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Erysipelas with preferential brain and skin involvement in a Mediterranean bottlenose dolphin *Tursiops truncatus*

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ABSTRACT: Infections by *Erysipelothrix rhusiopathiae* occur in domestic animals and cause the disease known as 'erysipelas'. The ubiquity of *Erysipelothrix* spp. makes infection possible in a wide range of vertebrates and invertebrates. Cetaceans are highly susceptible to erysipelas, especially those under human care. The number of cases documented in wild cetaceans is low, the pathogenesis is incompletely understood, and the full spectrum of lesions is not well defined. The possible serotypes and species of the genus that can cause disease are unknown. In October 2022, a common bottlenose dolphin *Tursiops truncatus* stranded in Vilassar de Mar (Catalonia) showing skin lesions consistent with 'diamond skin disease', a characteristic lesion of erysipelas shared by swine and cetaceans. Necropsy was performed following standardized procedures, and multiple samples were taken for histopathology and bacteriology. *Erysipelothrix* sp. grew in pure culture in many tissue samples. Genetic characterization by multi-locus sequence analysis identified the species as *E. rhusiopathiae*. Histologically, the main lesions were an intense suppurative vasculitis of leptomeningeal arteries and veins with abundant intramural Gram-positive bacilli and meningeal hemorrhages. Meningeal lesions were considered the cause of death. The affected skin showed moderate suppurative dermatitis. Herein we document a case of erysipelas in a Mediterranean common bottlenose dolphin with unusual lesions in the leptomeningeal vessels and marked skin tropism. To our knowledge, this is the first case of severe brain involvement in erysipelas in a cetacean. We also provide a review of available cases in wild cetaceans, to highlight the characteristics of the disease and improve future diagnosis.

KEY WORDS: Erysipelas · *Erysipelothrix* · Cetacean · Septicemia · Vasculitis · Diamond skin · Necropsy · Strandings

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1. INTRODUCTION

Infections by *Erysipelothrix rhusiopathiae* occur in domestic animals such as swine, poultry and small ruminants (Wang et al. 2010, 2021). The disease known as 'erysipelas' is well-known in swine (Oppriesnig & Coutinho 2019). In domestic pigs, *E. rhusiopathiae* is carried subclinically in tonsils, bone marrow, intestine and gallbladder with a high prevalence (Stephenson & Berman 1978, Takahashi et al. 1999, Wang et al. 2010, Craig et al. 2016). Stressing factors allow for entry, multiplication and dissemination of bacteria, leading to septicemia and, in some acute cases, sudden death (Wang et al. 2010). Hemorrhagic and necrotizing skin lesions are a common feature of erysipelas, and their characteristic quadrangular or rhomboidal shape, when present, allow for identification of the condition, called 'diamond skin disease' (Torrison & Cameron 2019). Whether these lesions are present in acute, subacute or chronic forms, and whether septicemia is required for its development, remains in discussion. Embolic nephritis and fibrinous polyarthritis are frequently seen in swine as a consequence of septicemia (Oppriesnig & Coutinho 2019). Chronic infections may also develop in pigs, and manifest as a persistent fibrinous polyarthritis and/or vegetative endocarditis (Wang et al. 2010, Craig et al. 2016). Endocarditis caused by *E. rhusiopathiae* is reported in dogs and sheep (Aslani et al. 2015, Nielsen et al. 2018, Cabrera-García et al. 2020). In sheep, percutaneous/umbilical entry causes localized skin lesions, and the bacteria may spread hematogenously and lead to a subacute or chronic fibrinopurulent polyarthritis, which is relatively common in lambs (Craig et al. 2016). Any avian species may be affected by *E. rhusiopathiae*, but the disease is most serious in turkeys, which develop cyanosis, muscle hemorrhages, diarrhea and death (Wang et al. 2010) and, in chronic cases, endocarditis (Bobrek et al. 2013). In humans, *E. rhusiopathiae* causes an occupational zoonosis, usually as a localized skin lesion called 'erysipeloid' (Wang et al. 2010). Rarely, septicemia in humans leads to vegetative endocarditis, osteomyelitis or epidural abscessation, among other conditions (De Narvaez et al. 2022).

The number of species in the genus *Erysipelothrix* is rising. At present, 8 species are recognized: *E. rhusiopathiae, E. tonsillarum, E. inopinata, E. larvae, E. piscisicarius, E. anatis, E. aquatica* and *E. urinaevulpis* (Pomaranski et al. 2018, 2020, Eisenberg et al. 2022). *E. tonsillarum* appears to be of little clinical relevance for mammals, as only few reported cases of specific serotypes have occurred in dogs and swine (Takahasi et al. 2000, Bender et al. 2011). *E. piscisicarius* has been found to cause disease in fish (Pomaranski et al. 2020) and humans (Huang et al. 2022). The pathogenic relevance of *E. inopinata, E. larvae, E. anatis, E. aquatica* and *E. urinaevulpis* remains unknown.

Virulence factors of *Erysipelothrix* spp. include the surface protective antigen (Spa) protein, subdivided in types A, B and C (To & Nagai 2007, Pomaranski et al. 2018), a neuraminidase, a hemolysin, a hyaluronidase and the capsular polysaccharide antigen (Shimoji et al. 1994, Wang et al. 2010). Adhesion molecules RspA and RspB allow bacteria to stick to endocardial valves (Shimoji et al. 2003, Doerner et al. 2018).

The ubiquitous nature of *Erysipelothrix* spp. makes infection possible in a wide range of vertebrates and invertebrates, even in the marine environment (Wood 1973, Fidalgo et al. 2000, Oppriesnig & Coutinho 2019). Erysipelas has long been recognized as a threat for cetaceans under human care, causing acute septicemia (Seibold & Neal 1956). Cetaceans are highly susceptible to septicemic disease, which is usually peracute (often without specific clinical signs), acute or subacute (Kinsel et al. 1997). Due to husbandry practices, animals under human care have a relatively high incidence of disease, and many facilities housing delphinids follow vaccination programs with swine vaccines to protect animals from the often fatal septicemic form (Lacave et al. 2001, Díaz-Delgado et al. 2015). However, there are few documented cases of erysipelas in wild cetaceans around the world.

The first report of erysipelas in wild cetaceans was published in 1975 and involved a long-finned pilot whale *Globicephala melas* from the French Atlantic Ocean. The infection resulted in human exposure during the necropsy and zoonotic transmission (Chastel et al. 1975). Since then, a total of 74 cases of *E. rhusiopathiae* isolation have been reported, including the present study (Table 1 and references therein). Additionally, *Erysipelothrix* spp. have been detected in intestinal content or feces of a southern right whale *Eubalaena australis* and a fin whale *Balaenoptera physalus* (Marón et al. 2019, Marangi et al. 2021). Despite the rise in information about *Erysipelothrix* spp. infections in wild cetaceans, there is no agreed disease case definition associated with this bacterium, and it is unknown whether there are differences in disease manifestation in different cetacean species. Knowledge gaps regarding the pathogenesis of erysipelas remain to be filled, and the full spectrum of lesions is not defined in cetaceans. The possible serotypes and species of the genus that can cause disease in ceta-

Table 1. Summary of the most frequent lesions observed in each species of free-ranging cetacean. In all cases, *Erysipelothrix rhusiopathiae* was isolated by culture or diagnosed by positive PCR and highly compatible lesions. N: number of individuals from which *Erysipelothrix* was isolated; CSF: cerebrospinal fluid

Species	N	Lesions	Reference(s)
Individual case reports with complete[a] gross and histological investigation			
Tursiops truncatus	4	Diamond-shaped skin lesions corresponding to suppurative dermatitis with or without vasculitis (n = 2). Cloudy CSF (n = 1). Cavitary effusions (n = 2). Generalized congestion, edema, hemorrhages in subcutaneous tissue, muscle and internal organs (n = 4). Lymphadenomegaly (lymphoid hyperplasia) (n = 2). Intravascular and interstitial bacteria with or without thrombosis (n = 4). Suppurative inflammation in internal organs (n = 1). Suppurative vasculitis with intramural bacteria (n = 1).	Melero et al. (2011), Díaz-Delgado et al. (2015), Ceccolini et al. (2021), this study
Phocoena phocoena	3	Cloudy CSF (n = 1). Generalized congestion and hemorrhage in internal organs (n = 3). Pulmonary edema (n = 3). Histologically, bacterial emboli in many organs (n = 2).	Ceccolini et al. (2021)
Stenella frontalis	1	Generalized hemorrhages. Lymphadenomegaly (lymphoid hyperplasia). Bronchointerstitial pneumonia with pulmonary edema. Acute cardiomyocyte necrosis. Intravascular and interstitial bacteria in all tissues, with thrombosis. Suppurative adrenalitis with vascular fibrinoid necrosis.	Díaz-Delgado et al. (2015)
Delphinus delphis	1	Congestion in multiple organs. Pulmonary edema. Acute hepatic necrosis. Intravascular bacteria in many tissues.	Ceccolini et al. (2021)
Steno bredanensis	1	Pustular and ulcerative dermatitis with hemorrhage. Pulmonary edema and congestion. Generalized lymphadenomegaly. Splenic petechiae. Intestinal edema and congestion. Bloody feces. Unilateral testicular abscess.	Lee et al. (2022)
Delphinapterus leucas	1	Mycotic dermatitis. Lymphadenomegaly. Pulmonary edema. Aortic valve vegetative endocarditis[b]. Suppurative and lymphocytic optic neuritis and choroiditis. Chronic-active encephalitis.	Rouse & Burek-Huntington (2023)
Total	11		
Individual case reports with incomplete[a] gross and/or histological investigation			
Tursiops truncatus	2	Generalized congestion (n = 1). Pulmonary edema (n = 1), hemorrhages (n = 2). Cavitary effusions (n = 2). Lymphadenomegaly (n = 1).	Ceccolini et al. (2021)
	2	Intracellular Gram-positive rods in cerebrum and spleen.	Nesbitt et al. (2022)
	1	Diamond-shaped skin lesions corresponding to acute dermatitis with vasculitis.	Sacristán et al. (2022)
Eubalaena australis	2	Diamond-shaped skin lesions corresponding to suppurative dermatitis and panniculitis, necrotizing vasculitis and thrombosis with bacteria.	Fiorito et al. (2016)
Globicephala melas	1	Hepatic necrosis with intralesional Gram-positive bacilli.	Chastel et al. (1975)
Total	8		
***Erysipelothrix* isolations from general mortality studies**			
Phocoena phocoena	38	Muscular abscesses (n = 6). Suppurative pneumonia/ bronchopneumonia[c] (n ⩾ 8).	Siebert et al. (2001, 2009), Neimanis et al. (2022)
Tursiops truncatus	1	Fishing line agglomerate in esophagus. Ventral blubber edema.	Grattarola et al. (2023)
Total	39		
Unexpected mortality events			
Phocoena phocoena	16	Non-specified lesions in mammary gland, spinal cord, lung	IJsseldijk et al. (2023)

[a]Complete: available gross and histopathological descriptions of a set of internal organs; incomplete: gross or histopathological descriptions unavailable

[b]Coinfection with other bacteria

[c]The direct relationship of *Erysipelothrix rhusiopathiae* as the causative agent of the lesion was not established

ceans are unknown. It is unclear in cetaceans, as well as swine, whether skin lesions are always present in case of septicemia, or whether septicemia can occur without skin lesions. Similarly, whether *Erysipelothrix* spp. can infect lymphoid organs subclinically is unknown (Stephenson & Berman 1978).

Here we document a case of septicemic erysipelas in a Mediterranean common bottlenose dolphin *Tursiops truncatus*, with unusual lesions in the central nervous system (CNS) vessels, suppurative meningitis and marked skin tropism. To our knowledge, this is the first case of severe brain disease in a free-ranging or human-cared cetacean. We also provide a review of *Erysipelothrix* spp. infection in wild cetaceans, to highlight the characteristics of the disease and aid in future diagnosis.

2. MATERIALS AND METHODS

2.1. Necropsy and histopathology

An adult male Mediterranean bottlenose dolphin stranded alive in Vilassar de Mar (Barcelona, Spain) on the afternoon of 21 October 2022. The dolphin died a few minutes thereafter, with no time for veterinary assistance. It was transported to the Veterinary School of Barcelona on the same day, refrigerated at 4°C, and necropsied on 24 October, 72 h after death. Blood was collected upon arrival by cardiac puncture, for bacteriology and serum collection by centrifugation. Necropsy was performed following standardized procedures (Pugliares et al. 2007, Cuvertoret-Sanz et al. 2020).

After removal of the dorsal neck muscles, cerebrospinal fluid (CSF) was collected with a syringe and needle by aspiration through the atlanto-occipital joint, prior to opening the skull. The brain was removed from the skull and swabs from third and fourth ventricles and small brain tissue samples were collected for bacteriology and molecular biology studies. The brain was prefixed in 10% buffered formalin, and 2 d later, transversal sections were obtained for complete fixation. Samples from a standard suite of organs were fixed in 10% buffered formalin and routinely processed for embedding in paraffin, sectioned with a microtome and stained with hematoxylin and eosin. Gram and Grocott stains were applied to specific sections when needed. Screening for cetacean morbillivirus (CeMV) was performed by immunohistochemistry on brain, lymph node and lung sections as previously described by Cuvertoret-Sanz et al. (2020).

2.2. Bacteriology, biochemical characterization and virology

Bacteriological culture was performed from 18 organic fluids, tissue samples and swabs, including skin lesions, blood, urine, CSF, lung, liver, spleen, kidney, mesenteric and diaphragmatic lymph nodes, brain (cerebrum and cerebellum), atlanto-occipital joint fluid, transudates in cavities (peritoneal, pleural), leptomeninges, blowhole and forestomach and intestinal contents. Homogenates of tissue samples, fluids and swabs were inoculated onto Columbia agar with 5% sheep blood (Difco) and MacConkey agar (Oxoid) and incubated overnight at 37°C in 5% CO_2.

Susceptibility to amoxicillin, penicillin and ciprofloxacin were tested as previously described (López-Serrano et al. 2020), using Neo-Sensitabs™ diffusion tablets (Rosco Diagnostica). Since no clinical breakpoints are available for these species, veterinary practice according to Clinical and Laboratory Standards Institute (CLSI) breakpoints was followed (EUCAST- and CLSI potency NEO-SENSITABS, Rosco Diagnostica) in the interpretation of the results.

Biochemical characterization of representative isolates was performed, first using an API Coryne (Biomerieux) identification system and then the Vitek 2 system (Biomerieux).

A PCR to study CeMV presence was performed as previously described by Cuvertoret-Sanz et al. (2020).

2.3. Genetic characterization of bacterial isolates

First, 16S rRNA sequencing was performed, followed by a multi-locus sequence analysis (MLSA) of the genome. For 16S rRNA amplification, DNA extraction was performed using Chelex-based Instagene™ Matrix (Bio-Rad Laboratories) following the manufacturer's instructions. Identification of isolates was attempted by partial sequencing of the 16S rRNA gene using the primers 358F (CTA CGG GAG GCA GCA GT) and 907R (CCG TCW ATT CMT TTG AGT TT) (Lane 1991). Sequences were analyzed by blasting against the NCBI database. Complete 16S rRNA gene amplification was performed with universal primers 8F (AGA GTT TGA TCC TGG CTC AG) and 1492R (CGG TTA CCT TGT TAC GAC TT) (Weisburg et al. 1991) and sequencing with 8F, 1492R, 358F and 907R primers. Sequences were aligned and assembled with the Fingerprinting II v3.0 software (BioRad), and a consensus sequence was obtained. Sequences were analyzed by blasting against the NCBI database.

For MLSA, DNA was extracted using the Zymo-BIOMICS™ DNA/RNA Miniprep kit following the manufacturer's instructions for DNA extraction. MLSA was performed using 7 housekeeping genes following the protocol of Pomaranski et al. (2020). Genes included galactokinase (*galK*), glycerol-3-phosphate-dehydrogenase (*gpsA*), d-lactate dehydrogenase (*ldhA*), ribose-phosphate-pyrophosphokinase (*prsA*), phosphate acetyl-transferase (*ptA*), adenylosuccinate synthetase (*purA)*, recombinase A (*recA*) and DNA gyrase B (*gyrB*). Products were amplified using Phusion hot-start II high-fidelity DNA polymerase (New England Biolabs) following the manufacturer's protocols. Conditions included an initial denaturation step of 98°C for 30 s; followed by 30 cycles of 98°C for 10 s, 55°C for 20 s and 72°C for 30 s; with a final extension at 72°C for 7 min. The PCR products were purified using a QIAquick PCR purification Kit (Qiagen) following the manufacturer's protocol and submitted to AZENTA (South Plainfield, NJ, USA) for Sanger sequencing using both forward and reverse primers. Sequences were concatenated and edited using BioEdit 7.2.5 (Hall 1999) and aligned with the ClaustralW Multiple Alignment in MEGA-X 10.2.1 (Tamura & Nei 1993). The phylogenetic analysis was performed using the maximum likelihood method and Tamura-Nei model (Kumar et al. 2018). Finally, the consensus tree was derived using 1000 bootstrapped replicates of the data set.

2.4. Review: pathological characterization of erysipelas in cetaceans

We entered the terms '[(cetacean OR dolphin OR porpoise OR odontocete OR mysticete) AND (erysipelas OR *Erysipelothrix*)]' into the PubMed central database search engine (https://pubmed.ncbi.nlm.nih.gov/). Papers were considered for review if they focused on wild cetaceans, comprising individual case descriptions of erysipelas, general population studies where *Erysipelothrix* had been isolated and mass mortality event investigations. From individual case reports, we considered 'complete' descriptions those with gross examination and multiple organs assessed by histopathology, in animals in very to moderately fresh condition.

3. RESULTS

3.1. Macroscopic lesions

At necropsy, the dolphin weighed 294 kg, with a total body length of 313 cm, and a maximum girth measured cranial to the dorsal fin of 164 cm. The conservation status of the carcass was mildly to moderately autolytic, which did not affect the pathological evaluation significantly. Body condition was slightly reduced (2.5/4, according to Joblon et al. 2014), with 9 mm thickness of dermal fat layer caudal to the flipper. Skin of approximately 1/5 to 1/6 of the body surface showed quadrilateral lesions between 4 and 8 cm a side, and often with an inner, smaller, slightly raised quadrangular area (Fig. 1), with a partially sloughed epithelial layer. The dorsal fin, flukes and flippers were not affected. Intraspecific healed rake tooth marks in intermediate number were observed on the flanks. A moderate amount of sand was found in the mouth as a consequence of the live stranding.

Around 100 ml of serohemorrhagic transudate was found both in the thoracic and abdominal cavities. The pharynx and nasal sinuses also contained sand. No recent ingesta were present in the forestomach, which had only a moderate quantity of sand, several squid beaks and a fishhook with a ball of line without associated pathological changes (Fig. 2). The secretory main stomach was empty, and the pyloric stomach contained a small amount of yellow liquid. No specific lesions were found in the abdominal organs. *Clistobothrium* morphotype *grimaldii* was found in the ventral retroperitoneal space and around the testes.

The trachea contained frothy fluid. The lungs were congested and showed small whitish nodules (suspected parasitic granuloma). Approximately 12 ml of yellowish, turbid CSF was collected from the atlanto-occipital joint. The meninges showed an intense congestion and multifocal hemorrhages, especially in the frontal and parietal lobes; when sectioned, the leptomeningeal space and the sulci were severely distended by blood (Fig. 3).

3.2. Microscopic findings

The most relevant microscopic lesions were found in the CNS and the skin. Leptomeningeal medium-caliber blood vessels, both arteries and veins, showed congestion, extensive leukocyte margination, endothelial hyalinization and intense suppurative inflammatory infiltration within the tunica media and adventitia (vasculitis) (Fig. 4A,B). Inflammation multifocally extended to the meninges (suppurative meningitis) (Fig. 4D). Abundant clumps of Gram-positive bacilli were found intramurally, within the tunica media, and occasionally adhered to the

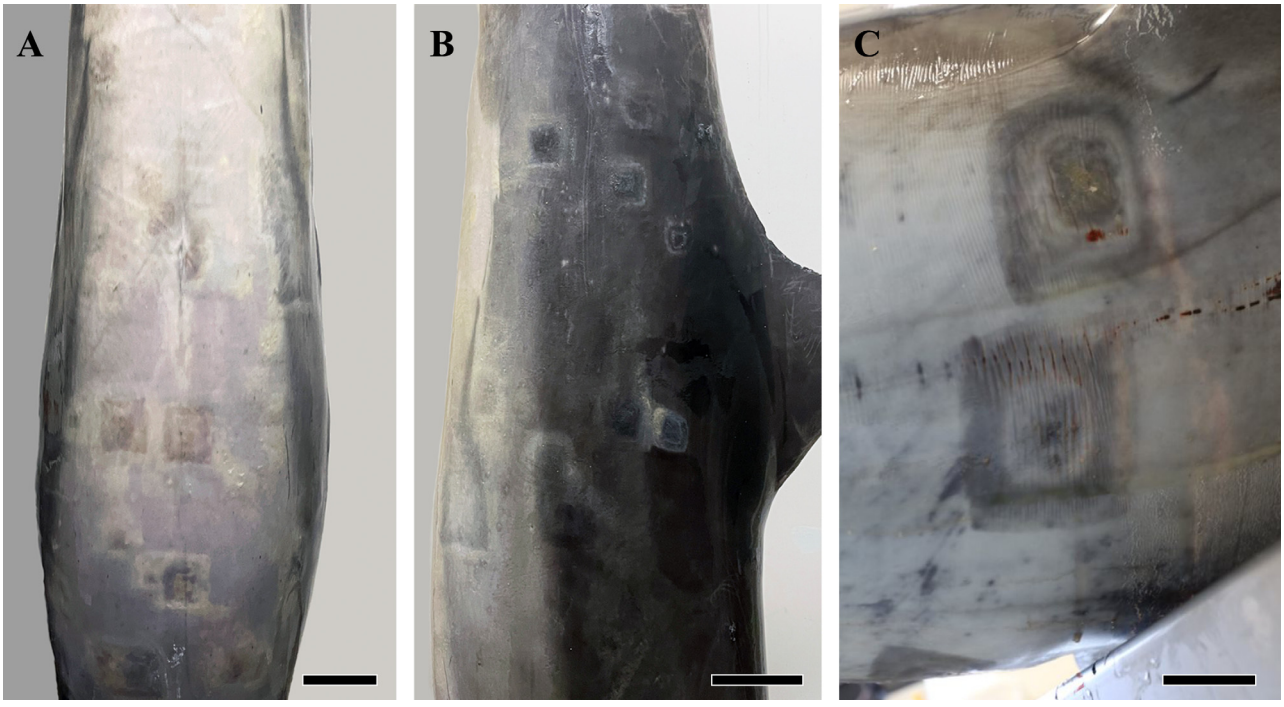

Fig. 1. Skin lesions of erysipelas in a bottlenose dolphin *Tursiops truncatus*. Quadrangular ('diamond') lesions measuring 4–8 cm a side. (A) Ventral view. (B) Lateral view. (C) Closer view of ventral side. Lesions have raised central squares with epidermal sloughing. Scale bars = (A,B) 5 cm, (C) 3 cm

endothelium. The perivascular space was occupied by extensive hemorrhage, extravasated leukocytes and proteinaceous fluid. Medium- and small-caliber blood vessels of the neuroparenchyma presented similar vascular changes of milder intensity, with associated necrotic changes of neurons. Meningeal lesions were considered the cause of death for this individual.

The affected skin showed a moderate perivascular and interstitial neutrophilic dermatitis within the superficial dermis, and, with less intensity, in the middle dermis and the panniculus. We observed epidermal hyperplasia, multifocal exocytosis of neutrophils to the epidermis, occasional intracorneal pustules and vesicles, and mild stratum corneum necrosis. No bacterial clumps or thrombi were found with Gram staining in any of the multiple sections. No overt vasculitis was observed (Fig. 4).

As an incidental finding, there was also an intense necrotizing tracheitis affecting the mucosa and submucosa, with severe vessel thrombosis, suppurative vasculitis and fibrinoid degeneration. Vessel walls and the detached tracheal epithelium presented fungal forms, positive in Grocott stain, sometimes forming hyphae of 6–7 µm in thickness, with variable shape and occasional irregularly dilated structures of 10–60 µm in diameter. No species identification was achieved. Fungi were not seen in any of the lung and CNS sections performed, so mycotic infection remained localized to the trachea. Similarly, Gram staining of tracheal sections revealed no bacteria as the cause of the vasculitis.

Systemically, there were no relevant findings besides a generalized increase in circulating leukocytes, a moderate to marked congestion in many organs and scant circulating bacteria.

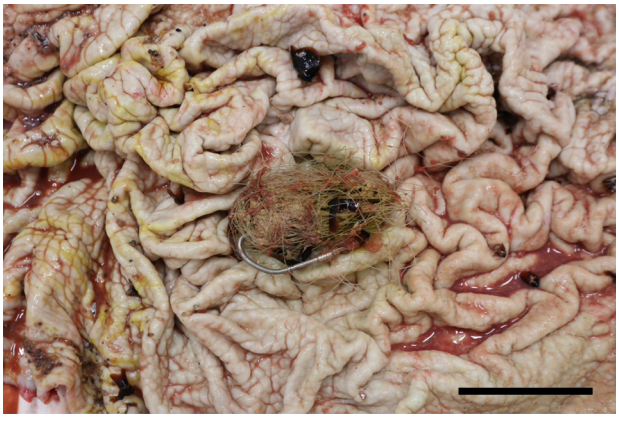

Fig. 2. Hook and line in the first stomach of a bottlenose dolphin. There was no other content besides a small amount of sand and a few squid beaks. There was no associated injury to the mucosa. Scale bar = 3 cm

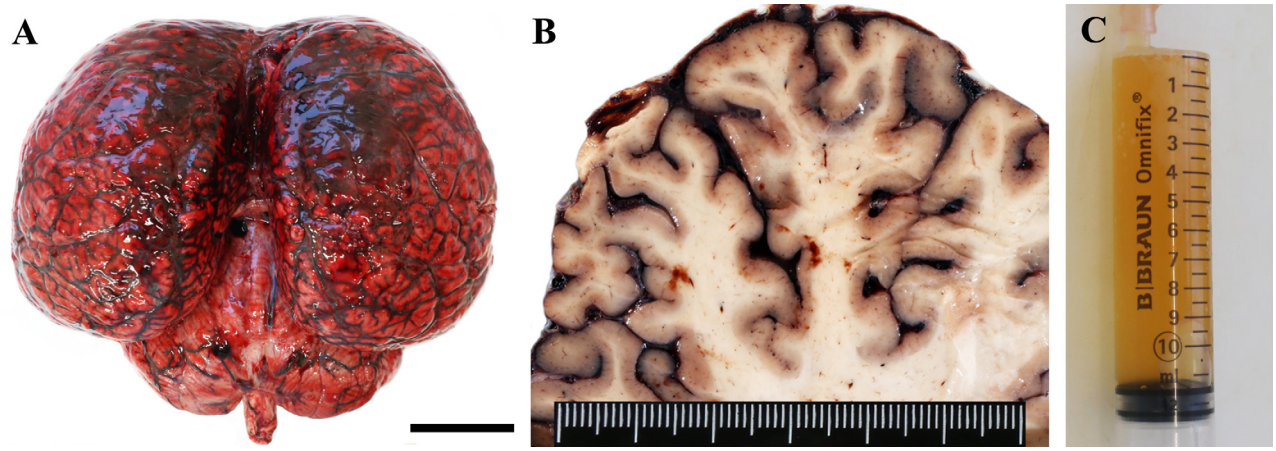

Fig. 3. Encephalon, gross lesions. (A) Dorsal view of the brain with marked congestion and hemorrhage of leptomeningeal vessels. Scale bar = 5 cm. (B) Partially formalin-fixed section of cerebral cortex. Hemorrhages extend to the sulci. (C) Cerebrospinal fluid (CSF) obtained by puncture of the atlanto-occipital joint, with a yellowish, turbid color

3.3. Bacteriology, biochemical characterization and virology

Growth in pure culture compatible with *Erysipelothrix* was found in samples or swabs from blood, abdominal and thoracic transudates, atlanto-occipital joint, liver, spleen, mesenteric and diaphragmatic lymph nodes, urine (>100 000 CFU ml^{-1}), brain and leptomeninges and superficial dermis from skin lesions. A mixed growth of abundant colonies of *Erysipelothrix* and other bacteria were cultured from lung (*Photobacterium damselae* and *Vibrio alginolyticus*), from a blowhole swab (*V. alginolyticus* and *Enterococcus* sp.), kidney (*Plesiomonas shigelloides, Escherichia coli* and *Proteus* sp.) and CSF (with *P. shigelloides*). Gastric or intestinal content culture yielded *P. shigelloides* without *Erysipelothrix* growth. Bacterial colonies of *Erysipelothrix* were small (0.5 mm) and non-hemolytic at 24 h of incubation, becoming α-hemolytic after 48 h. They were catalase- and oxidase-negative and characteristically produced H_2S only at the inoculation line of triple sugar iron (TSI) slant. They were first identified as *E. rhusiopathiae* with 99.7% identity using the API Coryne (profile 4120340) identification system. The Vitek system identified the *Erysipelothrix* isolate as *E. rhusiopathiae*, although fermentation of lactose, D-maltose and D-raffinose (all negative) seemed to disagree with the common biochemical properties of this bacterial species (Table S1 in the Supplement at www.int-res.com/articles/suppl/d157p031_supp.pdf). The studied isolate was susceptible to amoxicillin, penicillin and ciprofloxacin. Immunohistochemistry and PCR for CeMV yielded negative results.

3.4. Genetic characterization of the bacterial isolate

Sequencing of the 16S rRNA gene amplicon obtained with 358F and 907R allowed the assignment of the isolate to the genus *Erysipelothrix*, with similar homology (98–99%) to *E. rhusiopathiae*, *E. muris*, *E. piscisicarius* and *E. tonsillarum*. When a sequence of 1443 nucleotides obtained with primers 8F and 1492R was used for identification, no further discrimination was possible, again showing more than 98% homology (and an e value of 0) with all species indicated above.

Phylogenetic relationships delivered by MLSA (Fig. 5) suggested that the isolates recovered from this case belong to the *E. rhusiopathiae* spaB-positive sub lineage.

3.5. Review: pathological characterization of erysipelas in cetaceans

Since 1975, there have been 74 reports of infected free-ranging cetaceans, including our case (see Table 1). Affected species include, ordered by frequency, harbor porpoises *Phocoena phocoena* (n = 57), common bottlenose dolphins (n = 10), southern right whales (n = 2), a long-finned pilot whale, an Atlantic spotted dolphin *Stenella frontalis*, a common dolphin *Delphinus delphis*, a rough-toothed dolphin *Steno bredanensis* and a beluga whale *Delphinapterus leucas* (see references in Table 1). These cases represent individual reports of disease (n = 19), isolations retrieved in population mortality studies (n = 39) or mass stranding events (n = 16). The individual cases had a variable degree of pathological description depending on the availability of internal organs and decomposition status.

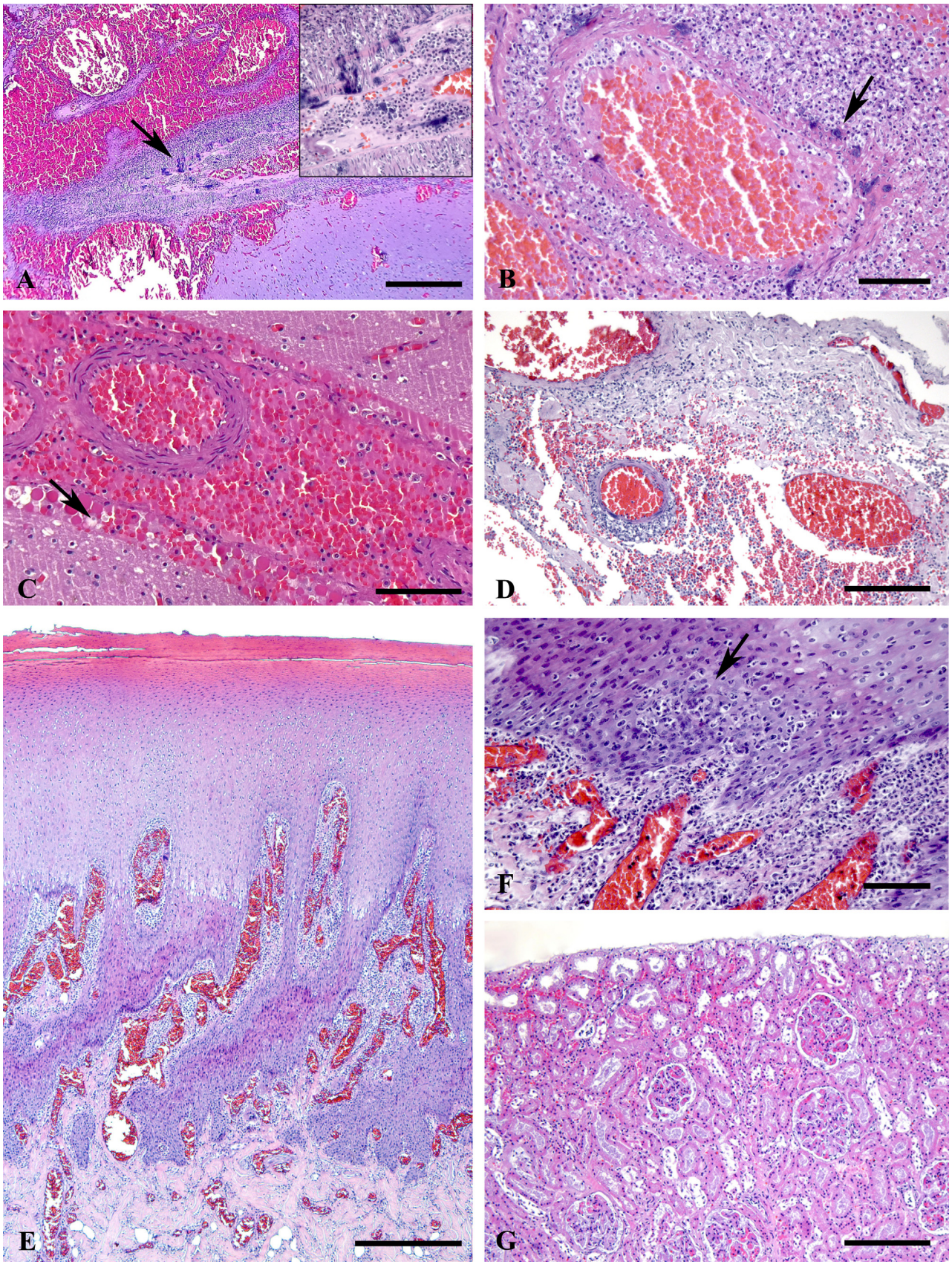

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Fig. 4. (A–D) Cerebral cortex, hematoxylin/eosin (H&E): (A) Intense suppurative vasculitis with intramural clumps of bacteria (arrow) and hemorrhage in a medium-caliber meningeal artery. Scale bar = 500 µm. Inset: detail of intramural bacteria. (B) Similar changes in a smaller vessel, higher magnification. Scale bar = 100 µm. (C) Subpial hemorrhage and edema. Scale bar = 100 µm. (D) Extensive hemorrhages and leukocyte extravasation in the meninges, with suppurative meningitis. Scale bar = 200 µm. (E,F) Skin, H&E: (E) Superficial epidermis, showing mild signs of necrosis. Perivascular spaces are expanded by inflammatory cells and vessels are hyperemic. Scale bar = 500 µm. (F) Skin at higher magnification. Neutrophils are within the epidermal layers (exocytosis; arrow). Scale bar = 100 µm. (G) Kidney, H&E. No histologic alterations. Scale bar = 200 µm

From all individual cases, including ours (n = 19, see Table 1), diamond skin lesions were reported in 2 bottlenose dolphins, including our case. Cloudy CSF was observed in a harbor porpoise, and in our case. In internal organs, predominant gross lesions were cavitary effusions (n = 5), generalized lymphadenomegaly (n = 5), generalized congestion and edema, mainly in the lung (n = 5), CNS (n = 3) and subcutaneous tissue (n = 2), but also in skeletal muscle, adrenal glands and thyroid. Generalized hemorrhages were a common feature, especially in subcutaneous tissue (n = 2), CNS (n = 2), pancreas (n = 2) and myocardium (n = 2) but also blubber, spleen, adrenal glands and stomach. There was a single report of vegetative valvular endocarditis in a beluga whale, also associated with *Streptococcus viridans* and *Clostridium* sp. (Rouse & Burek-Huntington 2023). Macroscopic lesions may be absent in some cases (Ceccolini et al. 2021).

Histopathology was complete in 11/19 of these cetaceans. Generalized congestion, hemorrhages and thrombosis were present in 5 cetaceans. Congestion was more prevalent in spleen (n = 5), lung (n = 3) and liver (n = 3). Hemorrhages were found in the CNS (n = 3), myocardium (n = 2), lung (n = 2), dermis, pancreas, kidney, urinary bladder and adrenal glands. Lymphadenomegaly corresponded to a reactive lymphoid hyperplasia (n = 2). Suppurative inflammation was described in dermis (n = 3), myocardium, adrenal glands, testicles, blood vessels, eye and meninges. Histologically, dermal lesions correspond to suppurative necrotizing dermatitis with vasculitis, capillary thrombosis and bacterial emboli. Fibrinoid necrosis with vasculitis has also been reported in the adrenal glands of an Atlantic spotted dolphin (Díaz-Delgado et al. 2015). In our case, a severe suppurative and necrotizing vasculitis was exclusively found in the CNS. Necrotizing lymphadenitis and acute renal tubular injury were among other lesions observed in cetaceans (Ceccolini et al. 2021).

Bacteria were found histologically in 9/11 animals. In 7 of them, septic embolization was present in multiple tissues, affecting the glomerular capillaries (n = 5), dermis (n = 2), lymph nodes (n = 2), CNS (n = 2),

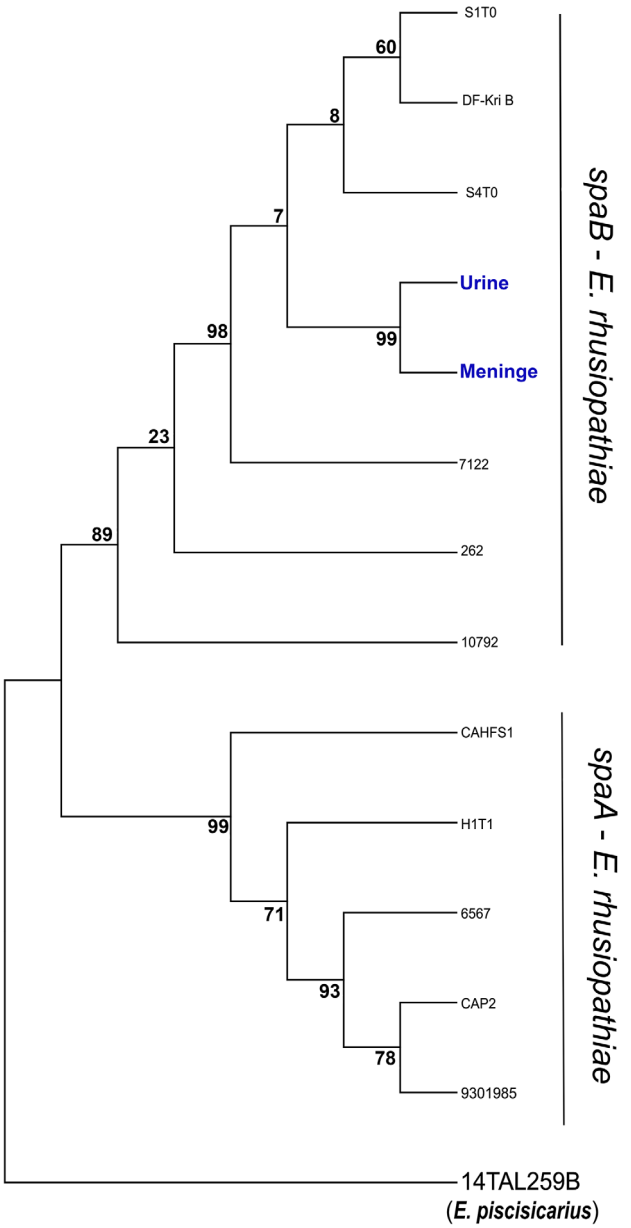

Fig. 5. Multi-locus sequence analysis maximum-likelihood tree. Values at nodes show percentage of replicate trees in which the associated sequences clustered together in the bootstrap test (1000 replicates). Genes used for comparison were *galK*, *gpsA*, *ldhA*, *prsA*, *ptA*, *purA*, *recA*, and *gyrB*. Reference sequences used in this analysis were selected from Pomaranski et al. (2020)

adrenal glands, liver, myocardium, lung, spleen, pancreas, urinary bladder, eye, aortic valve and intestine. In a common bottlenose dolphin and a harbor porpoise (Ceccolini et al. 2021), emboli were exclusively found in adrenal vessels. Detailed pathological information about all cases can be found in Table S2.

Sampling and description in the remaining 63 reported cases of erysipelas was inconsistent and often incomplete due to autolysis or lack of internal organs (Chastel et al. 1975, Fiorito et al. 2016, Nesbitt et al. 2022, Sacristán et al. 2022, IJsseldijk et al. 2023). Sometimes *E. rhusiopathiae* was found and reported as an ancillary finding without further elaboration on associated pathology (Siebert et al. 2001, 2009, Neimanis et al. 2022, Grattarola et al. 2023). Besides the 2 common bottlenose dolphins mentioned in the individual cases, diamond-shaped skin lesions without evaluable internal organs have been found in a common bottlenose dolphin and 2 southern right whale calves (Fiorito et al. 2016, Sacristán et al. 2022). In these whales, lesions were contiguous to gull-inflicted wounds, probably direct inoculations (Fiorito et al. 2016). Other lesions mentioned in these incomplete cases include diagnosis of septicemia with bacteria in brain and spleen samples in bottlenose dolphins (Nesbitt et al. 2022), multifocal necrotizing hepatitis with intralesional bacteria in a pilot whale (Chastel et al. 1975) and suppurative pneumonia in harbor porpoises (Siebert et al. 2001, 2009, Neimanis et al. 2022).

4. DISCUSSION

We describe the first confirmed case of erysipelas in a cetacean live-stranded on the Catalonian coast of Spain. To our knowledge, there is an additional confirmed case in the Western Mediterranean Sea, a common bottlenose dolphin from the coast of Valencia (Melero et al. 2011). A common bottlenose dolphin stranded at the Balearic Islands in 2013 represents a suspected third case. This dolphin had characteristic macroscopic skin lesions suggesting erysipelas, but the dolphin could not be necropsied and thus the infection was not confirmed (Balearic Island Stranding Network unpubl.; see Fig. S1).

The diagnosis of erysipelas in our case was based on the characteristic skin lesions and the isolation of *Erysipelothrix* spp. from multiple samples, including the skin lesions. Sequencing of 16S rRNA was not able to discriminate the accepted species in the genus *Erysipelothrix*, and a final etiologic diagnosis of *E. rhusiopathiae* was achieved after genetic characterization by MLSA. Taxonomy of the genus *Erysipelothrix* is constantly changing, with new species reclassified every year. Neither biochemical analyses nor traditional 16S rRNA sequencing provide a reliable species definition, and whole-genome sequencing or MLSA are indispensable for this purpose.

4.1. Lesion characterization of erysipelas in free-ranging cetaceans

Lesions in the CNS in free-ranging cetaceans, grossly, comprise brain congestion, hemorrhage and turbid CSF (Melero et al. 2011, Díaz-Delgado et al. 2015, Ceccolini et al. 2021). A peculiarity of our case, not described previously in cetaceans, was the severe damage to arterioles and venules of the meninges, with high numbers of bacteria inside the vessel walls and severe suppurative vasculitis and meningitis. This led to massive leakage of fluid and blood to the Virchow-Robin space and beneath the pia mater, resulting in a fatal increase in intracranial pressure. *E. rhusiopathiae* has been previously isolated from CNS samples in cetaceans, but the only reported lesions histologically present in the CNS were congestion and bacterial emboli (Ceccolini et al. 2021).

CNS involvement in *E. rhusiopathiae* infections is observed in humans and domestic animals, although it is considered rare (Kim et al. 2007). In humans, septicemic forms include septic embolic strokes and meningitis (Ko et al. 2003, Kim et al. 2007, De Narvaez et al. 2022). There is a case report of a sheep with complicated nasal *Oestrus ovis* infestation that presented bacterial contamination with *E. rhusiopathiae* and extension of the infection to the brain, causing malacia and meningoencephalitis (Lara-Pérez et al. 2015). In pigs, CNS vessel involvement, with vasculitis and emboli, is described and attributed to embolization of bacteria from heart valves (Karstrup et al. 2011). In our case, however, heart valves showed no macroscopic abnormalities.

From cases with complete pathological examination, characteristic diamond-shaped skin lesions were found in 2 of 4 common bottlenose dolphins including our case, which demonstrates that, as characteristic as these lesions can be, they are not always present. Although harbor porpoises are the species with a higher number of isolations, no skin lesions are reported, which suggests a predisposition for skin involvement in common bottlenose dolphins, as suggested by others (Ceccolini et al. 2021). However, skin could not be assessed in all studies including harbor porpoises due to decomposition.

Intralesional and circulating bacteria in multiple organs is a common finding in cetaceans. Our case presented bacteria only in CNS vessels, causing lesions, and circulating in small quantities in other tissues. Bacteria were not found histologically in the most commonly affected organs in other cases (glomeruli, dermis, and adrenal glands). Systemic congestion is frequently described and could be a consequence of stranding-related stress or of septicemic process.

4.2. Epidemiology and pathogenesis

Although it is assumed that knowledge on the disease in terrestrial animals, especially swine and humans, may generally apply to wild cetaceans, there are still knowledge gaps in the pathogenesis and epidemiology of erysipelas in wild cetaceans that need to be clarified. In swine, it is presumed that bacteria enter mainly via skin lesions such as conspecific injuries and through the tonsils after ingestion (Harada et al. 2013, Oppriesnig & Coutinho 2019). This has not been studied in dolphins. *E. rhusiopathiae* has been isolated from healthy harbor seals *Phoca vitulina* and fish slime, so an oral route of infection could be considered (Wood 1973, Wang et al. 2010, Oppriesnig & Coutinho 2019). In 10 of 74 cetaceans documented with *Erysipelothrix* spp. infection, discontinuities in skin or digestive system were observed, including a dermic pustule (Chastel et al. 1975), gull-inflicted wounds (Fiorito et al. 2016), gastric or esophageal ulcers, a dental abscess, a bony callus in the rib (Ceccolini et al. 2021), skin wounds and severe *Anisakis* parasitization with gastric ulceration (Lee et al. 2022), and mycotic dermatitis (Rouse & Burek-Huntington 2023). With only 10 of 74 cases demonstrating the potential cutaneous or digestive route of infection, alternative pathophysiology needs to be explored. Our case presented a necrotizing tracheal lesion associated with fungi. The absence of bacteria in Gram stain led us to consider it unlikely as the respiratory route of entrance of *Erysipelothrix*. Unfortunately, no tracheal tissue was available for culture. Although *Erysipelothrix* spp. were not isolated from a swab of gastrointestinal content in our case, the presence of bacteria in other parts of the digestive tract cannot be ruled out. Small discontinuities could have facilitated the entrance of the pathogen from the environment or commensal localizations.

In summary, erysipelas in cetaceans, from the pathological perspective, causes septicemia and, in some cases, characteristic diamond skin lesions, mainly in common bottlenose dolphins, but apparently not frequently observed in harbor porpoises. Our case shows that severe vasculitis in the brain may also occur as part of this disease. An important peak of publications of erysipelas in wild cetaceans was recorded in 2021–2023, with, to our knowledge, 8 available articles, including the present work. In contrast, the disease was only sporadically described over a 41 yr period, from 1975 to 2016, with a total of 5 publications (see Fig. S2). We do not know whether this sudden increase corresponds to a higher incidence of erysipelas in cetaceans in the last years, or to a deeper study of population health, improvement of diagnostic methods or involvement of veterinary research in stranding networks. Recently, a mass mortality event was attributed to *E. rhusiopathiae* in harbor porpoises (IJsseldijk et al. 2023), showing that an epidemic scenario is also possible. Similarly, erysipelas in porcine pathology is now considered a re-emerging disease (Oppriesnig & Coutinho 2019). All of these observations highlight the pathogenic role of *Erysipelothrix* for wild cetacean populations.

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