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Trouble in the Tank: A Case Report of Fatal Scuticociliate Encephalitis in a Whitetip Reef Shark (*Triaenodon obesus*)

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Abstract

This case report presents a recent case of scuticociliatosis in a whitetip reef shark (*Triaenodon obesus*), housed at a zoo (Haus des Meeres Aqua Terra Zoo, Vienna, Austria). Clinical signs such as uncoordinated swimming and body tilt were observed prior to death. Postmortem examination and magnetic resonance imaging (MRI) revealed significant brain lesions consistent with granulomatous or necrotising encephalitis. Histopathology and molecular diagnostics confirmed the presence of the scuticociliate *Miamiensis avidus* and/or *Philasterides dicentrarchi* in the brain, with extensive tissue invasion. This case underscores the pathogenicity of scuticociliates in elasmobranchs, highlighting the need for effective management practices in aquaria to prevent or mitigate such infections. In this study, we present the first documented infection with scuticociliates in the whitetip reef shark.

1 | Introduction

Sharks are one of the highlights in every public aquarium. However, they are susceptible to various pathogens, including several scuticociliates (Ciliophora: Scuticociliatida) (Cheung 1993; Goertz 2004). These unicellular eukaryotes inhabit freshwater, marine and soil biospheres and many of the species are nonpathogenic free-living organisms (Pan et al. 2020). Nevertheless, others are known to be facultative parasites, for example, *Miamiensis avidus*, *Philasterides dicentrarchi*, *Uronema marinum* and *Anophryoides haemophila* (Cawthorn et al. 1996; Cheung et al. 1980; Harikrishnan et al. 2010; Thompson and Moewus 1964) and can cause a severe disease, called scuticociliatosis. This disease was reported in both captive and wild shark populations: in captive zebra sharks (*Stegostoma tigrinum*), Port Jackson sharks (*Heterodontus portusjacksoni*), Japanese horn sharks (*Heterodontus japonicus*) (Li et al. 2017; Stidworthy et al. 2014), as well as in a common thresher shark (*Alopias vulpinus*), a brown smooth-hound shark (*Mustelus henley*) (Chang and Okihiro 2024) and wild smooth dogfish (*Mustelus canis*) (Newton et al. 2019). Garner (2013) reports neuro-invasive ciliate infection of swell sharks (*Cephaloscyllium ventriosum*), zebra sharks and horn sharks (*Heterodontus francisci*), but without further details. In contrast, a mass mortality of leopard sharks (*Triakis semifasciata*) in the San Francisco Bay was unambiguously traced back to the scuticociliate *M. avidus* (Retallack et al. 2019).

In 2017, *M. avidus* was recognised as nonsynonymous with another pathogenic species, *P. dicentrarchi* (De Felipe et al. 2017). Since they are closely related species, it is difficult to distinguish them at the species level. *M. avidus* has three different life stages, during which it feeds mainly on bacteria (microstome stage), on other protozoans or host tissue (macrostome stage) and a smaller, nonfeeding, spreading stage (tomite stage). The macrostome stage is not described in *P. dicentrarchi* and the morphology of the microstome and tomite stages of the two mentioned scuticociliate species

differ (De Felipe et al. 2017). *P. dicentrarchi* is known to be a microaerophilic scuticociliate that typically feeds on bacteria in its free-living form. Nevertheless, upon encountering a suitable host, it can also change to a histophagous parasitic stage (Steverding 2022). The complex interactions between fish host, environment and parasite, which determine the development, course and severity of the disease, are not well understood. However, the role of extracellular proteinases as virulence factors for scuticociliates has been reported (Narasaki et al. 2018; Paramá et al. 2004). In addition to elasmobranchs, systemic infections with histophagous scuticociliates have also been observed in a variety of marine teleosts in aquaculture and in the wild, partly with relevant economic impact (Harikrishnan et al. 2010). Affected species include olive flounder (*Paralichthys olivaceus*) (Jee et al. 2001; Jung et al. 2005, 2007; Kim et al. 2004a, 2004b; Song et al. 2009; Yoshinaga and Nakazoe 1993), turbot (*Scophthalmus maximus*) (Dykova and Figueras 1994; Iglesias et al. 2001; Puig et al. 2007; Sterud et al. 2000), southern bluefin tuna (*Thunnus maccoyii*) (Garza et al. 2017; Munday et al. 1997, 2003; Power et al. 2019), sea bass (*Dicentrarchus labrax*) (Dragesco et al. 1995), New Zealand grouper (*Polyprion oxygeneios*) (Anderson et al. 2009; Smith et al. 2009), yellowtail kingfish (*Seriola lalandi*) (Smith et al. 2009), large yellow croaker (*Larimichthys crocea*) (Lin et al. 2024), black rockfish (*Sebastes schlegelii*) (Whang et al. 2011) and the threatened handfish (Nowak et al. 2024), among others. Of the reported scuticociliate species, *M. avidus* is regarded as the predominant scuticociliate pathogen affecting cultured finfish (Song et al. 2009; Whang et al. 2013).

In addition to its relevance in aquaculture, scuticociliatosis in aquaria-housed fish can pose serious threats to the health of valuable and endangered species, particularly elasmobranchs such as sharks and rays, where infections often involve the central nervous system. Several earlier reports of *M. avidus* and/or *P. dicentrarchi* infections in sharks in aquariums have been documented (Li et al. 2017; Stidworthy et al. 2014), underscoring the parasite's specific impact on captive shark populations. Most recently, Chang and Okihiro (2024) identified bacterial or protozoal meningoencephalitis as the leading cause of death in stranded or captive elasmobranchs and emphasise the importance of thorough postmortem examinations, including dissection of the chondrocranium. Here we present the first report of scuticociliatosis in a whitetip reef shark, with the diagnosis based on clinical, histopathological and molecular examinations. Moreover, we demonstrate serious brain lesions that were caused by the parasite, using magnetic resonance imaging (MRI).

2 | Case Processing and Results

2.1 | Case History

The affected whitetip reef shark was estimated to be born in 2016 and was caught in the wild in 2018. Since then, it was kept in a 15.5×7.5 m rectangular walk-around indoor tank in the Haus des Meeres Aqua Terra Zoo in Vienna, Austria (Figure 1A). The aquarium held 330,000 L of seawater with salinity ranging from 23% to 27% and a temperature of 23.5°C ± 1°C. A closed filtration system with protein skimming, ozonation and three parallel sand filters guaranteed appropriate water quality. The tank housed four species of elasmobranchs: blackchin guitarfish (*Glaucostegus cemiculus*), blacktip reef shark *(Carcharhinus melanopterus)*, zebra shark (*Stegostoma tigrinum*) and a single whitetip reef shark (*Triaenodon obesus*). The majority of 30 other fish species in the tank were Osteichthyes of the genus *Acanthochromis*. Three times a week, targeted feeding with Atlantic and Indian mackerel, hake fillets, calamari, saithe fillets, sprats, sardines and white tiger shrimp was offered to the elasmobranchs, while a variety of food was provided for other species in the aquarium according to the species-specific demands.

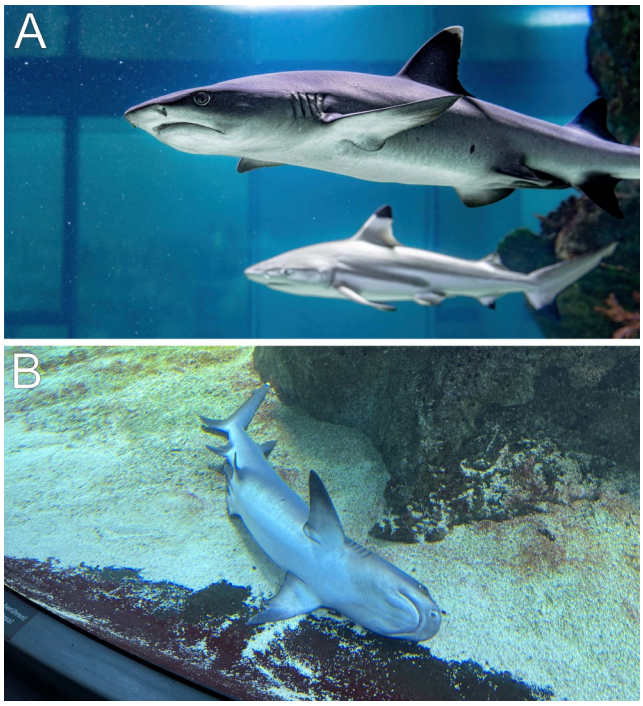

FIGURE 1 | (A) The male whitetip reef shark (*Triaenodon obesus*) prior to its illness was kept at the Haus des Meeres since 2018 in the 360° shark tank with four other elasmobranch species, such as the Blacktip reef shark (*Carcharhinus melanopterus*) seen in the back. (B) The shark showed sudden neurological abnormalities, such as impaired swimming behaviour and lateral recumbency on the ground 2 days before its death.

Showing no signs of external lesions, the whitetip reef shark began to exhibit uncoordinated swimming behaviour in 2024, colliding uncontrolled with objects such as rocks and walls. The animal displayed a body positioning tilted to the left with a right-hand twist (Figure 1B). No abnormalities were observed prior to this event, and the animal was considered clinically healthy until then. None of the other sharks showed signs of disease.

Within an hour, the shark was separated and placed in a tank of approximately 50 000 L for 2 days. The condition did not improve, and 2 days later, the animal died and was taken to the Fish Health Division (Vetmeduni Vienna) for a postmortem examination.

2.2 | Diagnostic Imaging

Upon arrival at the clinic, the shark had been dead for approximately 8 h.

The postmortem MR images were acquired using a high-field MRI unit (Magnetom Espree, 1.5 T, Siemens Healthcare, Erlangen, Germany) with the shark placed in sternal recumbency. Following a scout examination, the positioning of the shark was adjusted and the isocentre was placed on the level of the animal's eyes. The following sequences were acquired: transverse T2- and T1-weighted turbo spin echo (TSE), transverse T2-weighted fluid attenuation inversion recovery (FLAIR), sagittal 3D T2-weighted TSE, transverse and sagittal T1-weighted gradient echo (GRE). Slice thickness was set from 1 to 2.5 mm.

An oval lesion with mildly irregular-shaped edges was detected intra-axially in the right rostral section of the telencephalon (Figure 2a). The lesion exhibited well-defined margins and a T2W hypo- and T1W hypo- to isointense centre with a thick T2W hyper- and T1W isointense rim when compared with the cranial musculature. Such findings may indicate either a necrotic area or abscess formation within a larger brain lesion. Dorsally and medially adjacent to this lesion, a second ill-defined, T2W hypointense and T1W hyperintense, thick band-like lesion was visible, which may have corresponded to a second area of necrosis or abscessation at a different maturation stage. The surrounding tissue of the telencephalon's lesions on the right was T2W hyperintense, indicating oedema. This oedema caused a mass effect, which resulted in a mild midline shift of the telencephalon to the left, particularly in the rostral aspect. Additionally, mild cranial compression of the diencephalon and mesencephalon

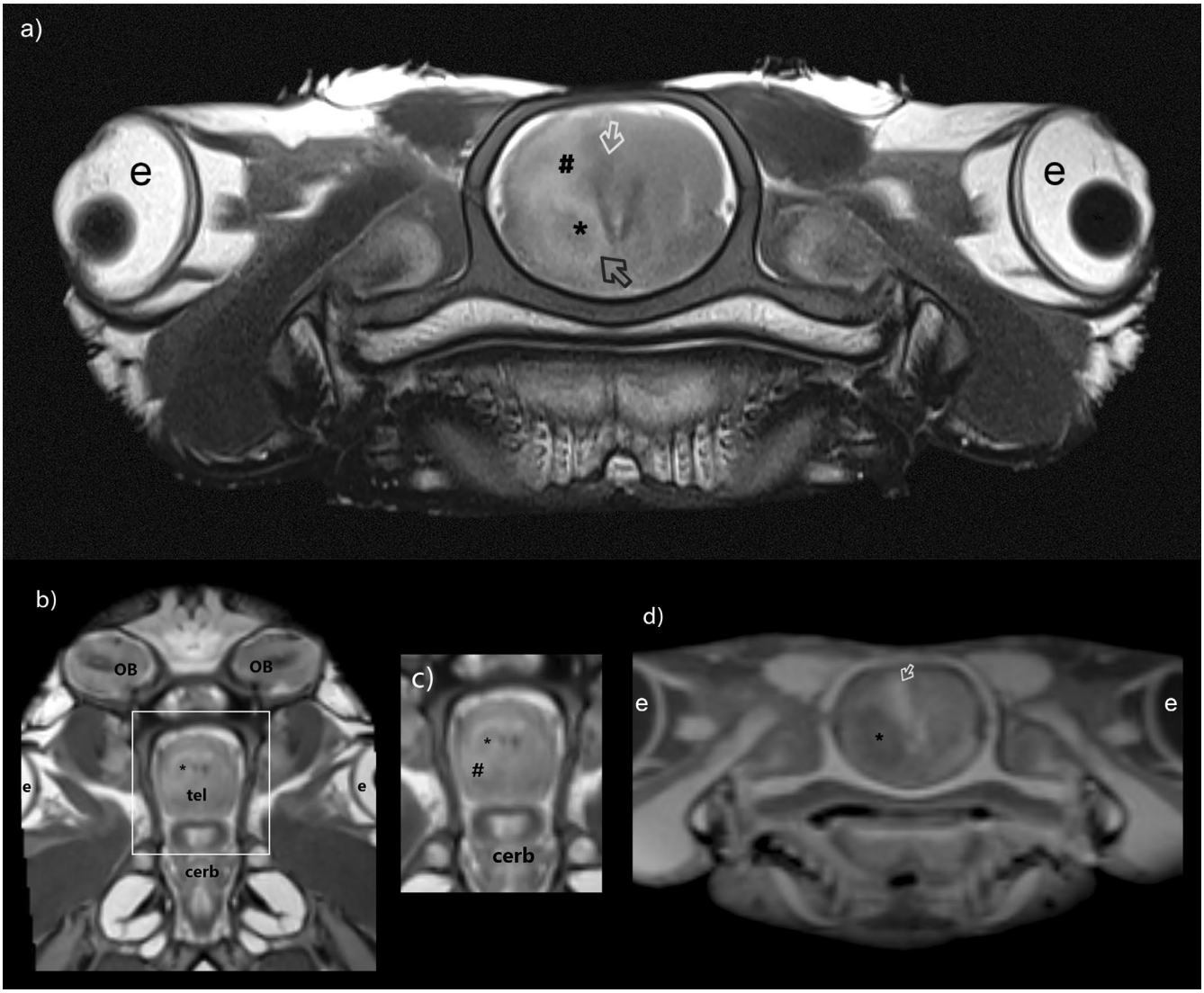

FIGURE 2 | MRI images (1.5 T) of the brain of the whitetip reef shark (*Triaenodon obesus*) on the level of the eyes. (a) transverse and (b) 3D dorsally reconstructed T2-weighted TSE images with the white-marginated, rectangular circumscribed area magnified in c). (d) transverse reconstructed 3D T1-weighted GRE image at the same level as a). Right is to the left. Oval-shaped T2W hypointense, T1W hypo- to isointense area (*) with a T2W hyperintense rim (open black arrow) in the right telencephalon. Second ill-defined, T2W hypointense, T1W hyperintense, band-like region (open white arrow) in the right telencephalon, –consistent with granulomatous/necrotising encephalitis. The lesions are surrounded by T2W hyperintense brain parenchyma, – consistent with oedema (#). The main lesion, including the surrounding oedema, measures approximately 11 mm in diameter. Telencephalon (tel), cerebellum (cerb), olfactory bulb (OB), eye (e).

and mild displacement of the cerebellum caudally were suspected. The brain parenchyma of the left telencephalon section was mildly heterogeneous in the T1W and T2W TSE sequences. The cerebellum and the structures of the left diencephalon and mesencephalon were inconspicuous, except for the aforementioned mild displacement and compression due to the mass effect (Figure 2a–d).

2.3 | Necropsy

The shark had a total body length (TL) of 133 cm and a weight of 12.8 kg. The shark presented oligofocal haemorrhages on the ventral surface of the body, particularly in the oral region, around the pectoral girdle and near the pelvic fins. The gills were covered with an excessive amount of mucus. Wet mounts of skin and gills did not show any parasites. The gross anatomy of the internal organs was inconspicuous, with a pale pink spleen, ochre liver and a moderate quantity of food residues (kelp and pulpy ingesta) within the gastrointestinal tract.

Due to the findings from the diagnostic imaging, the skin was removed from the dorsal section of the head, and the chondrocranium was opened using bone-cutting forceps. About 3 mL of a slightly sanguineous fluid was aseptically removed from the cranial cavity. The right hemisphere of the telencephalon was slightly enlarged compared to the left side, showed prominent vascularisation and presented structural loss at the rostral part (Figure 3). Sterile swabs of the cerebrospinal fluid were cultured for bacteriology on Columbia sheep blood (COS) agar plates (Thermo Fisher Scientific, Oxoid) and incubated for 48 h at 22°C. The bacterial isolates were analysed with MALDI TOF MS (Matrix-assisted laser desorption ionisation time-of-flight mass spectrometry; Bruker Daltonic GmbH, Bremen, Germany) and identified low numbers of *Vibrio harveyi* in the cerebrospinal fluid.

The whole brain was aseptically extracted, and samples of the brain, affected and unaffected parts, the cerebrospinal fluid, and a swab from the nasal cavity were taken for microscopic examination. In the sample of the affected brain tissue, numerous organisms resembling scuticociliates were observed (Figure S1). An unambiguous morphological assignment of the organisms was not possible, most likely because the time of death had occurred several hours before. In the samples from unaffected brain parts and from the nasal cavity, no such organisms were detected.

2.4 | Histopathology

For histopathology, tissues of the brain, kidney, spleen, gonads, rectal gland, gills, gastrointestinal-intestinal tract, pancreas, liver and heart were collected and transferred to 4% neutral-buffered formalin. Brain tissue was selected from different regions to compare the obviously altered regions from the seemingly unaffected ones. After 24 h, tissues were embedded in paraffin wax, and 4 μm sections were stained with haematoxylin and eosin (HE) and additionally with Giemsa stain for protists and amoeba, periodic acid-Schiff (PAS) stain for intracellular storage dysfunctions and fungal infections, Ziehl–Neelsen stain for acid-fast bacteria, Taylor's stain to detect bacteria and Grocott's stain for the detection of fungal infection.

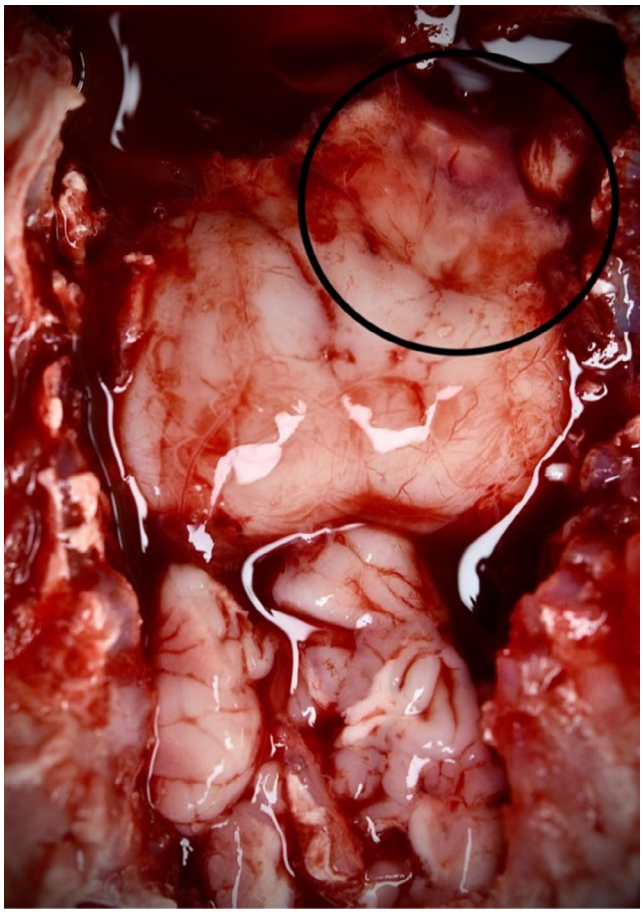

FIGURE 3 | Brain of the whitetip reef shark (*Triaenodon obesus*) in situ after opening of the chondrocranium: Bloody fluid in the cranial cavity, structural loss and vascular injection in the right hemisphere of the rostral telencephalon (black circle).

The investigated tissues showed shark-specific morphology with no relevant alterations, except for the brain, particularly the telencephalon (Figure 4). Large areas of the telencephalon showed massive disruption of tissue architecture due to multifocal to coalescing foci of neuropil rarefaction and liquefaction, and neuron loss with prominent interlacing blood vessels. Only sparsely scattered inflammatory cells, mainly eosinophilic granulocytes and lymphocytes, were observed in the affected regions. These regions contained a huge number of elliptical, unicellular organisms measuring approximately 20 × 15 μm, with numerous, partly eosinophilic, intracytoplasmic droplets (Figure 4B). In many of the organisms, a macronucleus, and in some, additionally a micronucleus was evident. The presumptive scuticociliates were observed only in tissue slides of the affected brain regions, which were clearly separated from less or nonaffected regions. In the transition area from total structure loss to intact brain tissue, no demarcation was present (Figure 4A). The adjacent tissue with preserved architecture was infiltrated with a moderate number of inflammatory cells, especially eosinophilic granulocytes and lymphocytes forming perivascular cuffs (Figure 4D). The histopathological findings in the brain were consistent with an acute, severe, oligofocal necrotising encephalitis.

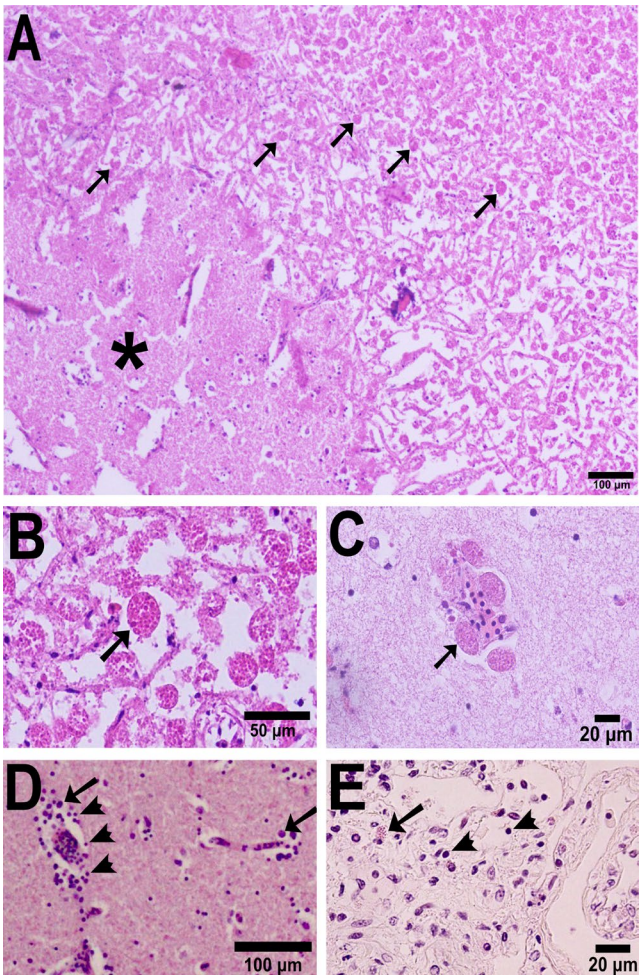

FIGURE 4 | Histopathology showing the Telencephalon of the whitetip reef shark (*Triaenodon obesus*), H&E staining. (A) The right part shows a massive ciliate infestation (arrows) with structural loss of the nervous tissue, which is clearly distinguishable from the noninfiltrated tissue (*). (B) Detail from A) with scuticociliate (arrow); the scuticociliates are clearly visible, with characteristic eosinophilic intracytoplasmic droplets (erythrophagocytosis) (arrow) (C) vascular-associated scuticociliates (arrow) (D) accumulation of eosinophilic granulocytes (arrows) and lymphocytes (arrowheads) around blood vessels (perivascular cuffs) (E) detail of the meningitis with eosinophilic granulocytes (arrows) and lymphocytes (arrowheads).

In the meningeal tissues, eosinophilic granulocytes and lymphocytes were present in moderate to high numbers, accompanied by a severe hyperaemia and parasites, focally attached to the meningeal structures, indicative of a moderate to severe, oligofocal to coalescing, predominantly eosinophilic meningitis (Figure 4E).

A contribution of other pathogens such as bacteria, mycobacteria and fungi was ruled out by special stains.

2.5 | Molecular Characterisation and Ciliate Identification

Samples for molecular identification were taken from the affected brain tissue, from cerebrospinal fluid as well as from nasal scrapings and stored at −20°C until further use. DNA extraction from the homogenised tissues was performed with the DNeasy Blood & Tissue Kit (QIAGEN) according to the manufacturer's protocol. The concentration of the extracted DNA was measured using a NanoDrop (ThermoFisher Scientific). For confirmation of the presence of scuticociliates, molecular methods targeting the small-subunit (SSU) rRNA gene region and the internal transcribed spacer 2 (ITS-2), respectively, were used. SSU amplification was performed according to protocols specified by Jalenques et al. (2021) and Chi et al. (2023). The largest amplicon was obtained using the primers SSU244-R: 5′-GTGAATCATAGTAACTGATCGA-3′ and SSU1117-F: 5′-TCCTTAAGTTTCAGCCTTGCG-3′ (Chi et al. 2023), which target an 870 bp fragment of the SSU rRNA gene. For ITS-2 amplification, we used the primers designed by Sueiro et al. (2022) fITS2: 5′-TCC CGC TAA ACT CGA AAA GC-3′ and rITS2: 5′-AGC CGA GAT CAC TTT CTG TG-3′ which target a 78 bp sequence.

PCR conditions were as follows: DreamTaq Green PCR Master Mix (Thermo Scientific), 12.5 µL; DNA (100 ng/µl); forward and reverse primer (10 pmol/µl), each 1 µL; and PCR grade water 9.5 µL. Initial denaturation was set at 94°C for 5 min, followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 54°C for 10 min, elongation at 72°C for 1 min, and a final elongation step at 72°C for 10 min.

Amplification products were visualised on a 1.5% agarose gel (Serva Electrophoresis GmbH) containing 10 µL Gel Red (Biotium). Bands of the expected sizes were excised, purified with a MinElute Gel Extraction kit (Qiagen) and sequenced by the Sanger method (LGC Genomics, Germany). Sequencing results were identified using BLAST-n through a search in the GenBank database (www.ncbi.nlm.nih.gov) and showed 100% identity to the SSU rRNA gene of *M. avidus* deposited in GenBank under accession number JN689230.1 from base pair 272 to 1062 and 100% identity to a sequence of the ITS-2 gene of *M. avidus* (accession number: KY082894.1) from base pair 350 to 377 as well as 100% identity to the corresponding sequences of *P. dicentrarchi*. The resulting ITS-2 sequence was only 28 bp in length, which is shorter than the expected amplicon size, likely due to limitations in sequencing read quality. All samples (brain, cerebrospinal fluid and nasal cavity) tested PCR positive.

3 | Discussion

Neurological symptoms in aquarium-housed sharks pose a diagnostic challenge and often require rapid therapeutic intervention. In our case, the diagnosis was facilitated by the fact that the whitetip reef shark (*Triaenodon obesus*) was already deceased at the time of the examination, allowing for a comprehensive, multidisciplinary diagnostic approach. Still, even in live sharks, a thorough clinical and neurological examination, diagnostic imaging and the collection of suitable samples may provide at least an organ-specific diagnosis, and in the best case, determine the aetiology of the disease. Clinical examination and diagnostic imaging methods of live sharks require meticulous preparation and special equipment. For the evaluation of nervous tissues, MRI provides excellent results, but the use in live fish is restricted due to limited availability, longer duration of the examination

compared to other imaging procedures, need of immobilisation and high costs. Consequently, information regarding the use of computed tomography (CT) and magnetic resonance imaging (MRI) for live sharks is restricted to few reports (Columbus Zoo and Aquarium 2019; Denver Zoo Conservation Alliance 2024; Dumonceaux et al. 2010; Dumonceaux et al. 2012; Hill and Geach 2025; Montero-Hernández et al. 2024), or available in elasmobranch husbandry manuals (Mylniczenko et al. 2017; Stetter 2004). Instead, the acquisition of MR images is currently mostly performed for anatomical studies on dead or seemingly healthy live animals (Ito et al. 2023; Perry et al. 2007; Winkel et al. 2024) and on fixed shark brain specimens (Kim et al. 2021; Yopak and Frank 2009). However, scientific reports that combine the results of clinical history, MRI examination, pathogen detection and postmortem investigations (necropsy and histopathology) of diseased shark are not available. The devastating effect of scuticociliates on nervous tissue has been documented by histopathology before (Jalenques et al. 2021; Li et al. 2017; Retallack et al. 2019; Rossteuscher et al. 2008; Stidworthy et al. 2014), but here we demonstrated the lesions by MRI for the first time. Based on the MRI findings of the current case, granulomatous or necrotising encephalitis or abscess formation were the considered main differential diagnoses. Oval-shaped areas of necrotic tissue or abscess formation, as observed in this case, may contain the causative agent or its degradation products.

When necrotising and lytic lesions in the brain of sharks are suspected or observed, bacterial, viral and fungal causes must be considered, besides parasitic invasion. Infectious meningoencephalitis has been reported in wild, stranded elasmobranchs, notably caused by the scuticociliate *M. avidus* and the Gram-positive bacterium *Carnobacterium maltaromaticum*, which have caused epizootic and enzootic strandings but are also the most common cause of death of aquarium-housed elasmobranchs (Chang and Okihiro 2024). Meningoencephalitis in common thresher sharks (*Alopias vulpinus*) associated with *Carnobacterium maltaromaticum* was reported by Steele et al. 2022. In the cerebrospinal fluid, we found low numbers of *Vibrio harveyi*, a gram-negative potential pathogen, which is ubiquitous in marine environments. Most likely, it did not contribute to the disease, since bacteria-specific stains of histological slides did not reveal a visual presence of bacterial organisms in the brain lesions.

Following the exclusion of other pathogens in the brain, our findings were consistent with descriptions from similar cases of scuticociliatosis (Alvarez-Pellitero et al. 2004; Li et al. 2017; Ramos et al. 2007; Rossteuscher et al. 2008; Stidworthy et al. 2014; Tao et al. 2016).

The visually observed presence of scuticociliates was confirmed by molecular identification. Differential molecular diagnostics for *M. avidus* and *P. dicentrarchi* are to date unavailable. These taxa have been demonstrated to have identical SSU and ITS-2 rDNA sequences (De Felipe et al. 2017; Sueiro et al. 2022). This highlights the genetic similarity of these scuticociliates and the limitations of molecular identification using ribosomal markers alone. Moreover, possibly wrongly identified and reported sequences lead to further confusion as well as the synonymous use of both species names (Gao et al. 2012). A search for new gene targets is essential to be able to differentiate and better understand potential differences in the pathology of the two species, with focus on the histophagous macrostome stage found only in *M. avidus* (De Felipe et al. 2017).

An important result of the present study is that we were able to detect and diagnose scuticociliates molecularly in nasal swabs of the shark. This indicates a potential noninvasive sampling method for live animals, and its potential for testing animals before admission to aquarium facilities, hence avoiding possible transmission to other elasmobranchs held in large multi-species show aquaria.

Unfortunately, the origin of pathogenic scuticociliates in the aquarium remains unclear in our case. In Japan, *M. avidus* was described as 'naturally occurring' in four different aquariums, causing skin- and general infections in 26 different fish species (Yanagisawa et al. 2018). Stidworthy et al. (2014) described the fatal disease of wild-caught sharks, kept in mixed-species marine tanks in Europe and North America, and Rossteuscher et al. (2008) identified the pathogen from wild-caught sea-dragons. Jalenques et al. (2021) found conclusive evidence of scuticociliatosis in 12 individual marine aquarium-kept fish, representing 10 different species. Among them, the authors identified *M. avidus/P. dicentrarchi* in three samples using molecular methods.

It may be speculated that the pathogen is indeed naturally occurring in many marine systems, and environmental factors such as temperature shifts may trigger the transformation of the parasite to the histophagous stage and initiate the attack of suitable hosts. This would be in accordance with the observations of Jalenques et al. (2021) who suggested a rise of water temperature caused a severe outbreak of the disease. Interestingly, it seems that not only temperature alone plays a crucial role, since outbreaks have been reported at temperatures varying from 13°C (Jalenques et al. 2021), 14°C–18°C (Rossteuscher et al. 2008), 16°C–20°C (Yanagisawa et al. 2018), to 22.5°C–24.5°C (this study). Generally, a range of 18°C–23°C has been reported as optimal for the proliferation of scuticociliates (Moustafa et al. 2010; Ramos et al. 2007; Takagishi et al. 2009; Tao et al. 2016), and at 27°C proliferation ceases (Yanagisawa et al. 2018). In aquaria with mixed populations, water temperature may not meet the temperature optimum for each of the housed fish species; therefore, some species may be more prone to the disease.

Another factor which may contribute to outbreaks of the disease is a high organic load, including bacteria and other suitable nutrients for scuticociliates (Urrutxurtu et al. 2003). This is reflected in a special vulnerability of recirculating aquaculture systems (RAS), which are especially prone to scuticociliatosis (Budiño et al. 2011); it is certainly also true for aquaria.

The cases of scuticociliotasis reported from elasmobranchs in aquaria (Jalenques et al. 2021; Rossteuscher et al. 2008; Stidworthy et al. 2014; Yanagisawa et al. 2018) included mostly lesions of the central nervous system, but in contrast to our findings, also parasitic invasion of skin, muscle and other organs. The route of infection is not clear, but entry points through the gills, the skin, the nares and the olfactory nerve have been suggested for *M. avidus/P. dicentrarchi* (Iglesias et al. 2001; Moustafa et al. 2010; Paramá et al. 2006). In our case, the parasite most likely invaded its host via the nares, where we were able to detect the pathogen's DNA. Though the parasite was also present in low numbers in blood vessels, no lesions were observed in any

other organs than the brain. Possibly, the shark succumbed to the disease before a systemic infection could develop.

Since the control of the pathogen plays a major role in marine aquaculture and aquaria, several methods have been developed. Besides the use of chemicals and pharmaceuticals (Iglesias et al. 2002; Kim et al. 2022), the application of dinoflagellates for the elimination of selected scuticociliates was successfully tested in vitro (Kim et al. 2017). For marine aquaria, where mixed populations of sensitive fish and invertebrates such as corals are often maintained together, the use of chemicals is limited. On the other hand, they may be successfully applied to individuals with early stages of superficial infections in quarantine tanks.

Once scuticociliates are established in a system, achieving medium- or long-term control is extremely challenging—'control' refers to reducing parasite levels to a point where they no longer cause disease, minimising transmission and preventing recurrent outbreaks—challenges that are particularly difficult in large, biologically complex systems. To prevent scuticociliatosis in captive shark populations, targeted monitoring and proactive environmental management might be helpful. Control strategies might help to prevent disadvantageous fluctuations in parameters like water chemistry quality, temperature and salinity, which can facilitate the proliferation of scuticociliates and other pathogens. Keeping records of the mentioned environmental parameters is additionally recommended to trace back trigger factors if a disease breakout happens. High concentrations of organic matter in tank systems provide food sources for ciliates, increasing infection risks. Maintaining strict hygiene practices and minimising nutrient buildup in captive environments can significantly reduce this potential (Lamas and Leiro 2020).

In conclusion, this is the first report of fatal scuticociliatosis in a whitetip reef shark. Clinical, necropsy, histopathological and molecular findings were complemented by magnetic resonance imaging, demonstrating the high value of combining diverse diagnostic tools. In conjunction with targeted health management, advanced diagnostics via nasal swabs may minimise the risk of transmission and fatal scuticociliatosis in captive elasmobranchs in the future.

Author Contributions

Hella Schwegler: investigation (equal), methodology (equal), visualization (lead), writing – original draft preparation (lead). **Jeff Schreiner:** writing – original draft preparation (supporting). **Maria Prüllage:** investigation (equal), writing – original draft preparation (supporting). **Karoline Lipnik:** investigation (equal), methodology (equal), writing – review and editing (supporting). **Astrid S. Holzer:** writing – review and editing (equal). **Eva Lewisch:** conceptualization (lead), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Native preparation of cerebrospinal fluid from the deceased whitetip reef shark (*Triaenodon obesus*) showing scuticociliates (white circles). Some organisms appear partially degraded, likely due to postmortem autolysis. Note the presence of intracytoplasmic droplets within the ciliates, which are characteristic features aiding in their recognition.