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The significance of shark tooth from the Late Miocene Tukau Formation, northwest Sarawak, Malaysia

Yi Ning Fong*, Dominique Dodge-Wan, Prasanna Mohan Viswanathan

Department of Applied Sciences, Faculty of Engineering and Science, Curtin University Malaysia, CDT 250, 98009 Miri, Sarawak, Malaysia
*Corresponding author email address: yn0503@live.com

Abstract: An incomplete shark tooth was discovered from the Late Miocene Tukau Formation outcrop along the Sungai Rait Road in the Miri region, Sarawak, Malaysia. The specimen represents the first documented occurrence of vertebrate remains from the formation, which was referred to as the "Barren Series" due to the absence of fossils in most samples. Previous studies have reported limited brackish water foraminifera with no biostratigraphic value. The discovery of the fossil could help with the reconstruction of the palaeoenvironment of the formation. The shark tooth was recovered from a muddy heterolithic bed at a log height of 17.6 m above the base of the sequence at the outcrop. The tooth specimen is an upper right lateral tooth belonging to the genus *Carcharhinus* (Carcharhiniformes, Carcharhinidae) based on its overall morphology. A detailed comparison of its morphological features with specimens from previous studies suggests that the tooth may belong to one of the following potential species: *C. amboinensis*, *C. leucas*, or *C. limbatus.* These shark species are commonly found in continental and insular shelf waters, often nearshore, in estuaries, bays, lagoons, and coastal environments, with some species tolerating varying salinities or migrating seasonally. Bulk sampling could be envisaged to gain further knowledge of the vertebrate fossil record from the Tukau Formation.

Keywords: Clastic sediments, *Carcharhinus*, tooth morphology, Miri

INTRODUCTION

The Tukau Formation is part of the Neogene Baram Delta succession, comprising the Setap Shale, Lambir, Miri, Tukau and Liang formations (Togunwa *et al*., 2015). The Neogene successions comprise a 9 to 12 km thick sequence of primarily progradational to strongly aggradational coastal-deltaic to shelf deposits (Sandal, 1996), which is possibly a storm-flood-influenced deposition (Collins *et al*., 2017; 2018). The Tukau Formation dates from the Late Miocene to Pliocene age (Lee *et al*., 2004).

The Neogene marine vertebrate fossil record of Borneo Island, particularly that of elasmobranchs, has garnered limited attention, with only a few localities in Sarawak and Brunei yielding recorded findings (Kocsis *et al*., 2019). James (1984), Sandal (1996), and Wannier *et al*. (2011) reported the presence of shark teeth in the Miri and Sibuti formations. Subsequently, Kocsis *et al*. (2019) synthesised this earlier literature, examining the photographs and descriptions provided, and identified the occurrence of genera such as *Carcharhinus*, *Hemipristis* and *Otodus* (*Megaselachus*) *megalodon* in the region.

Kocsis *et al*. (2019) and Razak & Kocsis (2018) reported numerous shallow-water elasmobranch assemblages from Ambug Hill in Brunei, exhibiting various states of preservation. Their study provided detailed taxonomical descriptions and numerical abundance of genera, including *Otodus* (*Megaselachus*), *Hemipristis*, *Galeocerdo*, *Carcharhinus*, *Glyphis*, *Pristis*, *Rhina*, *Rhynchobatus*, *Himantura*, *Pastinachus*, *Taeniurops*, *Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Rhinoptera*.

Kocsis *et al*. (2021) reported several reworked elasmobranch remains, comprising six sharks and one ray taxa, from Penanjong Beach in Brunei. A summary of the elasmobranch fossil record in the Indo-Australian Archipelago (IAA) by Kocsis (2024), Mediodia *et al*. (2025) revealed that the IAA fossil fauna encompasses over 40 taxa distributed across four orders and 17 families. Specifically, in Brunei, during the Miocene, 31 elasmobranch taxa from five different orders have been identified, including Orectolobiformes, Lamniformes, Carcharhiniformes, Rhinopristiformes, and Myliobatiformes. Among these elasmobranch remains reported, the Carcharhiniformes represent the most prevalent order (Kocsis, 2024).

The present study aims to provide detailed taxonomic and ecological descriptions of a shark tooth found in a Tukau Formation outcrop Rait 2 (V3) in the Sungai Rait region (4°16'17.1"N 114°00'53.5"E). Refer to Fong *et al*. (2024) for the description of outcrop V3.

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Geological setting

The Tukau Formation lies within the Miri Zone, which is the youngest of the three tectonostratigraphic zones in onshore Sarawak, including the Kuching, Sibu, and Miri Zones (Liechti *et al*., 1960; Madon, 1999). The Miri zone comprises the Rajang Group, the Mulu, Kelalan, and Tatau Formations, the Melinau Limestone Formation, the Nyalau Formation, the Setap Shale Formation, the Subis Limestone, and the Lambir, Belait, Tukau, Miri, Seria, Bergrih and Liang Formations (Jong & Kessler, 2019). While some researchers have combined the Lambir and Tukau formations due to their lithostratigraphic similarities and uncertain ages (Banda & Honza, 1997; Collins *et al*., 2020), this study follows the formation boundaries delineated by Liechti *et al*. (1960), recognising them as distinct formations.

The Tukau Formation was known as 'the Barren Series' due to its general lack of fossils. It does, in some places, contain some brackish-water fauna with no chronostratigraphic values (Liechti *et al*., 1960, Wilford, 1961; Hutchison, 2005), and these authors listed foraminifera in the formation, including *Ammobaculites* sp., *Glomospira* sp., *Haplophragmoides* sp., and *Trochammina* sp. Recent studies by Collins *et al*. (2020) have revealed the presence of ichnofossils in the formation, including *Asterosoma*, *Chondrites*, *Cylindrichnus*, *Diplocraterion*, *Gyrolithes*, *Macaronichnus*, *Ophiomorpha*, *Palaeophycus herberti*, *Palaeophycus tubularis*, *Phycosiphon*, *Planolites*, *Psilonichnus*, *Rhizocorallium*, *Rosselia*, *Schaubcylindrichnus coronus*, *Siphonichnus*, *Skolithos*, *Taenidium*, *Teichichnus*, *Thalassinoides* and *Fugichnia*. Indications of these species suggested that the deposition environment of the Tukau Formation is under marginal marine conditions.

The Tukau Formation is relatively heterolithic compared to other adjacent formations and was deposited in a coastal plain environment with fluvial and tidal influences (Collins *et al*., 2020). The formation comprises mudstone, massive silt/sandstone, and mud/siltstone containing irregular quartz pebbles (Nagarajan *et al*., 2017, Togunwa & Abdullah, 2017). Carbonaceous materials are common in the formation (Collins *et al*., 2020).

There are several well-exposed outcrops along the Sungai Rait Road. These outcrops, including the study area of this paper, are detailed in Kessler *et al*. (2023) (refer to Figure 1A for the location of Rait 2 outcrop, also referred to as outcrop V3). This study covers a single shark tooth specimen recovered from Rait 2 outcrop (or V3). In this study and Fong *et al*. (2024), the outcrop is referred to as Rait 2 (or, in short, V3). In Kessler *et al*. (2023), the same outcrop is labelled as outcrop Sg-5.

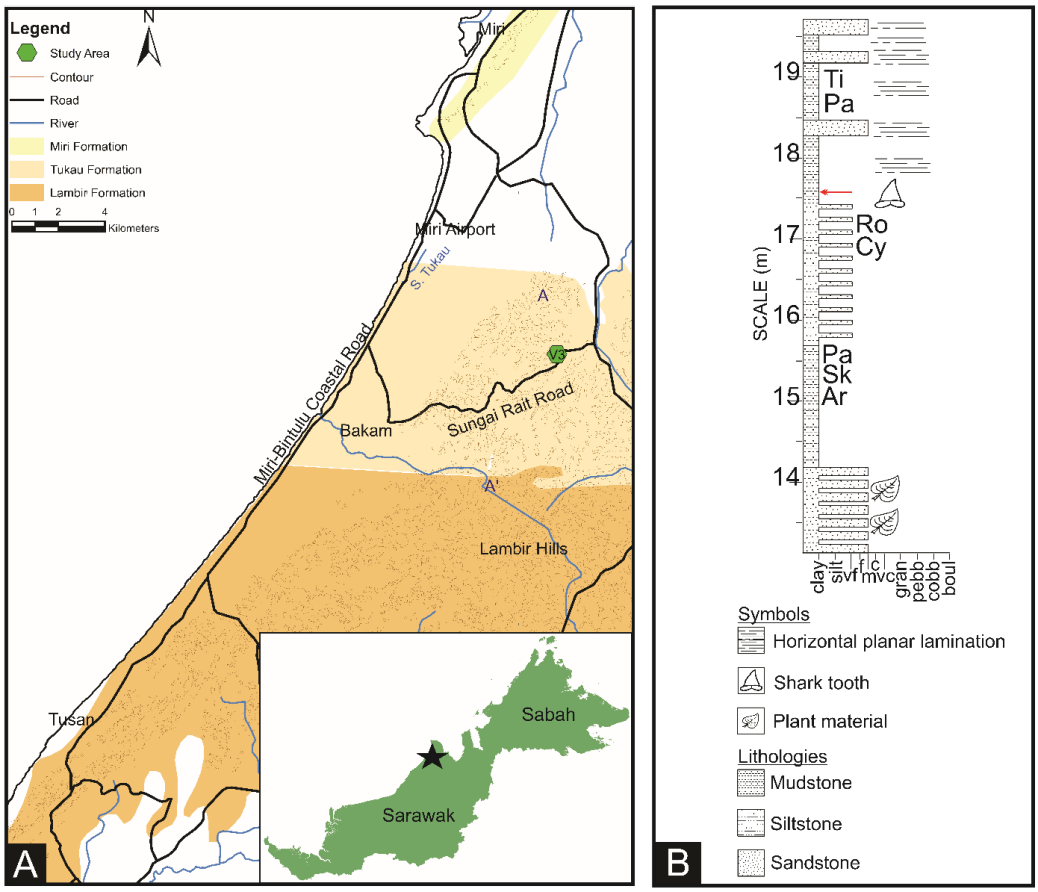


Figure 1: A. The location of the study area in the Miri region, NW Sarawak. Geological details were modified in accordance with Liechti *et al*. (1960). B. The selected sedimentary section of the studied outcrop with the bed bearing a shark tooth at 17.6 m on the log. Refer to Hutchison (2005), page 111, Figure 42 for the stratigraphic column at a broader regional scale, and Fong *et al*. (2024) for the strata logs of the Tukau Formation. Abbreviations: Ar: *Arenicolites*, Cy: *Cylindrichnus*, Pa: *Palaeophycus*, Ro: *Rosselia*, Sk: *Skolithos*, Ti: *Tisoa*.

METHODOLOGY

The material examined in this study consists of a single tooth fragment, designated as Specimen V3-17.6m. The specimen was studied, analysed and curated in Curtin University Malaysia. This specimen was found in a muddy heterolithic bed located at a log height of 17.6 m within the stratigraphic sequence (refer to Figure 1B for the context). The bed is characterised by centimetre-to decimetre-thick dark grey silty mudstone to carbonaceous mudstone interbedded and interlaminated with centimetre-to decimetre-thick siltstone to very fine-grained sandstone. Trace fossils are observed, but are all unidentified.

No additional fossil remains were found in this bed or the immediately adjacent strata. Although direct fossil evidence is limited at this outcrop, palynological analysis conducted at the same outcrop (Rait 2) provides information about the palaeoenvironment. Specifically, samples analysed from log heights of 3.5 m and 11.5 m reveal a diverse assemblage of palynomorphs. The composition of this assemblage is characterised by a majority of palynomorphs from the hinterland, followed by mangroves, spores and seasonal or montane ecological groups (Fong *et al*., 2024).

Specimen V3-17.6m was extracted from the surrounding rock using a geological hammer and chisel, cleaned with an ultrasonic cleaner and studied with an SMZ745T Nikon Stereo Microscope equipped with a Nikon camera. The position of the tooth in the jaw (either lower or upper jaw) was identified based on the tooth shape and relative size (Purdy, 2006). The anatomical descriptions and terminology followed the definitions provided by Purdy (2006) and Cappetta (2012). Refer to Figure 2 for the tooth terminology used in the description.

RESULTS

Specimen V3-17.6m is a worn or incomplete tooth. The tooth specimen is a crown without the preservation of its root. It has no cusplets, and the absence of cusplets is unlikely due to incomplete preservation of the tooth root. According to the shark teeth illustration of various shark species by Ebert *et al*. (2021), cusplets usually grow right beside the cusp, along the heel of the tooth. Figure 2 shows that the specimen has relatively well-preserved heels, with no cusplets growing out from the heels. Figure 2A shows both the lingual and labial side of Specimen V3-17.6m, while Figure 2B illustrates the sketches of the specimen on both sides. The lingual side is slightly convex, referring to the side facing inside the jaw, whereas the labial surface is flatter and faces outside of the jaw (Underwood *et al*., 2015).

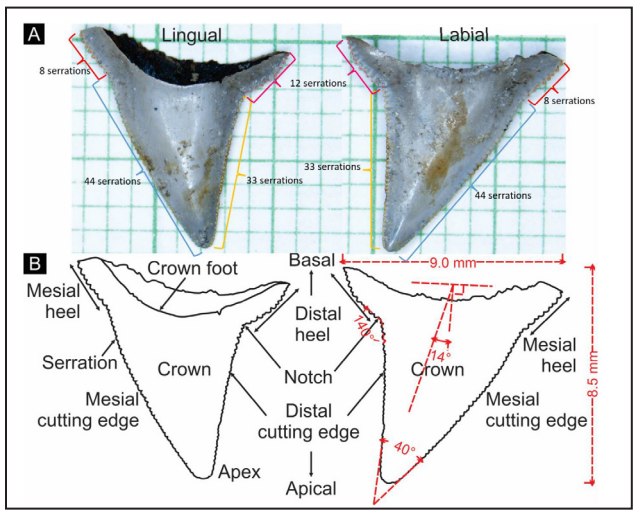


Figure 2: Specimen V3-17.6m. A. Photographs under a microscope. B. Sketches with labels, angles and dimensions.

The crown is 8.5 mm, 9.0 mm and 1.0 mm in height, width, and thickness. In the lateral view, the apex of specimen V3-17.6m exhibits a slight curvature towards the labial side. The crown is inclined slightly towards the distal side. The angle between the distal and mesial cutting edges is about 40 degrees, and the crown is deflected at about 14 degrees distally (Figure 2). Assuming there was no further breakage after losing its root, the enameloid of the crown foot is more extended on the labial side than on the lingual side.

The cutting-edge morphology is distinguished by fine serrations visible to the naked eye, but the number of serrations is not easily countable. There is a total of 97 countable serrations on the cutting edges of the specimen, with 12 on the distal heel, eight on the mesial heel, 33 on the distal cutting edge, and 44 on the mesial cutting edge. Some of the serrations are broken, thus not countable. Specimen V3-17.6m has a more convex mesial cutting edge basally, which tends to become straight towards the apex of the crown. The mesial cutting edge joins the mesial heel with continuous serrations and lacks a notch. The distal cutting edge is nearly straight to very weakly concave, forming a shallow and angular notch of around 140 degrees with the distal heel (refer to *Galeocerdo cuvier* in Figure 3 for a deeply notched tooth). It exhibits a complete serration pattern along all cutting edges, encompassing the main cusp and the heels. The serrations are coarser at the base or on the heels but finer towards the apex of the crown, ranging from 4.5 to 6 serrations per mm.

Specimen V3-17.6m exhibits a grey colouration corresponding to Munsell 5PB 6/2 on the Munsell colour chart, and the iron staining or coating on the specimen is characterised by a distinct hue identified as Munsell 5Y 5/2 (Munsell, 2000).

DISCUSSION

The Specimen V3-17.6m is the first-ever reported vertebrate remains in the Tukau Formation. This finding is a significant addition to the existing literature, which previously only reported brackish water faunas. The reported shark tooth from the overlying Miri Formation belongs to the *Carcharhinus* (Carcharhiniformes, Carcharhinidae). The shark teeth from the lower Sibuti Formation are attributed to the *Carcharhinus* and *Hemipristis* (Carcharhiniformes, Hemigaleidae) (Wannier *et al*., 2011, Kocsis, 2024).

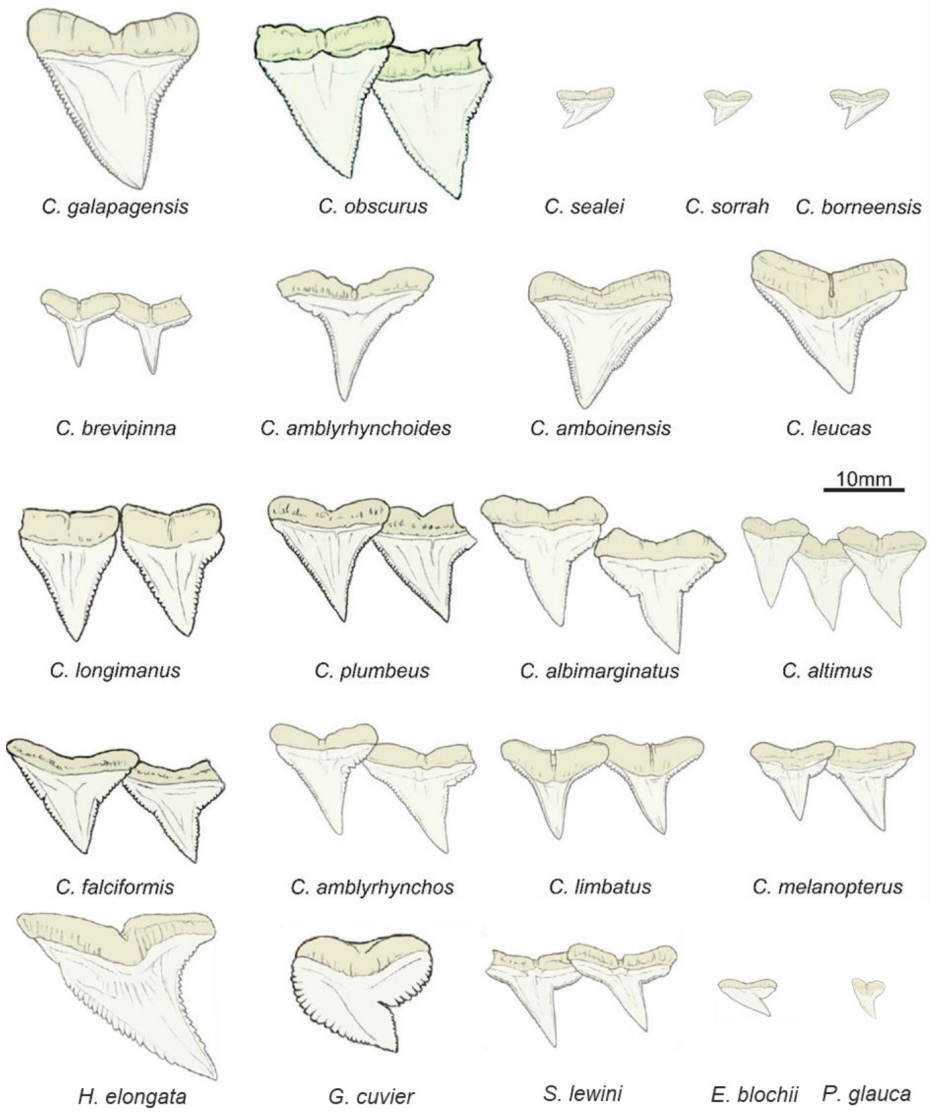


Figure 3: Illustration of several shark teeth of the Carcharhiniformes sharks found in Southeast Asia. 10 mm scale. Adapted from Ebert *et al*. (2021).

In Ambug Hill, Brunei, shark teeth from the orders Lamniformes, Carcharhiniformes, Rhinopristiformes and Myliobatiformes were reported, with the Carcharhiniformes dominating, comprising four families and 13 species (Kocsis, 2024, Kocsis *et al*., 2019). Kocsis (2024) reported multiple species of the shark genus *Carcharhinus*, including *C. amblyrhynchoides*, *C. amblyrhynchos*, *C. amboinensis*, *C. borneensis*, *C. falciformis*, *C. limbatus*, *C.* aff. *melanopterus*, *C. sealei* and *C.* spp.

As stated by Purdy (2006), the accurate application of the taxonomic key for shark tooth identification necessitates the examination of complete specimens possessing both root and crown. Worn or incomplete specimens cannot be accurately identified to an appropriate taxonomic level. Hence, the key to common genera of Neogene shark teeth is not applicable in this case.

In this study, comparative analysis is carried out to identify specimen V3-17.6m to the taxonomic level. Figure 3 shows the morphological comparison of shark teeth between different species of shark under the order of Carcharhiniformes. The Carcharhinidae family exhibits a wide variation in dental morphology (Cappetta, 2012; Ebert *et al*., 2021). However, a principal evolutionary trend is the acquisition of serrated cutting edges on the teeth, particularly pronounced in *Carcharhinus* (Cappetta, 2012). Collareta *et al*. (2022) describe the *Carcharhinus* teeth as having a triangular crown shape, slightly crenulated, and serrated. The design enables the carcharhines to cut through flesh like a trimmer efficiently (Collareta *et al*., 2022). Among the *Carcharhinus* species, *C. sealei*, *C. sorrah* and *C. borneensis* differ from the others by having deeply notched teeth. The species *Galeocerdo cuvier*, which belongs to the family

Galeocerdonidae and the order Carcharhiniformes, has a serrated, strongly notched lateral tooth (Ebert *et al*., 2021). It is a common characteristic among sharks that belong to the family of Galeocerdonidae, including *G. aduncus*, *G.gajensis*, and *G. latidens.*

H. elongata belongs to the family of Hemigaleidae, under the order of Carcharhiniformes. The upper lateral tooth is larger and more compressed labiolingually than the lower tooth, exhibiting a hooked shape with strong serrations on both sides (Chappell & Séret, 2020). The lateral tooth of *Prionace glauca,* shown in Figure 3, is elongated with fine serrations along the cutting edges, and the heels are smooth. The species also belongs to the family Carcharhinidae, within the order Carcharhiniformes (Ebert *et al*., 2021). Similar to the tooth morphology of *C. falciformis* and *C. plumbeus*, it also shows a slightly notched, triangular shape, with serrations on cutting edges. However, the lateral tooth of *P. glauca* exhibits an elongated shape, with relatively smooth heels.

Sphyrna lewini belongs to the family Sphyrnidae, which is part of the order Carcharhiniformes (Ebert *et al*., 2021). The family of Sphyrnidae often has lateral teeth with a triangular shape that curves distally, and the differences in tooth shape across species reflect adaptations to their distinct diets (Berkovitz & Shellis, 2023). From Figure 3, the lateral tooth of *S. lewini* exhibits a narrow triangular shape that is oblique, without serrations on the edges. However, larger individuals may have slightly serrated edges (Miller *et al*., 2014). *Eusphyra blochii*, which is also grouped under the family Sphyrnidae, shows similar tooth morphology, however, with smaller tooth size and a more deeply notched lateral tooth. Alike tooth morphology is also described by Villafaña *et al*. (2020), based on fossils of *Sphyrna* sp. from the early Miocene. The differences in tooth morphology are attributed to different dietary habits of the sharks (Berkovitz & Shellis, 2023).

An evaluation of the tooth crown morphology, such as the tooth shape and size, the presence of a notch, curvature on the labial and lingual surfaces, and the surface of the cutting edge, suggests the shark tooth specimen can potentially be assigned to the genus *Carcharhinus* based on its tooth characteristics, summarised in Table 1.

Carcharhinidae is the most prominent family in Carcharhiniformes (Naylor, 1992), *Carcharhinus* is the most diverse genus among the other 12 in the family, encompassing 36 species (Naylor, 1992; Naylor & Marcus, 1994; Froese & Pauly, 2024). All species of *Carcharhinus* are typically found in coastal waters, except for *C. longimanus*, *C. falciformis*, and *C. leucas*. *C. longimanus* and *C. falciformis* are oceanic species, while *C. leucas* demonstrate a unique ability to tolerate coastal and freshwater habitats (Naylor & Marcus, 1994). Some *Carcharhinus* species are distributed in Southeast Asia, as studied by Garrick (1982), Naylor & Marcus (1994), and Ebert *et al*. (2021). The characteristics of these species are summarised in Table 2 and Figure 3.

The tooth potentially originated from the upper right jaw quadrant, as evidenced by these vital morphological features: 1) Specimen V3-17.6m exhibits a relatively wide crown base in labiolingual view, with a crown width-to-height ratio of approximately 1.06, with a blade-like shape. In

Table 1: Comparison of the characteristics of the upper tooth of the *Carcharhinus* shark (Garrick, 1985; Marsili, 2007; Cappetta, 2012) and the Tukau shark tooth specimen obtained in this study.

Characteristics of Carcharhinus shark upper tooth (with height up to 2 cm) summarised in Garrick (1985), Marsili (2007) and Cappetta (2012)	**Characteristic of the Specimen V3-17.6m observed in this study**
Triangular.	Simple triangular shaped.
It has a relatively broad crown.	9.0 mm crown width and 8.5 mm crown height.
The cusp is separated from the distal and mesial heels, or only the distal heel, with a distinct notch or angle.	The distal heel is separated from the cusp by a shallow notch.
Flat labial, without a basal bulge on the root.	The labial surface is the flattest side of the tooth; however, the tooth specimen has no root.
Slightly convex lingual face.	The lingual side of the tooth is slightly convex.
Both mesial and distal cutting edges are usually serrated in Neogene and Recent forms, except for some species, e.g., *C. isodon* and *C. leiodon*, which exhibit smooth to weakly serrated mesial and distal cutting edges.	Both mesial and distal cutting edges are regularly serrated.
The root is relatively flat, with a high basal face that bears a distinct furrow.	The tooth specimen has no root, and cannot be compared.

Table 2: Shark species of the *Carcharhinus* genus distribution, with their common names, geographic distributions, and comments comparing their tooth morphology to the Tukau Formation tooth specimen. Information is based on Garrick (1982), Naylor & Marcus (1994), Purdy *et al*. (2001), Kocsis *et al*. (2019), Ebert *et al*. (2021), Lin *et al*. (2022), Malyshkina *et al*. (2023), and Kocsis (2024). Abbreviations: Wo: Worldwide, T: Tropical, I: Indian Ocean, P: Pacific Ocean, A: Atlantic Ocean, IP: Indo-Pacific Ocean, M: Mediterranean, W: West, C: Central. Green shade: Present; Grey shade: Uncertain.

Species name	Geographic distributions							Key features	Comparison with specimen V3-17.6m
	Wo	T	I	P	A	IP	M		
C. albimarginatus					W			Elongated cusp with an apical hooked tip, and a marked variation in serration size along cutting edges.	V3-17.6m lacks serration size variations and apical curvature.
C. altimus								Finely serrated, upright crown with a minimal distal notch development, and a distally bent apex.	V3-17.6m differs by having a distal notch and lacking apical curvature.
C. amblyrhynchoides			W			C		Coarsely serrated cutting edges with larger basal serrations that grade from heavy to fine, extending along the entire cusp length to just before the apex.	V3-17.6m lacks the distinct heavy to fine serration pattern and is more uniform in size.
C. amblyrhynchos								Sometimes referred to as *C. wheeleri*. Exhibits an almost horizontal basal margin labially.	V3-17.6m differs by having a more concave labial basal margin.
C. amboinensis				W				Large, broad, triangular tooth with serrated cutting edges.	Possible match (comparable).
C. borneensis						C		Displays coarser serrations mesially.	V3-17.6m differs by having finer, more uniform serrations on both cutting edges.
C. brachyurus								A more pointed crown with a distally inclined apex and displaying coarser serrations mesially.	V3-17.6m differs by having more uniform serrations on both cutting edges.
C. brevipinna								Serrations along the cutting edges are absent or weak.	V3-17.6m exhibits well-developed and clearly defined serrations along both cutting edges.
C. falciformis								Straight mesial cutting edge with a noticeable gap in the serrations mesially.	V3-17.6m has a shallowly notched mesial cutting edge with continuous serrations and no gap.
C. galapagensis								Elongated cusp and narrow overall teeth shape with coarse serrations.	V3-17.6m differs by having a triangular cusp and exhibits finer serrations.
C. leucas								Straight to slightly wavy mesial cutting edge, becoming weakly convex near the cusp tip.	Possible match (comparable).
C. limbatus								Slightly convex mesial cutting edge.	Possible match (comparable).
C. longimanus								Elongated cusp and straight basal margin of the root.	V3-17.6m differs by having a triangular cusp with a more concave labial basal margin.
C. melanopterus				W				Narrow cusp oriented erect to oblique with serrated cusplets.	V3-17.6m differs by having a more upright triangular cusp.
C. obscurus								Coarser serrations along the middle section of the cutting edges.	V3-17.6m differs by having a finer, more evenly serrated size along both cutting edges.
C. plumbeus								Narrower and more elongated crown compared to *C. leucas*, *C. longimanus*, *C. obscurus*, and *C. amboinensis*.	V3-17.6m differs by having a more triangular crown.
C. sealei						C		The basal half of the mesial cutting edge has serrations and becomes smooth distally.	V3-17.6m differs in that it has serrations continuously present along the entire cutting edge.
C. sorrah				W				Coarsely serrated distal cutting edge.	V3-17.6m differs by having a uniform serration size on both cutting edges.

shark dentation, distinct tooth forms in the upper and lower jaws represent one of the common forms of heterodonty (Berkovitz & Shellis, 2023). The crowns of upper teeth are usually more "compressed or blade-like" than those of the teeth from the lower jaw (Purdy, 2006). Only a minimum number of shark species show homodont teeth, where the size and shape of the teeth are similar regardless of the position of the teeth on the jaws, the same position of teeth during different life stages, and the same position of teeth in different genders. Species such as *Cetorhinus maximus* and *Rhincodon typus*, which are plankton-feeders, whose teeth are not used for catching prey, are some examples of homodont teeth sharks (Ebert *et al*., 2021). Most of the lower teeth of the *Carcharhinus* species are narrow (Garrick, 1982). 2) The apex of Specimen V3-17.6m exhibits a slight curvature towards the labial side in lateral view. Purdy (2006) reported that the upper teeth may recurve toward the labial side of the tooth, while the apex of the lower teeth usually recurve lingually. 3) The cusp is inclined to the right in lingual view. Shark tooth variation demonstrates high bilateral symmetry, and teeth on the right jaw are approximate mirror images of those on the left jaw (Naylor & Marcus, 1994). Based on a comparison of shark teeth from different *Carcharhinus* species with tooth crowns towards the top in the labial view, the teeth from the upper right tend to incline towards the right, while the upper left teeth are towards the left (Naylor & Marcus, 1994).

The morphological characteristics of Specimen V3-17.6m suggest its potential classification as a lateral tooth despite the absence of root lobes forming obtuse angles, which is typically a defining feature of the lateral tooth. This identification is based on eliminating other possible tooth positions within the jaw. The tooth does not exhibit parasymphyseal, symphyseal, anterior, intermediate and posterior teeth characteristics. According to Purdy *et al*. (2001) and Purdy (2006), parasymphyseal teeth are typically small and often symmetrical, while asymmetrical roots characterise symphyseal teeth and are usually found in the lower jaw. Anterior teeth generally display an erected, awl-like crown morphology. The blade-like nature of Specimen V3-17.6m further supports its potential origin from the upper jaw, as lateral teeth from the upper jaw tend to exhibit a more blade-like morphology compared to those from the lower jaw (Purdy, 2006). The posterior tooth of a shark often has a smaller, less well-developed crown as the Specimen V3-17.6m has a well-developed crown, which suggests that the tooth in the posterior position could be excluded (Purdy, 2006).

To further identify Specimen V3-17.6m to species level, the *Carcharhinus* species' geographical distribution patterns and distinctive morphological characteristics were considered. Some species were eliminated from consideration due to the occurrence locality of the Tukau tooth specimen in Northwest Sarawak, East Malaysia (e.g., *C. acronotus*, *C. cautus*, *C. cerdale*, *C. coatesi*, *C. dussumieri*, *C. fitzroyensis*, *C. humani*, *C. isodon*, *C. leiodon*, *C. macloti*, *C. porosus*, *C. perezi*, *C. signatus*, *C. tilstoni*, and *C. tjutjot*). Multiple *Carcharhinus* species remain as potential candidates. *Carcharhinus* shark tooth images were documented in previous studies, and the descriptions of each possible species were compared with Specimen V3-17.6m. Some species were eliminated due to their narrow tooth shape, coarser serrations mesially, horizontal basal margin, etc. (refer to the detailed descriptions in Table 2). *C. albimarginatus* tooth is a moderately triangular shape, with a slightly elongated cusp, an apical hooked tip, and a marked variation in serration size along the cutting edges. When compared to specimen V3-17.6m, variations in the serration size and apical curvature were not found. *C. altimus* differs from the specimen by bending distally at the apex and lacking the distal notch. *C. amblyrhynchoides* has coarsely serrated cutting edges, with larger serrations at the base and becoming smaller when moving towards the apex; however, the specimens show consistent, fine serrations throughout the cutting edges. *C. amblyrhynchos* exhibits an almost horizontal basal margin at the labial side; in contrast, the specimen has a more concave labial basal margin. *C. borneensis* tooth shows coarser serrations at the mesial cutting edge, which differ from the specimen. Compared to Specimen V3-17.6m, the tooth of *C. brachyurus* has a more pointed crown, a distally inclined apex, and coarser serrations on the mesial edge. *C. brevipinna* teeth have smooth or weakly serrated cutting edges, which contrasts with the specimen. The teeth of *C. falciformis* show a straighter mesial cutting edge, and an obvious gap in the serrations can be noticed. *C. galapagensis* exhibits longer and narrower teeth cusps, with coarser serrations when compared with the specimen. *C. longimanus* teeth differ from the specimen by having an elongated cusp and a straight basal margin near the root. The cusp of the *C. melanopterus* is narrower with serrated cusplets, and the shape could be oriented erect to oblique, depending on the position of the tooth, when compared with the specimen. *C. obscurus* shows coarser serrations along the middle section of the cutting edge. *C. plumbeus* shows a narrower and elongated crown, while the specimen has a more triangular crown. *C. sealei* shows a more deeply notched tooth, with serrations on the lower half of the tooth and smoother edges when moving towards the apex of the tooth. The fully grown tooth of *C. sealei* is also smaller compared to the specimen. *C. sorrah* also show smaller teeth, with more oblique cusps and coarsely serrated cutting edges at the distal side, compared to the specimen.

Based on the comparison in tooth morphology between Specimen V3-17.6m and previous studies, it can be concluded that the Tukau tooth specimen could belong to *C. amboinensis, C. leucas* or *C. limbatus*. However, it is essential to note the possibility of variation in tooth shape among individuals within a species. The variation might be due to 1) the differences in tooth size and morphology along the tooth row, 2) morphological differences between

teeth in upper and lower jaws, 3) geographic variation, 4) sexual dimorphism, 5) age-related changes which reflect a change in diet during life, and 6) individual variation (Naylor & Marcus, 1994; Berkovitz & Shellis, 2023). The morphological similarities between the teeth of *C. amboinensis*, *C. longimanus* and *C. leucas* present a significant challenge in their differentiation (Marsili, 2007; Kocsis *et al*., 2019; Lin *et al*., 2022; Kocsis, 2024). However, *C. longimanus* is eliminated due to its straighter crown foot compared to the other species (Lin *et al*., 2022). Compared to the upper teeth of *C. amboinensis*, the teeth of *C. leucas* are narrower, with a higher and less distally curved crown. The distal heel is less obviously separated from the teeth of *C. leucas*, with a smoother curve. The distal heel on *C. amboinensis* teeth is closer to the base of the crown and links to the distal cutting edge at an angle (Kocsis *et al*., 2019).

The ecological distribution of present-day *C. amboinensis* and *C. leucas* exhibit notable distinctions, potentially influenced by competitive exclusion between the two species (Ebert *et al*., 2021). *C. amboinensis* primarily inhabits continental and insular shelves, frequenting inshore areas near the surf line and along beaches, with a depth range of 0 to 100 meters (Ebert *et al*., 2021). In contrast, *C. leucas* demonstrates a broader ecological niche, occupying various coastal and estuarine environments. These include "hypersaline lagoons, bays, river mouths, passages between islands, coastal canals, near wharves, and along surf lines" (Ebert *et al*., 2021). *C. leucas* also ventures into warm riverine systems, often tolerating highly turbid conditions (Naylor & Marcus, 1994; Compagno *et al*., 2005; Ebert *et al*., 2021; Hasan *et al*., 2021).

Teeth, along with shells and bones are biomineralised tissues that have the highest potential to be preserved (Briggs, 2003). The fossilisation process of shark teeth typically involves rapid burial, wherein the surrounding sediment serves as a protective matrix against weathering, abrasion, and scavenging. It limits the tooth's exposure to oxygen, thereby inhibiting decay processes (Cappetta, 2012). The resultant anoxic environment is crucial in preserving the tooth and allowing the initiation of permineralisation processes that lead to fossilisation (Brett & Thomka, 2013). The colour variations observed in fossilised shark teeth depend on the mineral composition of the surrounding sediment during the fossilisation process (Brett & Thomka, 2013). Minerals such as calcite or silica may impregnate the tooth structure, contributing to its final colouration. In the case of Specimen V3-17.6m, the observed grey colouration is potentially caused by the clay matrix surrounding it. The reddish-brown colouration observed in Specimen V3-17.6m is commonly attributed to iron hydroxides, prevalent diagenetic minerals in fossilised remains. It indicates a fossilisation process occurring under oxidising environmental conditions (Zougrou *et al*., 2014).

In this study, no other parts of shark fossils were found in the same or nearby beds, suggesting that it is likely a product of tooth shedding. Bulk sampling is required to determine any other tooth fossils in the formation.

Proper bulk sampling is required to expand the fossil record, particularly in regions mentioned by Kocsis *et al*. (2019) and Kocsis (2024), including Sumatra, Peninsular Malaysia, Vietnam, and the Philippines, where Neogene and Pleistocene chondrichthyan data are poorly documented.

CONCLUSION

The tooth specimen (V3-17.6m) is the first reported vertebrate remains found in the Tukau Formation, where the literature only had records of some brackish water foraminifera. The fossil discovery could provide better insights into the depositional environment and biological diversity of the formation. Palaeoenvironment reconstruction is possible by identifying fossil species, as it allows for understanding the species' behaviour. Specimen V3-17.6m was examined closely and identified as a *Carcharhinus* shark's upper right lateral tooth based on morphology. Based on the literature review of Neogene to recent *Carcharhinus* species in tropical water from previous studies, the shark tooth could belong to one of the following species: *C. amboinensis*, *C. leucas* or *C. limbatus*. These shark species are commonly found in continental and insular shelf waters, often nearshore, in estuaries, bays, lagoons, and coastal environments, with some species tolerating varying salinities or migrating seasonally. This finding extends the known Neogene vertebrate record of Borneo, where fossil chondrichthyan data remain sparse, and it demonstrates the potential of the Tukau Formation as a new fossil-bearing unit, warranting targeted bulk sampling and systematic palaeontological investigation. Further work can be undertaken by bulk sampling and detailed taphonomic analysis to recover additional vertebrate remains and establish the stratigraphic distribution of fossil material.

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AUTHORS CONTRIBUTION

YNF (70%): fieldwork (strata logging, sampling, sample preparation), data analysis, writing original draft; DDW (25%): manuscript review and editing; MVP (5%): manuscript editing.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare relevant to the content of this article. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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