3D MODELING REVEALS FUNCTIONALITY OF A HEALED BUT MALALIGNED LEG FRACTURE IN A WHITE-FACED STORM PETREL *PELAGODROMA MARINA*

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ABSTRACT

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We describe a deformed tibiotarsus in a museum skeleton of a White-faced Storm Petrel *Pelagodroma marina* (Oceanitidae), probably resulting from a healed but malaligned fracture. Digital 3D modeling of intertarsal joint kinematics suggested that the affected leg could support neither terrestrial walking locomotion nor the usual foraging activities on open water. Nonetheless, the bird survived, presumably because it employed alternative feeding strategies. Considering this case in the context of previous studies on hindlimb injuries in other storm petrels, we conclude that these birds experience high frequencies of leg injuries but low frequencies of leg fractures.

Key words: bone fracture healing, long bone malalignment, 3D modeling, White-faced Storm Petrel, *Pelagodroma marina*, Ilhas Selvagens

INTRODUCTION

Birds often survive long bone fractures in the wild, but frequencies of healed fractures reported for various taxa vary considerably (Lidauer 1983, Brandwood *et al*. 1986, Goodman & Glynn 1988, Houston 1993). Segments of broken long bones may become oriented abnormally during the healing process (Tiemeier 1941, Atherton *et al*. 2012, Reichert *et al*. 2017b). The biomechanical and behavioural effects of such malalignments can be observed in live animals or deduced from geometrical analyses of bones and joints in skeletons (Reichert *et al*. 2017b). Because the affected birds survived the fracture event at least long enough for the bone to heal, each healed but malaligned fracture represents a natural experiment testing how far the biomechanical apparatus may deviate from the norm without fatal consequences.

Storm petrels, formerly considered a single family (Hydrobatidae, Procellariiformes), appear to represent two phylogenetically distinct taxa, Oceanitidae and Hydrobatidae. Both taxa are ecologically similar and are characterized by a pelagic lifestyle, except for their breeding season (Warham 1990, del Hoyo *et al*. 1992). The efficiency of their bipedal locomotion on land is notoriously poor (Warham 1996). However, when flying just above the water surface, especially the Oceanitidae use their feet to perform unique locomotory techniques (Withers 1979, Sugimoto 1998) that have been described as ‘pattering’, ‘walking’, or ‘standing’ on the water (del Hoyo *et al*. 1992; for videos, consult the Internet Bird Collection, www.hbw.com/ibc). One species, the White-faced Storm Petrel *Pelagodroma marina*, inhabits the Atlantic, Pacific, and Indian Oceans (del Hoyo *et al*. 1992). The North Atlantic subspecies, *P. m. hypoleuca*, breeds almost exclusively on the Ilhas Selvagens, a small archipelago between Madeira and the Islas Canarias (Campos & Granadeiro 1999). Here, we report a strongly deformed tibiotarsus in a White-faced Storm Petrel skeleton from this location and analyze the biomechanical consequences by optical 3D scanning and modeling.

METHODS

The bird skeleton collection of the Senckenberg Research Institute (Frankfurt am Main, Germany) includes 33 White-faced Storm Petrels. Here, we describe a skeleton with the catalogue number SMF 17899, which belongs to the subspecies *hypoleuca* and had been collected as a mummified cadaver on 06 October 2013 on Selvagem Grande (30°09′N, 015°52′W), Ilhas Selvagens, Portugal.

Tibiotarsi (one deformed) and tarsometatarsi were scanned using the 3D optical scanner Artec Spider controlled with the Artec Studio v9.2.3.15 software (Artec Group, Luxemburg) as described by Reichert *et al*. (2017a, 2017b). In short, each bone was scanned from two opposite sides, and pairs of scans were aligned using the software’s Rigid Alignment tool. 3D models were computed by Fine Serial Registration, Global Registration (min. distance 10, 40 000 iterations), and Sharp Fusion (resolution 0.2; fill holes by radius, max. radius 5). Models were exported as OBJ-files and visualized in Blender v2.6 (www.blender.org/features/2-73/). To directly compare the injured and healthy legs, bones of the healthy right leg were mirrored. Flexion of the intertarsal joints was modeled using single bone armatures. Images of the models for publication were designed with the free MeshLab software (www.meshlab.net). Planes in which tarsometatarsi rotated due to flexion of the intertarsal joints were calculated from the 3D coordinates of the distal ends of the tarsometatarsi at different flexion angles.

RESULTS

The skeleton of the White-faced Storm Petrel, SMF 17899, is complete and without apparent abnormalities, except for the left tibiotarsus (Fig. 1). The distal 7 mm of the bone with the articular surface are displaced from their normal position and are attached to the bone's shaft more proximally through a subtriangular mass of bone material (Fig. 1A). The long axis of the displaced distal bone portion forms an angle of ~53° with the shaft axis (Fig. 1B) and protrudes caudally. The straight distance from the proximal end of the tibiotarsus to the distal end of the tarsometatarsus at fully extended intertarsal joint is 16 mm shorter in the deformed leg than in the healthy leg. Thus, the functional length of the deformed leg (straight distance from the hip joint to the tip of the longest toe at full extension of all joints) was reduced compared to the healthy leg. The distal end of the deformed tibiotarsus is developed normally, including lateral and medial condyles and the supratendinal bridge over the extensor canal, but is axially rotated (Fig. 1B, C). As a result, the left foot moved at an angle with respect to the sagittal plane when it rotated around the intertarsal joint.

To obtain a clearer picture of the geometrical effects of the deformation, we generated 3D models from optical scans of the tibiotarsi and tarsometatarsi (Fig. 2). Mirroring the bones of the healthy right leg into their left counterparts enabled direct visual comparison of the deformed and the healthy legs. In the standing posture (20° flexion of the intertarsal joints; Fig. 2A-C), the foot of the deformed leg pointed backwards with the distal end of the tarsometatarsus some 25 mm higher above ground than that of the healthy leg (Fig. 2B). At increasing flexion of the intertarsal joints (70° in Fig. 2D-F), the foot of the deformed leg rotated upwards and outwards on a plane that obliquely intersected the parasagittal plane, in which the healthy foot would have moved, at an angle of about 75° (Fig. 2G).

DISCUSSION

The most plausible explanation for the deformation of the left tibiotarsus described herein (Fig. 1) is that the bone broke 7 mm from its distal end in an accident or predatory attack that the bird survived. The foot distal to the fracture was bent backwards, perhaps when the animal attempted to swim or crawl on land, and became fixed in this orientation when the fracture healed by periosteal callus formation and subsequent ossification. The duration of the healing process in the wild is hard to estimate, but based on general experience from veterinary practice it must have been four to eight weeks at least, and probably more (Doneley 2016). Alternatively, pathological conditions such as calcium deficiency disorders may cause bone deformations; however, these conditions would be expected to affect more than a single bone in one leg only. The normal morphology of the distal end of the deformed tibiotarsus (Fig. 1B, C) further supports the idea that the intertarsal joint had functioned normally before the deformation occurred.

Storm petrels can perform a digitigrade gait (i.e., walk on their toes) but rarely do. Rather, they shuffle forward on their tarsi when moving on land. A plantigrade posture also is their preferred resting stance (Warham 1996). The backward-pointing left tarsus (Fig. 2) certainly made digitigrade walking impossible for SMF 17899, but plantigrade resting and even movement may have been feasible if the bird could stand on the distal end of its deformed left tibiotarsus. Pattering White-faced Storm Petrels touch the water with both feet simultaneously as if jumping, or alternatingly as if walking, while the intertarsal joints flex and extend (del Hoyo 2013, de Groot Boersma 2016). In SMF 17899, the functional length of the deformed leg was reduced and the intertarsal joint did not operate in a sagittal plane (Fig. 2). Thus, if the bird was pattering at all, it must have done so in an asymmetric manner, maybe using only its healthy leg to interact with the water. The pattering bird may have counteracted the asymmetric foot movements by appropriate modifications of its wing action.

Tubenoses use their feet alternately when surface-swimming. The main action occurs at the intertarsal joints, while the tibiotarsi and femora hardly move (Warham 1996). Even under the doubtful assumption that the left intertarsal joint was fully functional in SMF 17899, alternating strokes of the legs would not have produced a simple forward-directed force. The left foot's oblique movement (Fig. 2G) would have rotated the swimming body's long axis to the right with every stroke, and the required compensatory actions would have decreased the efficiency of swimming locomotion.

Members of the Hydrobatidae appear capable of compensating for impediments that result from leg injuries, as such injuries hardly affect body mass (in Leach's Storm Petrel *Oceanodroma leucorhoa*, European Storm Petrel *Hydrobates pelagicus*; Love 1984) and breeding success (in the Band-rumped Storm Petrel *Oceanodroma castro*; Allan 1962, Harris 1969). The case of SMF 17899 suggests that this conclusion holds true for Oceanitidae as well. Sparsely available data on incubation spans in breeding White-faced Storm Petrels

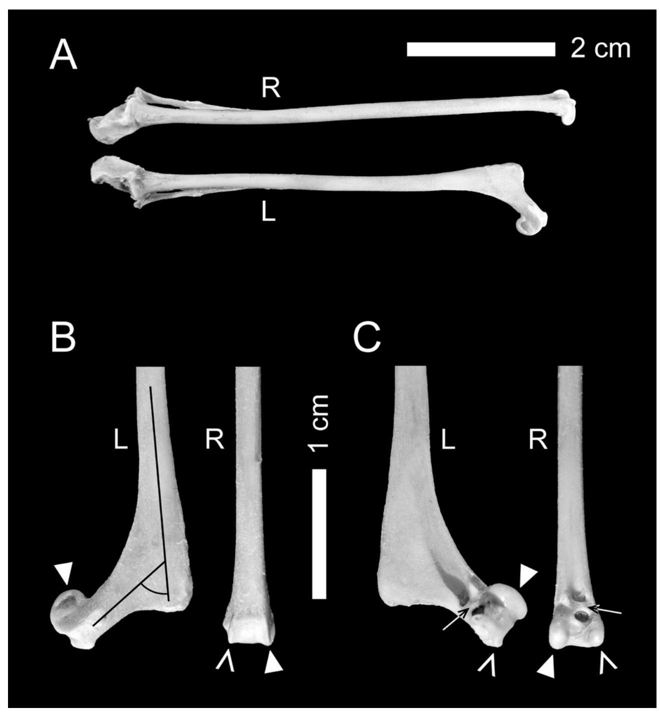

Fig. 1. Photographs of the tibiotarsi of the White-faced Storm Petrel, SMF 17899. A) The deformed left (L) and the healthy right (R) tibiotarsi, with the distal ends of the two bones also shown at higher magnification in caudal (B) and cranial (C) view. The angular malalignment of ~53° is highlighted in (B). Filled arrowheads, lateral condyles; open arrowheads, medial condyles; arrows, supratendinal bridges over the extensor canals.

indicate that well-fed birds can easily fast for five days (Richdale 1965), but this is only a fraction of the estimated duration of the healing process in SMF 17899. Therefore, the bird must have been foraging successfully while its leg fracture healed. Storm petrels are known to be pelagic surface feeders, but they readily exploit alternative sources, such as intertidal benthos (European Storm Petrel; d'Elbee & Hemery 1998, Thomas *et al.* 2006) and the beached remains of whales and fish (Fork-tailed Storm Petrel *Oceanodroma furcata*; Gill 1977, Robinson *et al*. 2018). Similar stationary food sources on solid ground may have enabled the survival of SMF 17899 on Selvagem Grande.

We are aware of only one census of leg injuries in Oceanitidae: Furness (1984) reported no injuries in a small sample (n = 35) of White-faced Storm Petrels from Gough Island. In contrast, significant proportions of larger samples had parts of their legs missing in several Hydrobatidae, including Band-rumped Storm Petrels (5.3 % of the combined sample of n = 414; Allan 1962, Harris 1969), Leach's Storm Petrels; (3.4 %, n = 5396; Waters 1964, Threlfall 1974, Morse & Buchheister 1977, Love 1984, Kirkham *et al*. 1987), and European Storm Petrels (1.5 %, n = 4789; Waters 1964, Love 1984, Mínguez 1996, Wojczulanis-Jakubas *et al*. 2014). The cause of the injuries remains conjectural, but infectious diseases and predatory attacks by fish on swimming or pattering birds have been implicated (Love 1984, Kirkham *et al*. 1987, Wojczulanis-Jakubas *et al*. 2014). The cited reports list >280 injured individuals but mention only two healed longbone fractures (Love 1984) and four 'deformed' feet (Threlfall 1974, Love 1984) without further details. Because pronounced deformations probably would not have passed unnoticed, cases like White-faced Storm Petrel SMF 17899 appear rare among Hydrobatidae. Notably, the leg bones of tubenoses are non-pneumatic and, thus, particularly strong (Warham 1996). In combination, these lines of evidence indicate high frequencies of leg injuries but low frequencies of leg fractures in storm petrels.

The legs protrude beyond the tail in flying Oceanitidae (except for White-bellied Storm Petrels *Fregetta grallaria*), but not Hydrobatidae (comprehensively documented by Brooke 2004, who did not formally separate the two taxa). Proportionally longer legs seem to facilitate pattering (Sausner *et al*. 2016), which appears to be more regularly observed in the Oceanitidae (Brooke 2004). Therefore, if hindlimb injuries are caused by attacks of predatory fishes on pattering birds, they may be expected to be more common in Oceanitidae than Hydrobatidae. Because the sample of procellariiform skeletons available to us is small, this hypothesis will have to be addressed in future surveys of larger museum collections and by field observations.

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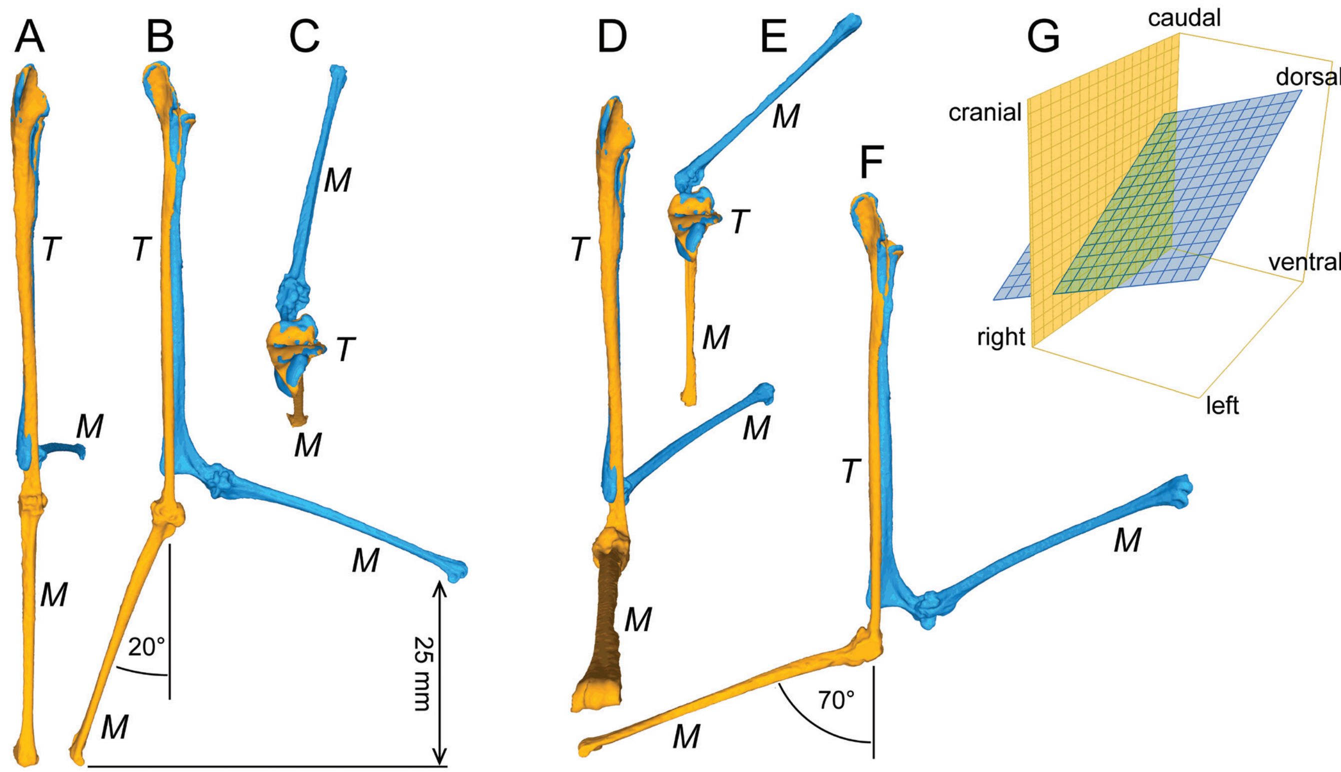

Fig. 2. Effects of the tibiotarsus deformation in the White-faced Storm Petrel, SMF 17899, on limb geometry and the kinematics of the intertarsal joint. Digital 3D models of the left and right tibiotarsi (*T*) and tarsometatarsi (*M*) are shown for flexions of the intertarsal joint of 20° (A, B, C) and 70° (D, E, F). The bones of the healthy right leg were mirrored, and the proximal ends of the tibiotarsi overlain, for direct visual comparison between the healthy (orange) and the deformed (blue) leg. Each combined model is shown in a frontal view in the caudal direction (A, D), in a lateral view (B, F; cranial is to the left), and in a view onto the proximal end of the tibiotarsus with the line of view along this bone's long axis (C, E; cranial is toward the bottom). (G) Comparison of the plane in which the left tarsometatarsus moved when the intertarsal joint was flexed in the deformed leg (blue) and the parasagittal plane in which this bone moves in a healthy leg (orange).

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