



Another look at tarsometatarsi of early penguins

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Abstract: The tarsometatarsus, a compound bone from the lower leg in birds, is the most important skeletal element in fossil penguin taxonomy, especially in the case of early members of this group. However, any attempt to go beyond the problem of mere classification obviously requires the better understanding of osteological traits under consideration. This in turn touches on the issue of interplay between bone and concomitant soft-tissue structures, such as muscles, tendons and vessels. This paper focuses on the more holistic comprehension of the tarsometatarsal section of the Eocene penguin foot, based on the analysis of the myology and the vascular system of its modern counterparts. A number of graphical reconstructions are provided with a discussion of the role of the hypotarsus and intermetatarsal foramina.

Key words: Antarctica, Eocene, Holocene, Sphenisciformes, foot anatomy, reconstruction.

Introduction

The avian tarsometatarsus is a product of the fusion of three metatarsals (II–IV) and a single distal tarsal bone (Baumel and Witmer 1993). In penguins (Aves: Sphenisciformes), this skeletal element (Fig. 1) is much shorter and wider medio-laterally relative to that in other birds (*e.g.*, Stephan 1979), and its compound character is especially conspicuous in immature bones (Fig. 2). The tarsometatarsus appears to be the most distinctive element of the penguin skeleton and has been extensively used in various studies (Jadwiszczak and Gaździcki 2014, and Chávez Hoffmeister 2014 as the most recent). It is often designated as the holotype of fossil species (Myrcha *et al.* 1990, 2002; Jadwiszczak 2009, and references therein). The oldest such bones attributable to Sphenisciformes come from the Paleocene epoch (66–56 Ma) and are rare (Slack *et al.* 2006). Penguin tarsometatarsi from the consecutive epoch (*i.e.*, Eocene in age; 56–34 Ma) are very numerous (several thousand specimens) and diverse (Jadwiszczak 2009; Ksepka and Ando 2011).

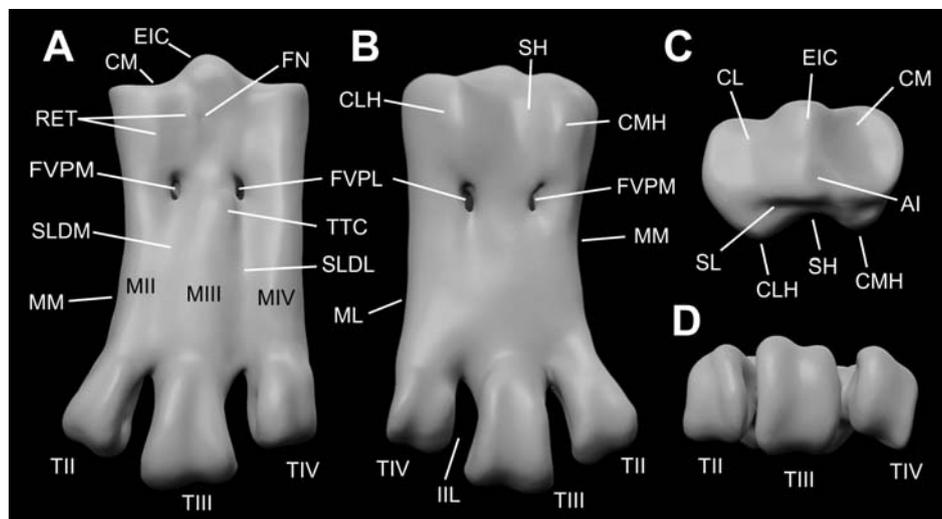


Fig 1. Osteology of the penguin tarsometatarsus. The model represents a left bone assignable to the extant Adélie Penguin, *Pygoscelis adeliae*. Dorsal (A), plantar (B), proximal (C) and distal (D) view. Abbreviations: AI – *area intercotylaris*, CM – *cotyla medialis*, CMH – *crista medialis hypotarsi*, CL – *cotyla lateralis*, CLH – *crista lateralis hypotarsi* (actually fused *cc. intermediae* and *c. lateralis hypotarsi*), EIC – *eminentia intercotylaris*, FN – *foramen nutricium*, FVPL – *foramen vasculare proximale laterale*, FVPM – *foramen vasculare proximale mediale*, IIL – *incisura intertrochlearis lateralis*, MII–IV – *os metatarsale II–IV*, ML – *margo lateralis*, MM – *margo medialis*, RET – *retinaculum extensorium tarsometatarsi* (attachment places), SH – *sulcus hypotarsi*, SL – *sulcus ligamentosus*, SLDL – *sulcus longitudinalis dorsalis lateralis*, SLDM – *sulcus longitudinalis dorsalis medialis*, TII–IV – *trochlea II–IV*, TTC – *tuberositas m. tibialis cranialis*.

Despite an extensive literature on fossil penguins, few attempts were undertaken to develop a more holistic view, not limited to an osteological aspect, of their lower hind limbs or even single components. To better understand the form and function of a given part, one must consider not only bones, but also muscles, vessels etc. This obviously poses considerable problems in the case of paleontological material, but some details can often be deduced based on the analysis of modern counterparts of an investigated animal. The objective of this paper is to provide help with regard to fuller comprehension of the tarsometatarsal section of the early penguin foot, focused on Eocene Antarctic representatives of these birds. The main reference point was osteology, myology and the vascular system of modern Sphenisciformes.

Material and methods

The osteological material (tarsometatarsi) examined here is housed in the collections at the Natural History Museum at Tring (UK) (modern penguins), Professor Andrzej Myrcha University Centre of Nature, University of Białystok (Poland), Natural History Museum, London (UK) and Museo de La Plata (Argentina) (fossil

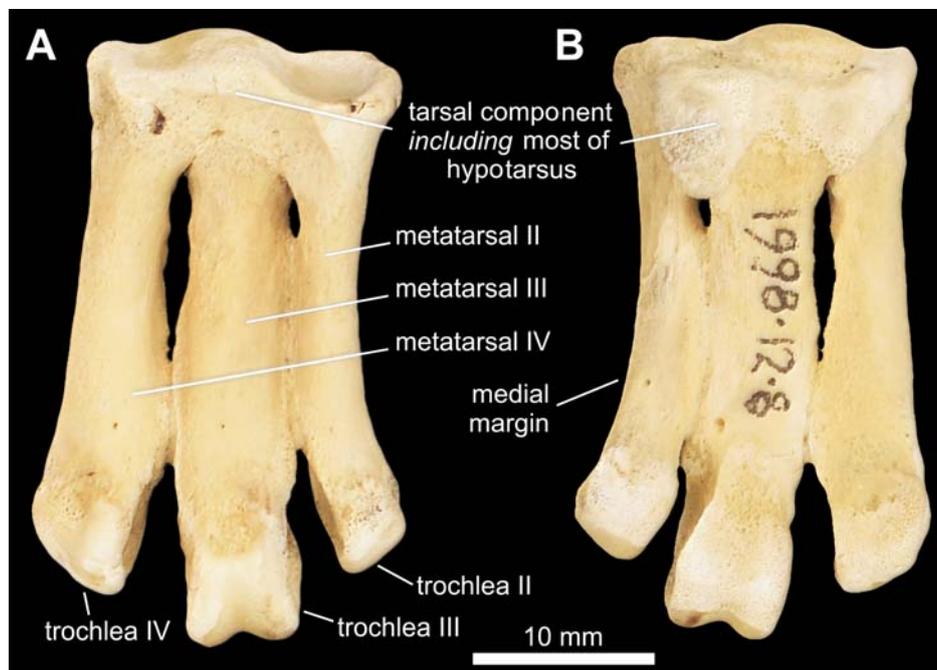


Fig. 2. Juvenile right tarsometatarsus of the extant Peruvian Penguin, *Spheniscus humboldti* (specimen NHM(T)UK 1998.12.8). Dorsal (A) and plantar (B) view.

penguins), abbreviated: NHM(T)UK, IB/P/B, NHMUK, MLP, respectively. Considering fossil Sphenisciformes, I concentrated on penguins (ten widely accepted species grouped into six genera) from the Eocene La Meseta Formation on Seymour Island (Antarctic Peninsula). Birds from four of these species, members of the genera *Anthropornis* and *Palaeudyptes*, were extremely large-sized or “giant”, whereas representatives of “*Archaeospheniscus*”, *Delphinornis*, *Marambiornis* and *Mesetaornis* did not exceed the size-range of extant sphenisciforms (Myrcha *et al.* 2002; Jadwiszczak and Chapman 2011). *Palaeudyptes antarcticus* from the Early Oligocene of New Zealand was another “giant” sphenisciform and Miocene *Palaeospheniscus bergi*, that comes from Argentine Patagonia, is assignable to the latter category. Tarsometatarsi attributable to each of these taxa are known. In the case of even earlier penguins, only the hypodigm of *Waimanu* from the Paleocene of New Zealand includes tarsometatarsi (Slack *et al.* 2006).

To examine the anatomy of tendons within the tarsometatarsal segment of a hind leg, I dissected three lower legs of extant pygoscelid penguins from the set housed at the University of Białystok (Fig. 3). Moreover, I widely used reconstructions and other data reported in the literature (see text). The 3D reconstructions were prepared using the Sculptris software (Pixologic Inc., <http://pixologic.com/sculptris/>). The anatomical terminology follows that by Baumel and Witmer (1993) (osteology), Schreiweis (1982) (myology) and Midtgård (1981, 1982) (vascular system).

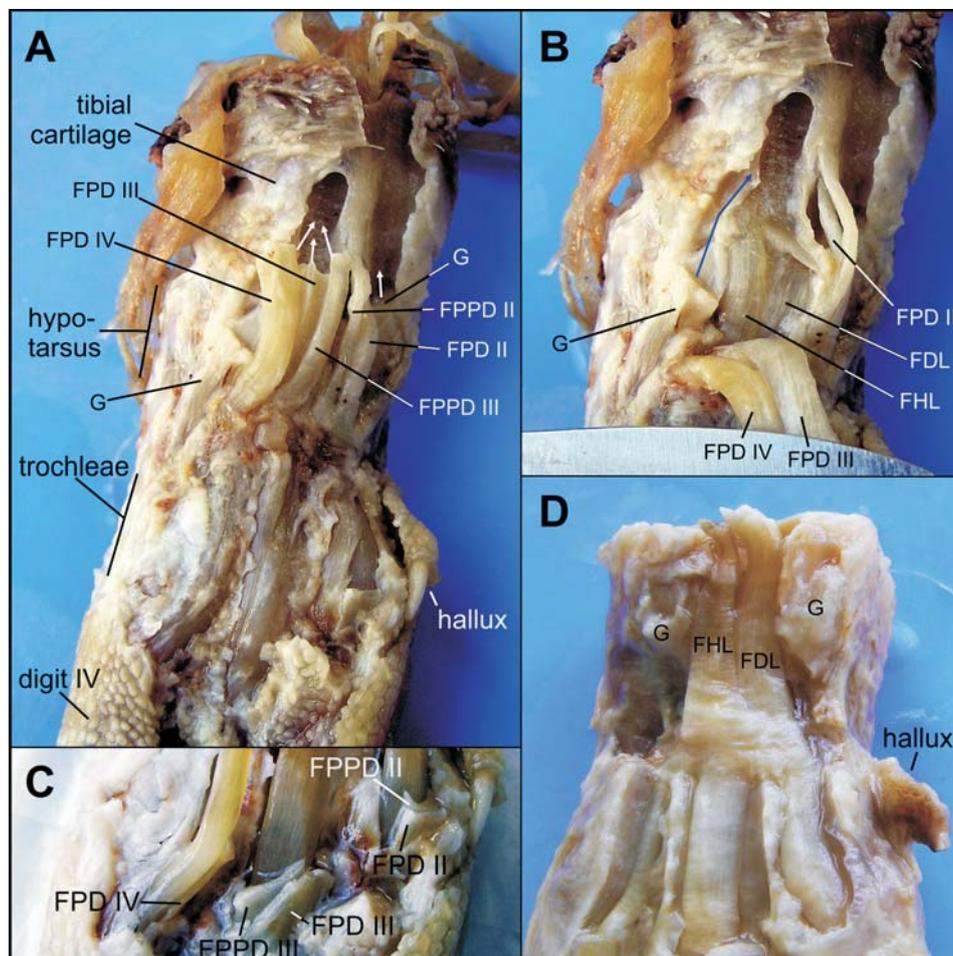


Fig. 3. The dissected left tarsometatarsus of a modern pygoscelid penguin, in plantar view, showing arrangement of main tendons. The overall view + tibial cartilage (A), intertarsal joint region showing deeply located tendons of *m. f. dig. longus* and *m. f. hal. longus* (B), close-up of distal tarsometatarsus (C) and the deepest tendons (D). Abbreviations: FDL – *musculus flexor digitorum longus*, FHL – *m. flexor hallucis longus*, FPD II – *m. flexor perforatus digiti II*, FPD III – *m. flexor perforatus digiti III*, FPD IV – *m. flexor perforatus digiti IV*, FPPD II – *m. flexor perforans et perforatus digiti II*, FPPD III – *m. flexor perforans et perforatus digiti III*, G – *m. gastrocnemius*.

Results

Myology. — In Sphenisciformes, most of tarsometatarsal muscles originate within its dorsal surface, whereas the overwhelming majority of passing tendons can be observed (after removal of superficial tendons of the *m. gastrocnemius*) on the plantar side. The medial branch of a tendon of the *m. gastrocnemius* has its insertion mainly on the *crista medialis hypotarsi*, the lateral branch passes over the lateral hypotarsal tubercle and inserts distally on the *margo lateralis*. Hence, this

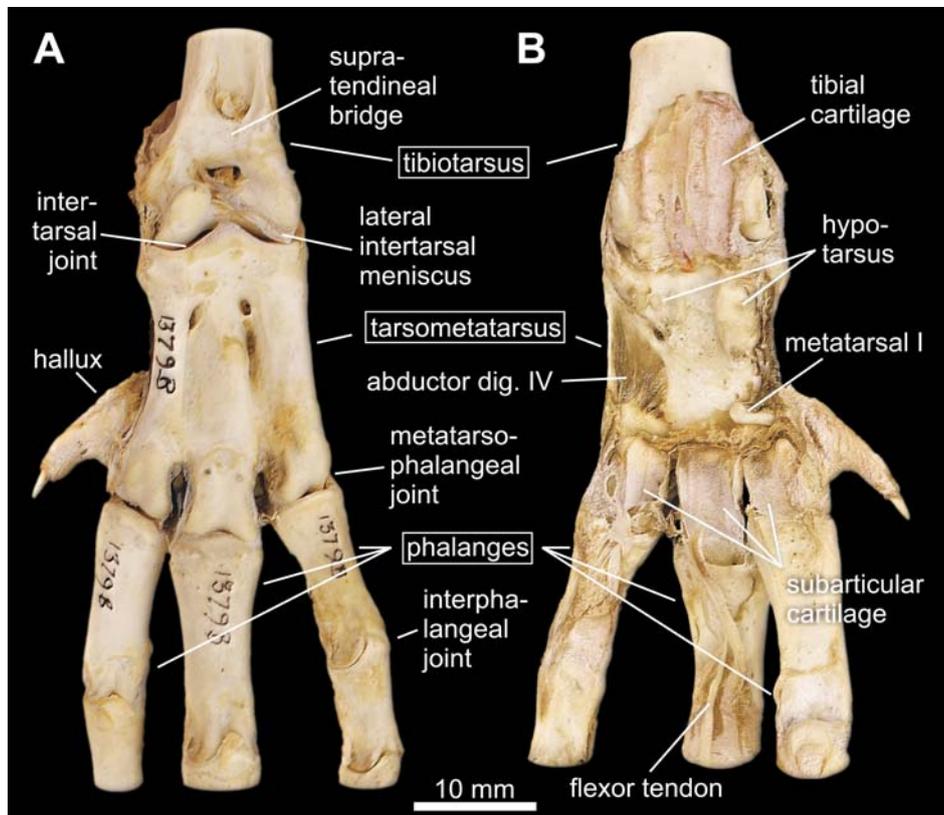


Fig 4. The partial left lower leg of the extant Rockhopper Penguin, *Eudyptes chrysocome* (specimen NHM(T)UK 13798). Dorsal (A) and plantar (B) view.

muscle is capable of moving the bone (*i.e.*, to extend it) without affecting movement of digits. The dorsal tarsometatarsus, in both modern and fossil bones, in most cases exhibits a conspicuous attachment point for a tendon of the *m. tibialis cranialis* and often also attachment sites for the *retinaculum extensorium tarsometatarsi*, which restrains the tendon of the *m. extensor digitorum longus*. The former tendon can act in the same direct manner like that of *m. gastrocnemius*, but, as a flexor, it moves the tarsometatarsus in an opposite direction. Two extensor muscles of the dorsal surface, the *m. extensor brevis digiti III* and *m. ext. brev. d. IV*, arise within the depression of the proximal metatarsals and intermetatarsal/longitudinal sulci, the third muscle, the *abductor digiti II*, originates more medially, within the metatarsal II, also its medial margin.

The plantar, dominated by tendons, side of the tarsometatarsus (Fig. 3) exhibits a conspicuous abductor muscle, the *m. abductor digiti IV* (Fig. 4), arising from a large portion of the metatarsal IV, laterodistal to the hypotarsus. The only part of the plantar tarsometatarsus clearly affected by passing tendons, especially those of the *m. flexor digitorum longus* and *m. flexor hallucis longus*, is the hypotarsus (au-

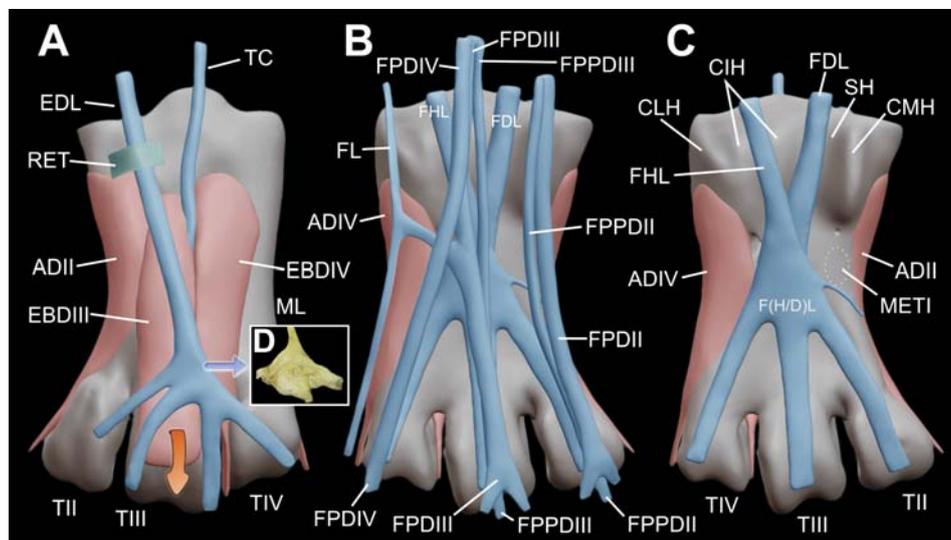


Fig. 5. Arrangement of main tarsometatarsal muscles and tendons superimposed on a generalized left *Palaeudyptes*-like bone. Dorsal (A) and plantar (B, C) view. The inset D shows the aponeurotic triangle created by EDL in modern Sphenisciformes (see Schreiweis 1982, p. 20; here in a pygoscelid penguin). Tendons of *m. gastrocnemius* removed in plantar view. Abbreviations: ADII – *musculus abductor digiti II*, ADIV – *m. abductor digiti IV*, CIH – *cristae intermediae hypotarsi*, CLH – *crista lateralis hypotarsi*, CMH – *crista medialis hypotarsi*, EBDIII – *m. extensor brevis digiti III*, EBDIV – *m. extensor brevis digiti IV*, EDL – *m. extensor digitorum longus*, FDL – *m. flexor digitorum longus*, FHL – *m. flexor hallucis longus*, FL – *m. fibularis longus*, FPDII – *m. flexor perforatus digiti II*, FPDIII – *m. flexor perforatus digiti III*, FPDIV – *m. flexor perforatus digiti IV*, FPPDII – *m. flexor perforans et perforatus digiti II*, FPPDIII – *m. flexor perforans et perforatus digiti III*, METI – putative attachment site of *os metatarsale I*, ML – *margo lateralis*, RET – *retinaculum extensorium tarso-metatarsi*, SH – *sulcus hypotarsi*, TII–IV – *trochlea II–IV*, TC – *m. tibialis cranialis*.

thor’s observation, in line with descriptions in Schreiweis 1982). Leaving the hypotarsus they fuse and then trifurcate. Three resulting branches connect to phalanges passing over the “robust” subarticular cartilages (Figs 3–4).

The location of muscles originating within the tarsometatarsus and layout of tendons of other muscles passing along this bone in Eocene Sphenisciformes, based on those in their modern counterparts (Fig. 3; see also the Material and methods section), and adjusted (where necessary) to conform with osteological details, are shown in Fig. 5. The most interesting aspects of the presented system seem to be the interaction between the hypotarsal ridges and sulci and respective tendons (Fig. 6) as well as the passage of the *m. extensor brevis digiti IV* within distal tarsometatarsus (Fig. 7).

Vascular system. — In penguins, the tarsometatarsal section of the vascular system for the blood circulation (main vessels) to the foot consists of two dorsal arteries (*aa. metatarsales dorsales II et III*) and two dorsal veins (by analogy to arteries: *vv. metatarsales dorsales*) merging proximally. It is closely related

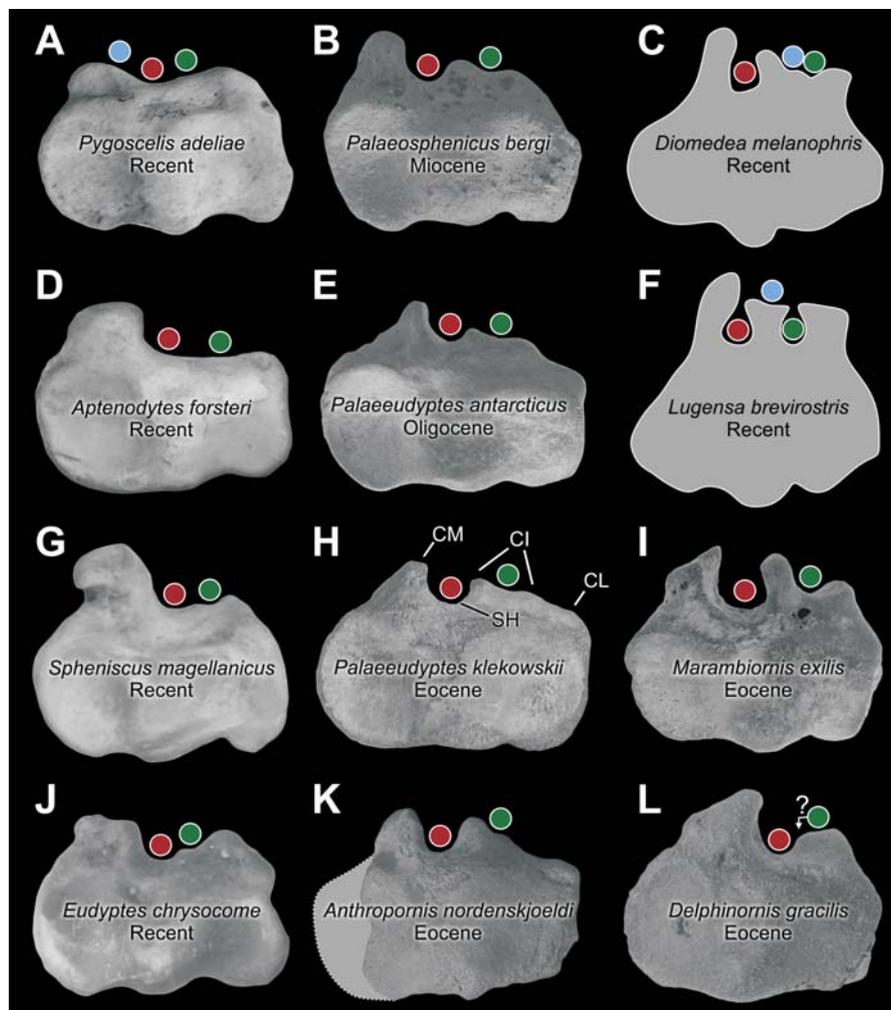


Fig. 6. Arrangement of selected tendons in hypotarsal region of tarsometatarsi of Sphenisciformes (A, B, D, E, G–L) and Procellariiformes (C, F). Proximal view, mirrored if needed. Specimens: unassigned from IB/P/B (A), NHMUK A694 (B), NHM(T)UK 1905.12.30.419 (D), NHMUK A1048 (E), NHM(T)UK 2001.45.1 (G), IB/P/B-0485 (H), IB/P/B-0490 (I), NHM(T)UK 1898.7.1.15 (J), MLP 95-I-10-142 (K) and IB/P/B-0279a (L). Arrangement of tendons in procellariiform birds, *D. melanophris* (C) and *L. brevirostris* (F), after Klemm (1969) and Mayr (2015). Red circles denote *m. flexor digitorum longus*, green – *m. flexor hallucis longus* and blue – *m. flexor perforatus digiti II*. Abbreviations: CM – *crista medialis*, CI – *cristae intermediae*, CL – *crista lateralis* and SH – *sulcus hypotarsi*. Specimens are not to scale.

to the following structures: the proximal and distal intermetatarsal foramina (which is reflected in their Latin names: *foramina vascularia proximalia* and *foramen vasculare distale*, respectively), dorsal intermetatarsal/longitudinal sulci and intertrochlear incisurae (author's observation, supported by descriptions in Midtgård 1981, 1982).

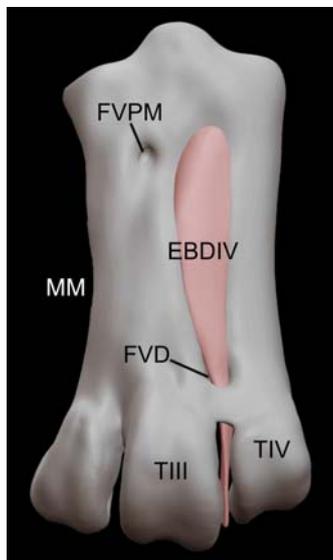


Fig. 7. Model of left *Delphinornis-larseni*-like tarsometatarsus showing a tendon of *m. extensor brevis digiti IV* (EBDIV) passing through *foramen vasculare distale* (FVD). Dorsal view. Other abbreviations: FVPM – *foramen vasculare proximale mediale*, MM – *margo medialis*, TIII–IV – *trochlea III–IV*.

The branching pattern and layout of both arteries and veins in Eocene Sphenisciformes, based on those in their modern counterparts (see the Material and methods section), and adjusted (where necessary) to conform with osteological details, are shown in Fig. 8. The most important aspect of the presented system appears to be the interplay between the medial proximal intermetatarsal foramen and the respective branch of one of two dorsal metatarsal arteries (*a. metatarsalis dorsalis II*) as well as that between the distal intermetatarsal foramen and a vessel branching from another dorsal metatarsal artery (*a. metatarsalis dorsalis III*). The above-mentioned foramina are simultaneously absent in some specimens attributable to *Palaeudyptes* and the distal foramen is lacking in the genera *Anthropornis*, *Palaeudyptes* and “*Archaeospheniscus*”. The particularly well-developed *foramen vasculare distale* can be observed in *Delphinornis larseni* and the oldest known penguins from the genus *Waimanu*.

Discussion

Myology. — The modern and fossil penguin tarsometatarsi, in general terms, do not differ substantially (author’s observation). Of course, they are larger or more elongate in some extinct taxa, some of them possess the distal intermetatarsal foramen or more complex hypotarsus (Myrcha *et al.* 2002; Chávez Hoffmeister 2014), like a majority of volant birds, including Procellariiformes – the closest living relatives of Sphenisciformes. Thus, the location of the homologous osteological characters in fossil bone observable in modern penguin tarsometatarsi does not exhibit any major deviations.

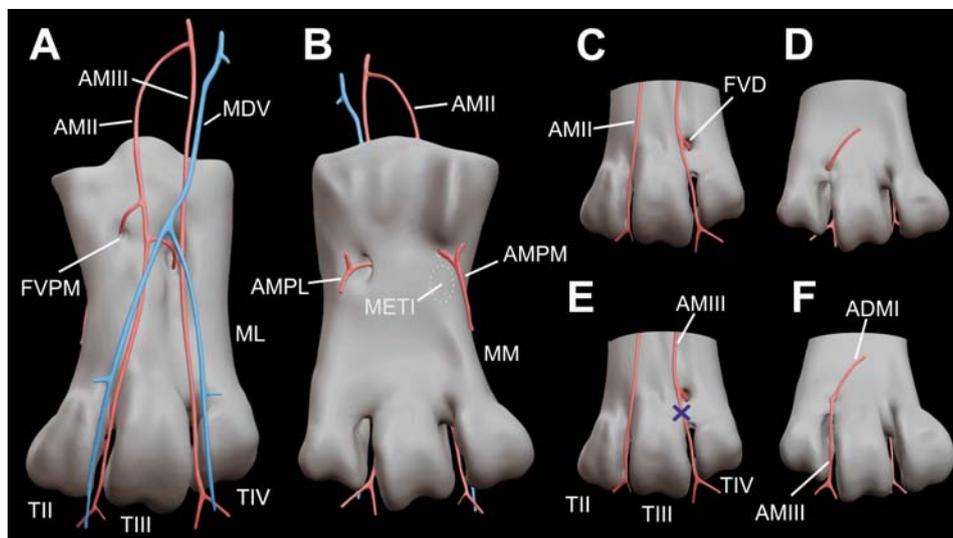


Fig. 8. Arrangement of main tarsometatarsal arteries and veins superimposed on a generalized left *Palaeudyptes*-like (A, B) and *Delphinornis-larseni*-like (C–F; two opposing variants) foot bones. Dorsal (A, C, E) and plantar (B, D, F) view. Abbreviations: ADMI – *arteria digiti I medialis*, AMII – *a. metatarsalis dorsalis II*, AMIII – *a. metatarsalis dorsalis III*, AMPL – *a. metatarsalis plantaris profundus lateralis*, AMPM – *a. metatarsalis plantaris profundus medialis*, FVD – *foramen vasculare dorsale*, FVPM – *foramen vasculare proximale mediale*, MDV – *main drainage vein* (a merger of *vv. metatarsales dorsales*), METI – putative attachment site of *os metatarsale I*, ML – *margo lateralis*, MM – *margo medialis*, TII–IV – *trochlea II–IV*.

The hypotarsus, a feature of the plantar side of the proximal tarsometatarsus, is of significance for penguin taxonomy, especially in extinct taxa (e.g., Myrcha *et al.* 2002; Ksepka *et al.* 2012; see also Acosta Hospitaleche and Jadwyszczak 2011). This structure, modeled by the interaction with tendons, in most present-day and some early (*Delphinornis*) penguins is, using Mayr's (2015) terminology, essentially monosulcate, utterly dominated by the hypotarsal sulcus bordered by the medial crest and lateral tubercle made of lateral and intermedial crests, barely recognizable or undistinguishable (Fig. 6). *Kairuku* from the Oligocene of New Zealand, devoid of the *crista medialis hypotarsi* (Ksepka *et al.* 2012), constitutes a separate case.

The relative location of tendons of *m. flexor digitorum longus* and *m. flexor hallucis longus* within the hypotarsus in modern penguins differs from that in Procellariiformes. In the former group, both tendons run more or less side by side (Fig. 6A, D, G, J), whereas in their volant relatives they are separated by bony crests and another tendon – a continuation of *m. flexor perforatus digiti II* (Fig. 6C–F). In most studied fossil Sphenisciformes, both “long” flexors were presumably separated by the *crista intermedia hypotarsi* (Fig. 6B, E, H, K; also in *Waimanu*, not presented here). Interestingly, penguins from the genus *Delphinornis* may have more resembled their extant counterparts (Fig. 6L). It is clearly not a function of bone dimensions, for *Marambiornis exilis*, an extinct species roughly similar in terms of body

size to *Delphinornis larseni*, possessed a very prominent intermedial crest (Fig. 6I). At any rate, the resulting deep (and relatively narrow) hypotarsal sulcus seems to represent an ancestral state. In Procellariiformes, the tendon of *m. flexor perforatus digiti II* appears to be much more lateral than in present-day penguins. Unfortunately, its location in early sphenisciforms is unrecognizable.

The well-developed *foramen vasculare distale* in tarsometatarsi attributable to *Delphinornis larseni* (and *Waimanu*) constituted not only a sharply defined passage for vessels (see above), but obviously also restrained a tendinous continuation of the *m. extensor brevis digiti IV* (Fig. 7). The tendon must have passed between dorsal and plantar bony bridges separating the foramen from the intertrochlear incisure. This prevents the disadvantageous increase of the moment arm of the muscle, as the metatarso-phalangeal joint becomes flexed. The similar mechanism acts more proximally, in the case of the *m. extensor digitorum longus* and *retinaculum* (Fig. 5A; see Currey 2002). The former structure is less developed (possibly partially unossified in some cases) in other species of *Delphinornis* as well as *Marambiornis exilis* and *Mesetaornis polaris*. It is not present in most fossil and all modern penguins.

Vascular system. — In modern penguins, the foot is completely supplied by the cranial (or anterior) tibial artery (*a. tibialis cranialis*), which splits into two metatarsal arteries (*aa. metarsales dorsales II et III*) prior to crossing the intertarsal joint (Fig. 8; Frost *et al.* 1975; Midtgård 1981, 1982). Such a pattern appears to be unique for Sphenisciformes (Midtgård 1982) and, for their tarsometatarsus attained its general shape by the Eocene, I see no reason to exclude the early penguins from the scope of this statement. In Procellariiformes and most other birds, *a. metatarsalis dorsalis III* is the sole large artery within this part of the lower leg (Midtgård 1982, fig. 11).

There is some ambiguity on the issue of the origin of the main lateral perforating vessel, *a. metatarsalis plantaris profundus lateralis*, that passes through the lateral proximal intermetatarsal foramen in extant penguins. According to Watson (1883), the above-mentioned artery branches from the “external digital artery” (*i.e.*, *a. metatarsalis dorsalis III*), whereas Midtgård (1982) points to the *a. metatarsalis dorsalis II* (or “internal digital artery” in Watson 1883). The methodology implemented by the latter researcher, Indian ink injections and making plastic corrosion casts, appears to be more convincing though.

Another perforating vessel, *a. metatarsalis plantaris profundus medialis*, branching from the *a. metatarsalis dorsalis II*, passes through the medial proximal intermetatarsal foramen and supplies the first (vestigial) toe in penguins (Midtgård 1982, fig. 11; see also Fig. 4B). Some tarsometatarsi attributable to Eocene *Palaeudyptes* possess virtually no medial foramen or it lacks its plantar opening. Interestingly, such a situation does not apply to representatives of another “giant” genus from the Eocene – *Anthropornis* (author’s observation; Myrcha *et al.* 2002). This observation poses an intriguing issue concerning the source of blood supply for the first toe. In procellariiforms, this toe is supplied plantarily by an artery branching from the *a. metatarsalis dorsalis III* after its passing through the distal

vascular foramen (Midtgård 1982, fig. 11). The Paleocene and some Eocene penguins, although not from the genus *Palaeudyptes*, had this foramen more or less developed, which is the ancestral trait. It cannot be definitely rejected here that individuals assignable to Paleocene *Waimanu* and Eocene *Delphinornis larseni* (relatively elongate tarsometatarsus, but not as much as in procellariiforms, combined with a patent distal vascular foramen) retained a pattern present in their volant ancestor (Fig. 8C–F). In *Palaeudyptes*, the tendency to diminish or lose the medial proximal intermetatarsal foramen can be associated with an alleged significant reduction of the first toe (see Jadwiszczak and Gaździcki 2014).

The main venous drainage of a penguin foot is via a large dorsal vessel resulting from the merger of two veins laying opposite (superficially) the main tarsometatarsal arteries (Fig. 8A; Midtgård 1981, 1982). Modern penguins are characterized by the presence of vascular counter-current heat exchangers. One of them, the humeral plexus, apparently arose at least 49 Ma (*i.e.*, during the Eocene epoch) (Thomas *et al.* 2011). In legs of most, if not all (Midtgård 1981), modern Sphenisciformes, the “extensive single-artery: multiple-vein” association exists as well (Frost *et al.* 1975). Importantly, this network of arteries and veins is not always limited to the tibiotarsus, as suggested by its name (*rete tibiotarsale*), and can expand distally beyond the intertarsal joint (Midtgård 1981, fig. 2). Unfortunately, the *rete tibiotarsale* (in the case of extant penguins – a simple *rete*; Midtgård 1981), unlike the brachial plexus, did not leave any impressions on fossil bones.

Concluding remarks

A better understanding of osteological traits touches on the issue of interaction between bone and concomitant soft-tissue structures. In the case of many fossils, one often has to deal with morphological differences between studied bones and their modern counterparts from the same genus, family or order. Most people are visualizers, hence the visualization can be an effective way to approach such a task. Figure 3 is a valuable supplement to the widely-cited paper on extant-penguin myology by Schreiweis (1982), who showed the plantar foot with “most tendons displaced”. A majority of models here presented (Figs 5, 7, 8) are largely unique for the paleontology of penguins and constitute the first step for further discussion.

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