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REVIEW

Recommendation of consensus definition of sea turtle fibropapillomatosis

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Abstract

Sea turtle fibropapillomatosis (FP) is an emerging transboundary contagious disease that affected concomitantly two different marine hot spots in the Northern Atlantic Ocean and in the South China Sea at the beginning of the twentieth century. FP reached a panzootic status in the 1990s in green turtle (*Chelonia mydas*) populations, with increased risks of emergence and spread of the disease which have been correlated with climate induced terrestrial and oceanic physical and chemical changes. During 2023–2024, scientific experts performed a bibliographic review and recommend the consensus definition of sea turtle fibropapillomatosis. FP is an emerging transboundary viral terrestrial and aquatic contagious neoplastic syndrome involving cancerous molecular transmission pathways, which may affect all species of sea turtles at all life stages. The diagnosis of the most common verrucous form of FP is pathognomonic by visual examination of a sea turtle. We summarize the main clinical characteristics of FP, moderated by a degree of confidence of research findings adapted from the Intergovernmental Panel on Climate Change (IPCC) assessment reports. We recommend the implementation of a universal and transparent monitoring strategy of sea turtle fibropapillomatosis in sentinel bays, under the governance of the World Organisation for Animal Health.

KEYWORDS

climate change, consensus definition, One Health, sea turtle fibropapillomatosis, World Organisation for Animal Health

INTRODUCTION

Sea turtle fibropapillomatosis (FP) is a transboundary emerging terrestrial and aquatic contagious viral disease that potentially affects all seven species of sea turtles listed as vulnerable, endangered, or critically endangered by the IUCN Red List™ at all life stages: loggerhead turtles *Caretta caretta*, green turtles *Chelonia mydas*, hawksbill turtles *Eretmochelys imbricata*, leatherback turtles *Dermochelys coriacea*, flatback turtles *Natator depressus*, olive ridleys turtles *Lepidochelys olivacea*, and kemp ridleys turtles *Lepidochelys kempii* (Aguirre & Lutz, 2004; Jones et al., 2016; Manes, Carthy, et al., 2023). FP not only alters the health of sea turtles' nesting ecosystems, but also alters sea turtles' keystone ecological roles in regulating the balance of coral reefs and blue carbon ecosystems (Aguirre & Lutz, 2004; Burge & Hershberger, 2020; Cooley et al., 2022; Du et al., 2019; Farrell et al., 2022; IPCC Annex V, 2022; Mashkour et al., 2020; Mycoo et al., 2022; Parmesan et al., 2022; Whilde et al., 2024). Moreover, clinical cases of FP were reported at the panzootic scale in *C. mydas* populations in the 1990s (Dujon et al., 2021; Hargrove et al., 2016; Herbst, 1994; Jones et al., 2016; Norton et al., 1990; Williams et al., 1994; Work et al., 2004). Despite extensive research, the etiology and pathogenesis of FP are not fully understood. FP continues to be observed in new geographic marine areas, likely due to the circum-tropical or highly migratory nature of sea turtle species and to climate change impacts profoundly altering the global oceanic hydrological cycle, shifting and expanding the spatial patterns of terrestrial and aquatic infectious diseases globally (Abreu-Grobois et al., 2008; Burge & Hershberger, 2020; Casale & Tucker, 2017; Christiaanse et al., 2024; Cooley et al., 2022; Du et al., 2019; IPCC Annex V, 2022; James et al., 2021; Lafferty, 2009;

Loganathan et al., 2021; Manes, Carthy, et al., 2023; Mortimer et al., 2008; Mycoo et al., 2022; Origlia et al., 2023; Parmesan et al., 2022; Patricio et al., 2012; Red List Standards & Petitions Subcommittee, 1996; Robben et al., 2023; Saladin & Freggi, 2024, Table 1; Seminoff, 2023; Wallace et al., 2013; Whilde et al., 2024; Wibbels & Bevan, 2019; Yetsko et al., 2020). Monitoring methods of FP and its putative etiological agent, alpha chelonid herpesvirus 5 (ChHV5), suffer from sparse, potentially biased, geographically limited, and unhomogenised approaches. The sound and transparent cooperation of the international community, away from financial conflict of interests and professional rivalry undermining sea turtle species conservation efforts, is essential to survey the disease and research for management actions to efficiently mitigate the dissemination of ChHV5 within and across sea turtle species, at the global scale (One Health High-Level Expert Panel (OHHLEP) et al., 2022; Saladin & Freggi, 2024; Whilde et al., 2024; Yetsko et al., 2020). We aim to clarify contradicting definitions of sea turtle fibropapillomatosis in the peer-reviewed literature, and to integrate novel research findings into a recommendation of consensus definition of the disease. This was done in the context of the international scientific forum of IUCN SSC MTSG Task Force on sea turtle fibropapillomatosis, although this communication does not represent an IUCN position statement, scientific experts expressed their professional opinions. Our objective is to provide precise recommendations of actions for the enhancement of standardized and transparent data collection to create a register of sea turtle fibropapillomatosis clinical cases and detection ratios of ChHV5, for all seven species of sea turtles globally, under the World Organisation for Animal Health (WOAH)'s governance (Mashkour et al., 2020; Whilde et al., 2024; World Organization for Animal Health [WOAH], 2023; Yetsko et al., 2020).

MATERIALS AND METHODS

During the scientific forum of IUCN SSC MTSG Task Force on sea turtle fibropapillomatosis (FPTF) in 2023 and subsequent reviews during 2024, scientific experts researched existing peer reviewed and gray literature documents relevant to drafting the consensus case definition of FP. In doing this, we took into consideration the geographical representativeness and reproducibility of reported and published studies. Our level of confidence of research findings is reported by indicating a (*very low*), (*low*), (*medium*), (*high*), (*very high*), or (*virtually certain*) level of confidence, which were adapted from the Intergovernmental Panel on Climate Change (IPCC) assessment reports (Cooley et al., 2022; Costello et al., 2022; IPCC Annex V, 2022; Mycoo et al., 2022; Parmesan et al., 2022). As reptiles are animals relevant to WOAH's Terrestrial Animal Health Code, results of our review are presented to precisely highlight the main characteristics of sea turtle fibropapillomatosis for the implementation of a universal reporting protocol. We apply the World Organisation for Animal Health (WOAH) standard operating procedure to assess a pathogenic agent of terrestrial animals against listing criteria of WOAH's Terrestrial Animal Health Code (OIE 2020; WOAH, 2023, Chapter 1.2.).

Practitioner points

- Sea turtle fibropapillomatosis (FP) is an emerging terrestrial and aquatic viral neoplastic disease involving cancerous genomic pathways, for which the diagnosis is pathognomonic upon the visual examination of a tumoral syndrome affecting a sea turtle.
- We recommend a universal transparent intergovernmental surveillance strategy of ChHV5 under the World Organisation for Animal Health (WOAH) governance, integrating standardized monitoring practices of FP in sentinel bays.
- Management actions to mitigate ChHV5's spread can include the creation of new marine protected areas (MPAs) or the implementation of reinforced conservation and biosecurity measures in existing MPAs.

RESULTS

Clinical characterization

Sea turtle' FP is clinically characterized by a potentially lethal tumoral syndrome, severely impairing sea turtles biological functions and ecological roles (*virtually certain*) (Jones et al., 2016; Manes, Carthy, et al., 2023). FP tumors are most commonly visible during a direct clinical examination and observed affecting the skin, oral and ocular mucosa, carapace and plastron of juvenile sea turtles, although FP tumors may also affect adult sea turtles (*virtually certain*) (Hargrove et al., 2016; Jones et al., 2016; Manes, Herren, et al., 2023; Page-Karjian et al., 2014). Internal FP tumors of sea turtles may affect their vital organs—(heart, lungs, kidneys)—, invade the coelomic cavity or the bones (*virtually certain*) (Hargrove et al., 2016; Norton et al., 1990; Stacy et al., 2017). There is an absence of reports of coelomic or bony FP tumors affecting sea turtles that are not impacted by skin tumors (*virtually certain*) (Ariel et al., 2017; Hargrove et al., 2016; Jones et al., 2016; Norton et al., 1990; Smith & Coates, 1938; Stacy et al., 2017; Work et al., 2004; Yetsko et al., 2021). Based on veterinary reports of sea turtle strandings, total area of skin/mucosa, and coelomic FP tumors increase with increasing straight carapace length (SCL), hence visceral and bony tumoral lesions are described to afflict mainly larger sea turtles, which may also be affected by a severe burden of skin tumors (*very high confidence to virtually certain*) (Hargrove et al., 2016; Herbst, 1994; Jones et al., 2016; Smith & Coates, 1938; Work et al., 2004; T.M. Norton pers. comm.). A tropism to particular organs may be dependent on geographic location (*low to medium confidence*) (Work et al., 2004). FP tumors may present

infiltrating macroscopic features towards adjacent tissues, and can, in particular, invade the eyes or bones of a sea turtle (*virtually certain*) (Work et al., 2004; B. Stacy pers. comm.). The clinical severity of FP can be characterized by scoring the tumor burden of a sea turtle (see the protocols described in Manes, Herren, et al., 2023; Page-Karjian et al., 2014, 2019; Rossi et al., 2016; Work & Balazs, 1999). Based on tumor scoring systems, there is strong evidence that severe disease leads to immunosuppression and complications such as emaciation or secondary bacterial infections (*virtually certain*) (Jones et al., 2016; Nash & Ryan, 2023; Perrault et al., 2021; Zwarg et al., 2014). Sea turtles afflicted with FP may exhibit a range of nonspecific anomalies in their blood profiles. These can include severe aregenerative anemia, variations of white blood cell count either as leukopenia or leukocytosis, increased levels of uric acid (hyperuricemia), elevated serum aspartate aminotransferase (AST), and a ionogram imbalance marked by low calcium (hypocalcemia) levels and high phosphate (hyperphosphatemia) levels. Additionally, bacteraemia attributed to immunosuppression, may be associated with the most severe clinical cases of the disease (*high confidence*) (Aguirre & Balazs, 2000; Norton et al., 1990; Work & Balazs, 1999; Yetsko et al., 2021; Zwarg et al., 2014; T.M. Norton pers. com.; B. Stacy pers. com.; D. Wrobel Goldberg pers. comm.).

Etiology—Epidemiology

FP is a significant seasonal disease to sea turtle species presenting neoplastic contagious and transboundary characteristics, affecting terrestrial and marine ecosystems worldwide. All seven species of sea turtles at all life stages including egg clutches, hatchlings and nesting sea turtles, recognized by the IUCN Red List as ranging from vulnerable to critically endangered, are at potential risk: *C. caretta*, *E. imbricata*, *C. mydas*, *D. coriacea*, *N. depressus*, *L. olivacea* and *L. kempii* (*very high confidence to virtually certain*) (Abreu-Grobois et al., 2008; Aguirre & Lutz, 2004; Ariel et al., 2017; Casale & Tucker, 2017; Dujon et al., 2021; Farrell et al., 2021; 2022; Hargrove et al., 2016; Herbst, 1994; Herbst et al., 1995; James et al., 2021; Jones et al., 2016; Li et al., 2017; Manes, Carthy, et al., 2023; Mashkour et al., 2020; Mortimer et al., 2008; Origlia et al., 2023; Red List Standards & Petitions Subcommittee, 1996; Robben et al., 2023; Seminoff, 2023; Stacy et al., 2017; Wallace et al., 2013). Juvenile *C. mydas* are the species and life stage reported as the most affected by FP, the disease has reached a panzootic status in *C. mydas* populations in the 1990s (*virtually certain*) (Duffy et al., 2018; Ene et al., 2005; Hargrove et al., 2016; Herbst, 1994; Jones et al., 2016; Nash & Ryan, 2023; Norton et al., 1990; Page-Karjian et al., 2014; Williams et al., 1994; Work et al., 2004).

FP is a complex multifactorial disease, strongly associated with the presence, and with the viral and immune response signaling dynamics of oncogenic Scutavirus chelonid alphaherpesvirus (ChHV5), subfamily *Alphaherpesvirinae,* in FP tumors (*very high confidence to virtually certain*) (Greenblatt et al., 2005; Herbst, 1999; Herbst et al., 1995; Lafferty, 2009; Burge et al. 2014; Dujon et al., 2021; Manes, Carthy, et al., 2023; Mashkour et al., 2021; Patricio et al., 2012; Whitmore et al., 2021; Yetsko et al., 2020). In FP-affected sea turtles, characteristic intranuclear viral inclusions indicative of herpesvirus infection can be observed in the epidermis and dermis using light and electron microscopy. The presence of ChHV5 may be concomitantly confirmed via in situ hybridization, immunohistochemistry, and/or molecular assays of FP tumor samples, FP tumored sea turtles seldomly showing an absence of infection by ChHV5 (Greenblatt et al., 2005; James et al., 2021; Loganathan et al., 2021; Mashkour et al., 2021; Matushima et al., 2001; Origlia et al., 2023; Whitmore et al., 2021; Work et al., 2009, 2015, 2017, 2020). Oncogenic ChHV5 can asymptomatically infect all species of sea turtles at all life stages, with transcriptionally active viral loads in nontumoral tissues (Alfaro-Nunez et al., 2014; Blackburn et al., 2021; Farrell et al., 2021, 2022; Loganathan et al., 2021; Page-Karjian et al., 2012; Quackenbush et al., 2001). *C. mydas* and *C. caretta* papillomavirus (CmPV1 and CcPV1), retrovirus, tornovirus 1 (STTV1), or a co-occurrence of CmPV1 and ChHV5, have been found in sea turtles affected by FP tumors and in healthy tissue samples of FP-afflicted sea turtles, without a clear correlation with FP (*medium confidence*) (Mashkour et al., 2020, 2021). FP is an infectious contagious viral disease, as evidenced by transmission in captive settings and experimental studies (*virtually certain*) (Greenblatt et al., 2004; Herbst, 1999; Herbst et al., 1995; Work et al., 2009, 2015, 2017). In the wild, transmission of ChHV5 probably occurs horizontally at foraging grounds through the water column (*high to very confidence*), or by direct contact (*high to very confidence*) (Herbst, 1999; Farrell et al., 2022; Jones et al., 2020; Lockley et al., 2020; Page-Karjian et al., 2022; Patricio et al., 2012). FP is also suspected to be transmissible by vectors such as marine leeches of the genus Ozobranchus (*medium to high confidence*) (Dujon et al., 2021; Farrell et al., 2021; 2005 Greenblatt et al., 2004; Jones et al., 2021; Lockley et al., 2020; Page-Karjian et al., 2020), spirorchid trematodes (*low to medium confidence*) (Norton et al., 1990; Herbst, 1994; Matushima et al., 2001; Work et al., 2004; Zwarg et al., 2014), cleaner fish, or saddleback wrasse *Thalassoma duperrey* (*low to medium confidence*) (Dujon et al., 2021; Jones et al., 2016). Contradicting studies exist concerning a secondary route of infection involving a vertical transmission of ChHV5, from sea turtle "parents" to egg clutches. The presence of ChHV5 has been detected in hatchlings through PCR assays, as well as in the environmental DNA (eDNA) analysis of sand from nesting areas and among hatchlings (*high to very high confidence*) (Farrell et al., 2022; Jones et al., 2020; Page-Karjian et al., 2022; Parmesan et al., 2022). Oncogenic ChHV5 is therefore, potentially affecting terrestrial ecosystems that are sea turtles' nesting sites (*high to very high confidence*) (Christiaanse et al., 2024; Farrell et al., 2022; Page-Karjian et al., 2022; Parmesan et al., 2022). In vitro culture of ChHV5 was recently achieved by replicating

the complex three-dimensional structure of sea turtle skin (Work et al., 2017). Elements of immunological proof of causation criteria have not been met (See Evans, 1976, Table 6). A serological response of sea turtles to ChHV5 infection occurs regardless of life stage or tumor status, and may be correlated with the causative ChHV5 viral strain in enzootic areas (*medium to high confidence*) (Evans, 1976; Farrell et al., 2022; Page-Karjian et al., 2020, 2022; Perrault et al., 2021; Work, 2020; Yetsko et al., 2020). Together, the Henle-Koch postulates are considered to not yet have been fulfilled to conclusively demonstrate a causative relationship between oncogenic ChHV5 infection and sea turtle fibropapillomatosis clinical symptoms (*virtually certain*) (Ariel et al., 2017; Blackburn et al., 2021; Evans, 1976; Farrell et al., 2021; Herbst et al., 1995; James et al., 2021; Jones et al., 2016; Matushima et al., 2001; Origlia et al., 2023; Rivers, 1937; Stacy et al., 2017; Work et al., 2017).

From an epidemiological perspective, the emergence and spread of FP in the beginning of the 20th century was reported from two distinct marine hot spots in the Northern Atlantic Ocean and in the South China Sea, occurring within a same sea turtle generation timeline (*very high confidence to virtually certain*) (Hendrickson, 1958; Smith & Coates, 1938). FP prevalences increased in 1980s (especially in *C. mydas* populations), due to the highly migratory nature of sea turtle species, to Ocean circulation and global hydrological cycle changes which shift the connectivity of sea turtle populations, and to the spread of infectious diseases globally in the Anthropocene epoch (*high to very high confidence*) (Burge & Hershberger, 2020; Cooley et al., 2022; Dujon et al., 2021; Lafferty, 2009; Manes, Carthy, et al., 2023; Norton et al., 1990; Parmesan et al., 2022; Simantiris, 2024; Work et al., 2004). Climate induced terrestrial and oceanic physical and chemical disruptions have impacted the Earth's systems since 1800s, shifting species geographic ranges and altering the timing of seasonal life events (*high to very high confidence*) (Aguirre & Lutz, 2004; Cooley et al., 2022; Costello et al., 2022; Du et al., 2019; IPCC Annex V, 2022; Manes, Carthy, et al., 2023; Manes et al., 2022; Mycoo et al., 2022; Parmesan et al., 2022). Climate-induced oceanic physical and chemical changes can be significantly correlated to the emergence and spread of FP. Increased and varying sea surface temperatures induce a thermal stress to ectothermic sea turtles, reduce thermal refugia, and disbalance sea turtle lymphoid structures' seasonal immune response to infectious threats (spleen and thymus). Disrupted salinity gradients alter osmoregulatory biological functions of sea turtles and higher mean photo-irradiances also impact sea turtle populations globally (*medium to high confidence*) (Bass, 2006; Cooley et al., 2022; Du et al., 2019; Duffy et al., 2018; Dujon et al., 2021; Hazel et al., 2009; Herbst, 1994; IPCC Annex V, 2022; López-Castro et al., 2013; Manes, Carthy, et al., 2023; Manes et al., 2022; Mycoo et al., 2022; Nash & Ryan, 2023; Reina & Cooper, 2000; Yetsko et al., 2021). *C. mydas* FP panzootic might be correlated to a reduced phenotypic and adaptive physiological plasticity of juvenile *C. mydas* under rapid climate change. Reduced adaptive possibilities of *C. mydas* turtles may be due to a lower immunogenomic repertoire compared to other sea turtle species, a higher sensitivity to disrupted salinity gradients and their related climatic oceanic processes, and a higher sensitivity of green turtles' skin tissue to photo-irradiance and to cytotoxic trace metallic elements (*low to medium confidence*) (Cooley et al., 2022; Dogruer et al., 2021; Du et al., 2019; Duffy et al., 2018; Finlayson et al., 2019; Fusco & Minelli, 2010; Hazel et al., 2009; IPCC Annex V, 2022; Manes, Carthy, et al., 2023; Manes et al., 2022; Martin et al., 2022; Nash & Ryan, 2023; Reina & Cooper, 2000; Stiebens et al., 2013). The hypothesis that a shift of virulence and/or a range shift of ChHV5 and/or its possible vectors, has been triggered by the terrestrial and oceanic impacts of climate change is supported by the fact that ChHV5 has been chronically asymptomatically infecting sea turtles since 300 million years. It is thought the most recent common ancestor of the actual ChHV5 variants infecting sea turtle populations globally exists since 193–430 years (*medium to high confidence*) (Alfaro-Nunez et al. 2014; Burge & Hershberger, 2020; Cooley et al., 2022; Du et al., 2019; Evans, 1976; Greenblatt et al., 2005; Herbst et al., 2004; IPCC Annex V, 2022; Jones et al., 2016, 2020; Lafferty, 2009; Lockley et al., 2020; Mycoo et al., 2022; Nash & Ryan, 2023; Page-Karjian et al., 2014, 2020; Patricio et al., 2012). Furthermore, there also exists a risk of shift of the terrestrial biome of sea turtles clutches under climate induced increased sand temperatures and humidity, triggering the activation or increased virulence of a latent ChHV5 infection of sea turtles' egg clutches (*low to medium confidence*) (Christiaanse et al., 2024; Farrell et al., 2021, 2022; Jones et al., 2020; Mashkour et al., 2020; Page-Karjian et al., 2022; Parmesan et al., 2022; Yetsko et al., 2020).

Physiological and ethological characteristics of *C. mydas* turtles might also explain higher FP occurrence and prevalence ratios in the species. *C. mydas* sea turtles spend most of their lives in coastal and nearshore marine areas which tend to be more polluted and have higher human activity levels than open oceans (*high to very high confidence*) (Aguirre & Lutz, 2004; Arthur et al. 2006, 2008; Cooley et al., 2022; Costello et al., 2022; Dogruer et al., 2021; Du et al., 2019; Dujon et al., 2021; Ene et al., 2005; Finlayson et al., 2019; IPCC Annex V, 2022; Jones et al., 2016; Lafferty, 2009; Manes, Carthy, et al., 2023; Manes et al., 2022; Monteiro et al., 2021; Mycoo et al., 2022; Parmesan et al., 2022; Pierce & Henry, 2009; Russet-Rodríguez et al., 2021; Yetsko et al., 2021). FP epizootic in juvenile sea turtle populations occurs during their recruitment at neritic shores affected by anthropogenic and climate change alterations (*high to very high confidence*) (Cooley et al., 2022; Ene et al., 2005; IPCC Annex V, 2022; Mycoo et al., 2022; Nash & Ryan, 2023; Page-Karjian et al., 2014). Changed or degraded nearshores environmental conditions can increase exposure levels of *C. mydas* to toxins, pollutants, and infectious agents as oncogenic ChHV5, and trigger an impaired immune response inducing the clinical expression of FP lesions in asymptomatic ChHV5 carriers (*high to very high confidence*) (Aguirre & Lutz, 2004; Arthur et al., 2006, 2008; Burge & Hershberger, 2020; da Silva et al., 2016; Dujon et al., 2021; Hazel et al., 2009; Manes, Carthy, et al., 2023; Manes et al., 2022; Martin et al., 2022; Nash & Ryan, 2023; Nelson

et al., 2013; Parmesan et al., 2022; Santos et al., 2011; Work et al., 2020; Yetsko et al., 2021). The feeding behavior and diet of *C. mydas* including seagrasses and algae found in coastal areas also increase their exposure to pathogens and eutrophic environmental conditions conducive to the clinical expression of FP (*high confidence*) (Aguirre and Lutz, 2004; Arthur et al., 2006, 2008; Dujon et al., 2021; Jones et al., 2016; Manes, Carthy, et al., 2023; Manes, Herren, et al., 2023; Nelson et al., 2013; Santos et al., 2011; Van Houtan & Hargrove, 2010; Van Houtan et al., 2014; Yetsko et al., 2021). A shift of marine reefs environment from coral dominated to algae dominated might be implicated in the pathogenesis and/or spread of FP (*low to medium confidence*) (Cooley et al., 2022; Nelson et al., 2013). Ocean warming induces mass coral reef bleaching events and coral disease outbreaks while Ocean's acidification decreases rates of calcification of corals and other calcifying reef organisms. These oceanic climate stressors reduce coral settlement and increase bioerosion and dissolution of reef substrates, while algae are more climate stressors-resilient species (*high to very high confidence*) (Cooley et al., 2022). An increase in macroalgae coverage of coastal shores might not be directly correlated to their eutrophication levels (*low to medium confidence*) (Cooley et al., 2022; Ramseyer et al., 2021). Macroalgae mainly present many phytopharmaceutical potentials, as antioxidant, antitumor, antiviral, anti-inflammatory, or antiinfectious activities. The phytopharmaceutical properties of the brown macroalgae Dictyota or the noncalcareous macroalgae Caulerpa for instance, are due to their high contents in medicinal phytochemicals: three types of cyclic diterpenes—(xenicanes, extended sesquiterpenes and dolabellanes)—, and sulfated polysaccharides such as fucans and fucoidans (*high to very high confidence*) (Nelson et al., 2013; Paul & Hay, 1986; Ramseyer et al., 2021; Rushdi et al., 2022; Saladin, 2021; J. Chalifour pers. comm.). Harmful red algae blooms that may be composed of toxic dinoflagellate Prorocentrum spp. producing okadaic acid, *Lyngbya majuscula* cyanobacteria, or *Karenia brevis* producing polyether neurotoxins, may be directly and/or indirectly involved in FP tumors formation (*low to medium confidence*) (Arthur et al. 2006, 2008; Dujon et al., 2021; Jones et al., 2016; Manes et al., 2022; Pierce & Henry, 2009). Invasive macroalgae outbreaks of *Hypnea musciformis* and *Ulva fasciata* might trigger herpesvirus infections within herbivorous species due to their ability to store environmental nitrogen as arginine, an essential amino-acid able to facilitate the formation of tumors through the activation of oncogenic ChHV5 (*low to medium confidence*) (Van Houtan & Hargrove, 2010; Van Houtan et al., 2014).

Studies of the etiology and environmental drivers triggering the clinical expression of FP are inconclusive (*virtually certain*) (Dujon et al., 2021; Jones et al., 2016; Manes, Carthy, et al., 2023).

Diagnosis

The diagnosis of a clinical case of the verrucous form of FP is pathognomonic upon the physical examination of a sea turtle affected by a tumoral syndrome of the skin and/or mucosa (*virtually certain*) (Hargrove et al., 2016; Jones et al., 2016; OIE 2021; T.M. Norton pers. comm.). Standardized noninvasive visual in-water monitoring of sea turtles therefore can allow the epidemiologic survey of the occurrence and prevalence of the verrucous form of FP in coastal marine areas (*very high confidence to virtually certain*) (Hancock et al., 2023). The effectiveness of surveys for FP monitoring is contingent on the quality and precision of underwater photographs acquired during field surveys. Photographs must be detailed enough to facilitate a thorough clinical examination of the encountered sea turtles. Additionally, the capture-mark-recapture technique (CMR) applied to a representative sample of a sea turtle population in sentinel bays represents a standardized approach to monitor the occurrence and prevalence of the verrucous form of sea turtle fibropapillomatosis and to determine the infection by, and exposure rate to, FP's putative causative agent, oncogenic ChHV5, of a sea turtle population (*virtually certain*) (Ene et al., 2005; Jones et al., 2020; Loganathan et al., 2021).

The diagnosis of an unspecific beginning skin lesion of a sea turtle—a plaque, erythematous, ulcerative or necrotic skin lesion—includes the differentiation from Gray Patch disease, Lung-Eye-Tracheal disease (with etiological agents ChHV1 and ChHV6, respectively), loggerhead genital respiratory disease, loggerhead orocutaneous disease, CmPV1, CcPV1, *Ozobranchus* spp., bacterial, and fungal dermatitis (including *Fusarium* spp. or *Vibrio alginolyticus* infections) and traumatic skin lesions (*high to very high confidence*) (Jones et al., 2016; Manire et al., 2008; Mashkour et al., 2020; Page-Karjian et al., 2020). A biopsy with histopathology is necessary and sufficient to diagnose a beginning skin lesion of a sea turtle as FP at plaque stage. A PCR analysis detection of ChHV5 from a sea turtle's skin biopsy can further confirm the identification of an FP lesion at plaque stage, although a negative result at the detection of ChHV5 PCR assay does not exclude an early FP stage (*very high confidence to virtually certain*) (Manire et al., 2008; Matushima et al., 2001; T.M. Norton pers. comm.). Diagnosis of bones and coelomic tumors in live sea turtles necessitates technical resources such as computed tomography (CT) scan, coelioscopy, ultrasound, or X-rays in severe cases. Internal tumors of deceased sea turtles can be detected during necropsy.

Histopathological characterization

Skin and mucosa FP tumors have been histologically characterized as benign fibroepithelial tumors that on microscopy consist of a fibroblast-rich collagenous matrix overlaid by orthokeratotic hyperkeratotic epidermis with occasional epidermal inclusions (*virtually certain*) (Ariel et al., 2017; James et al., 2021; Jones et al., 2016; Loganathan et al., 2021; Smith & Coates, 1938; Zwarg et al., 2014; T. Work pers. comm.). Coelomic and oral tumors have been classified as fibromas, myxofibromas, or fibrosarcomas of low-grade malignancy (*very high confidence*) (Jones et al., 2016; Norton et al., 1990; Work et al., 2004; Yetsko et al., 2021; T. Work pers. comm.).

Molecular genomic characterization of FP tumors

Although skin and mucosa FP tumors have mainly been reported as histologically benign lesions, recent gene expression studies revealed skin and coelomic fibropapilloma tumors present cross-species conserved oncogenic signaling pathways with human cancers, in particular with human basal cell carcinoma and "Kaposi sarcoma-associated herpesvirus infection" (*very high confidence*) (Blackburn et al., 2021; Duffy et al., 2018; Li et al., 2023; Yetsko et al., 2020, 2021). Metastatic molecular signaling pathways may be activated from all types of FP tumors, external and visceral, with kidney FP tumors showing a more severe metastatic pathway activation than skin FP tumors (*very high confidence*) (Yetsko et al., 2020, 2021). Robust laboratory PCR assays may detect oncogenic ChHV5 genetic material (-DNA or mRNA transcripts of ChHV5-) in FP tumors or healthy tissues samples of sea turtles (*virtually certain*) (Ariel et al., 2017; Blackburn et al., 2021; Farrell et al., 2021; Greenblatt et al., 2005; Work et al., 2009, 2015, 2017, 2020; Stacy et al., 2017). We recommend the development of a standardized PCR assay for the detection of ChHV5 and FP associated viruses for the implementation of a universal monitoring of the disease (OIE 2020; Okoh et al., 2023; WOAH, 2023; Yetsko et al., 2020; K. Jones pers. comm.; E. Labatisda Estrada pers.comm.). The ChHV5 genome has been entirely characterized and is available on GenBank through the accession number deposited as GenBank HQ878327 (Ackermann et al., 2012). Four distinct clades of ChHV5 variants are described at the global level—Eastern Pacific, Midwest Pacific, Western Atlantic and Eastern Caribbean, and Atlantic—(Greenblatt et al., 2005; Jones et al., 2020; Patricio et al., 2012; Whitmore et al., 2021), with possibly more localized phylogeographic variants of ChHV5 and a strong geographic influence on ChHV5 phylogeny, genetically diverse variants of ChHV5 sometimes co-infecting the same individual sea turtle (*high to very high confidence*) (Ene et al., 2005; Greenblatt et al., 2005; Jones et al., 2020; Patricio et al., 2012; Rodenbush et al., 2014; Whitmore et al., 2021).

Perspectives for treatment and prophylaxis

The natural regression of FP tumors has been consistently documented in the literature, independent of time or age class (*virtually certain*), and may be explained by the acquisition of an individual sea turtle immunity (*medium to high confidence*) (Guimarães et al., 2013; Hargrove et al., 2016; Manes, Herren, et al., 2023; Nash & Ryan, 2023; Page-Karjian et al., 2014; Patricio et al., 2016; Perrault et al., 2021; Work et al., 2020; Yetsko et al., 2021). The development of a cell or humoral immunity in a sea turtle population can explain a decrease in FP prevalence ratios in monitored bays (*medium to high confidence*) (Hargrove et al., 2016; Perrault et al., 2021; Work et al., 2020). Rescue, rehabilitation, and release of FP-affected sea turtles involves the surgical removal of tumors from the skin/mucosa (Burkhalter & Norton, 2019; Page-Karjian et al., 2014; Stacy et al., 2017). Precision oncogenic medicine has also been recently added to the therapeutic arsenal against FP (Burkhalter & Norton, 2019; Donnelly et al., 2019; Duffy et al., 2018). In vitro culture of ChHV5 was recently achieved by replicating the complex three-dimensional structure of sea turtle skin (Work et al., 2017), opening the path of FP prophylaxis research.

DISCUSSION

This work summarizes the many scientific perspectives of terrestrial and aquatic sea turtle fibropapillomatosis to recommend a consensus definition of the disease. Based on passive and targeted monitoring of sea turtle populations and robust PCR assays methods, sea turtle fibropapillomatosis is an infectious terrestrial and aquatic disease of which ChHV5 is the specific related pathogen. The disease has been reported to have superspread across sea turtles' migratory paths to new geographical areas since the beginning of the 20th century, likely due to the highly migratory nature of sea turtle species and climate-induced changes in sea turtle populations' oceanic connectivity. Zones considered free of FP clinical cases include for instance the Mediterranean Sea, the Persian Gulf, or the Seychelles. ChHV5 has nonetheless been detected in two marine areas where no clinical cases of FP were observed: the Mediterranean Sea and the Persian Gulf (WOAH Terrestrial Code Chapter 1.4. 2023; see Saladin & Freggi, 2024, Table 1). ChHV5 significantly affects all keystone species of sea turtles at all life stages and their ecological roles worldwide. We also integrate to our results the recent discovery of cancerous and metastatic molecular transmission pathways of the disease, analogous to those of a human basal cell carcinoma. Taking into account the facts that ChHV5 is the pathogen specifically related to FP clinical cases, that the virus does not occur in any other disease, and was recently cultured in vitro, we observe the Koch-Henle postulates as published in Evans, 1976 identifying ChHV5 as the etiological agent of FP are close to being met (See Evans, 1976, Table 1; Herbst, 1994 Work et al., 2017). Elements of immunological proof of causation criteria relevant to FP etiology, pathogenesis, and immunogenetic adaptation mechanisms of sea turtle populations to ChHV5 infection are persistent scientific knowledge gaps (see Evans, 1976, Table 6). The virus has been chronically infecting sea turtle populations, which renders difficult the study of the immunological dynamic of sea turtles to the ChHV5 infection threat in the wild. FP is complex, adding to the elusive nature of sea turtle species. We consider that Rivers alerted there might be "no rigid criteria" and that "to obtain the best results, however, this insecurity must be tempered by the priceless attributes of common sense, proper training and sound reasoning." We also recall unified criteria 10 of Evans, 1976 that, overall, "The whole thing should make biologic and epidemiologic sense" (Rivers, 1937;

see Evans, 1976, Table 13). Global sea turtle health can benefit from a standardized and transparent register of FP clinical cases occurrence, prevalence ratios, and ChHV5 detection ratios in sentinel bays. We therefore propose the listing of ChHV5 in WOAH's Terrestrial Code.

We hypothesize a reduced phenotypic plasticity of ectothermic sea turtles in response to rapid climate change may be involved in the pathogenesis of FP. The regression of the disease has been observed in some marine areas, suggesting a relative phenotypic and adaptive physiological plasticity, and a possible genetic accommodation of the species *C. mydas* (Fusco & Minelli, 2010). Sea turtles are reportedly impacted by sea surface temperatures and oceanic isotherms anomalies, oceanic stratification, reduced thermal refugia, ocean deoxygenation reducing their thermal tolerance, by a disruption of salinity gradients altering osmoregulation mechanisms, and by an increased photo-irradiance. Cumulative climate forcings may induce a lower immunity level and trigger an increased or varying metabolism activating a latent oncogenic ChHV5 infection in ectothermic sea turtle populations, especially in those also confronted with anthropogenic marine pollutants. A role of climate altered terrestrial and oceanic physico-chemical factors in the pathogenesis of FP has rarely been assessed (Burge & Hershberger, 2020; Christiaanse et al., 2024; Cooley et al., 2022; Costello et al., 2022; Dogruer et al., 2021; Du et al., 2019; Duffy et al., 2018; Dujon et al., 2021; IPCC Annex V, 2022; Jones et al., 2016; Manes, Herren, et al., 2023; Manes et al., 2022; Mycoo et al., 2022; Nash & Ryan, 2023; One Health High-Level Expert Panel (OHHLEP) et al., 2022; Parmesan et al., 2022; Reina & Cooper, 2000; Simantiris, 2024).

Sea turtle populations' immunogenetic adaptation to oncogenic ChHV5 infection within and across species is a scientific gap essential to be addressed. Gaps in knowledge about the disease include the following: the dynamic of the seroepidemiological response of sea turtle species to ChHV5 infection threat; the allelic diversity for genes of the major histocompatibility complex (MHC) within and across sea turtle species; the immune-related and apoptotic-related genes responses to oncogenic ChHV5 infection and environmental stressors; and the seasonal involution of sea turtles' lymphoid structures under rapid climate change (Evans, 1976; Blackburn et al., 2021; Farrell et al., 2021; Herbst, 1994; Martin et al., 2022; Nash & Ryan, 2023; Page-Karjian et al., 2022; Stiebens et al., 2013; Yetsko et al., 2021). The terrestrial impact of oncogenic ChHV5 at sea turtle nesting sites is also a significant scientific gap that needs to be addressed, via for instance the noninvasive technique of monitoring of the presence of ChHV5 environmental DNA (Farrell et al., 2022; Yetsko et al., 2020).

Historically, the World Organisation for Animal Health is the global veterinary authority who has been managing epizootic threats to the health of domestic and wild animal species. WOAH has been implementing targeted surveillance and management measures of animal pathogens at a global intergovernmental level for over a hundred years. For instance, *Batrachochytrium salamandrivorans* (*Bsal*) was assessed against listing criteria of the Aquatic Code in 2016 and an updated assessment in 2017 concluded *Bsal* met WOAH's criteria for listing. *Bsal* is a novel chytrid fungus that has infected fire salamanders *Salamandra salamandra* in the Netherlands since 2013 and that may affect several susceptible amphibian species (WOAH, 2024). *Bsal* is causing a serious threat to native *S. salamandra* population in the Netherlands and would have a significant detrimental effect in native fire salamanders population if the pathogen was introduced via the international trade: the fungus reduced the free-living fire salamander population of the Netherlands by 96% between 2010 and 2013 as a result of the unregulated international trade in salamanders (WOAH, 2024; OIE, 2016, see Annex 29; OIE, 2017, see Annex 29; Re:Wild, 2023; V.T. Grillo pers. comm.).

Concerning ChHV5, complementary and inclusive of specific research on sea turtle fibropapillomatosis, we also propose the creation of WOAH working group on sea turtle fibropapillomatosis. Veterinary, environmental, and interdisciplinary management actions can be catalyzed via WOAH's reinforced intergovernmental cooperation on FP: the identification of new marine protected areas and the implementation of reinforced area-based conservation and biosecurity measures in existing marine protected areas may be discussed (OHHLEP et al., 2022; Saladin & Freggi, 2024; Sustainable Development Goal [SDG] 13 "Climate Action," SDG 14 "Life below water" [United Nations, 2024] and SDG 15 "Life on land"; OHHLEP et al., 2022; United Nations Ocean Conference [UNOC, 2022]). Innovative and universal management actions are essential to efficiently contribute to the natural recovery from sea turtle fibropapillomatosis neoplasms of sea turtle coastal populations.

AUTHOR CONTRIBUTIONS

Claire Saladin: Conceptualization (lead); data curation (lead); formal analysis (lead); methodology (lead); writing—original draft (lead); writing—review and editing (lead); validation (lead). **Daniela Freggi**: Data curation (supporting); formal analysis (supporting); methodology (supporting); validation (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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