, and hearing in a protocetid whale. J Vertebr Paleontol. 2011;31(6):1173–1188. http://dx.doi.org/10.1080/02724634.2011.607985