

The digital tendon locking mechanism of the avian foot (Aves)

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Summary. Representatives of all avian orders were studied in order to establish that the tendon-locking mechanism (TLM), consisting of local specialization of the flexor tendons and the adjacent portion of the flexor tendon sheath, is by no means rare, but rather, constitutes the prevalent condition in a large majority of the avian species sampled. The areas of tubercles on the tendons and the adjacent sheath plications intermesh with one another thereby forming a true tendon-locking mechanism that maintains the distal and other interphalangeal joints of the digits in the flexed position. The TLM seems to function not only in perching, but in a wide variety of other activities of the avian foot including swimming, wading, prey-grasping, clinging, hanging, and tree climbing. The basic structural components of the mechanism are remarkably similar in the divergent avian groups adapted for these activities. Ultrastructural detail of the TLM was studied by means of scanning and transmission electron microscopy. Interdigital variation in distribution of the TLM in all of the digits of individuals were made as were comparisons of the interspecific distribution of the TLM. An analysis of the biomechanics involved in engaging the elements of the TLM and how they produce locking of the flexed joints of the digits includes a consideration of the roles of the podothecal pads, ungual flexor processes, and the elastic flexor and extensor ligaments of the toes. The components of the TLM are differentiated in early fetal development establishing that the TLM components are not acquired adventitiously in response to such factors as posthatching mechanical stresses.

A. Introduction

The surfaces of the digital tendons and the sheaths forming the tunnels in which they travel are usually covered

with smooth slippery synovial membranes that reduce friction between the surfaces in contact with one another. Nearly a century ago, it was discovered that certain birds possess roughened patches on the plantar surfaces of some of the flexor tendons of the digits, and a series of transverse folds on the adjacent flexor tendon sheath (Ranvier 1889), yet this fact is not widely known. These elaborations of tendon and sheath have been referred to as a locking mechanism (Schaffer 1903).

The present study of the occurrence and distribution of the tendon locking mechanism (TLM) does not include a consideration of the so-called automatic digital flexor mechanism; this mechanism is said to contribute to flexion of the digits by stretching the flexor tendons that traverse the tibial cartilage and hypotarsus as the intertarsal joint is flexed. This topic has been dealt with by several authors including Watson (1869), Schaffer (1903), Schranke (1930), and Bock (1965).

B. Materials and methods

The flexor tendons and sheaths of the entire foot or the third toe of specimens representing the 26 avian orders (Table 1) were carefully dissected in order to display the tendons and sheaths. The plantar podotheca, i.e., the digital pads and folds and the fatty subcutis, were removed exposing the intact outer (plantar) surface of the fibrous tendon sheath. The sheath was then incised along one side of its attachments to the phalanges and the plantar ligaments of the interphalangeal joint capsules, then reflected in order to examine its inner surface and the plantar surface of the tendons.

All of the digits of the foot were dissected in 21 specimens representing 13 orders (Table 1). The presence or absence of the TLM was noted and drawings were made of the pattern and distribution of the TLM. The remainder of the specimens consisted of only the third toe which was dissected and/or prepared for scanning electron microscopy (SEM) or transmission electron microscopy (TEM).

Methods of primary fixation varied. All specimens to be used for SEM study were dehydrated in a graded ethanol series up to 100%, and dried in liquid CO₂ in a Polaron critical point drier. Tissue was then coated with AuPd alloy in a Polaron E5100 coating unit.

Table 1. Summary of the presence or absence of the tendon-locking mechanism (TLM)

			TLM present	Whole foot dissection
Struthioniformes	Struthionidae	<i>Struthio camelus</i>	—	—
Rheiformes	Rheidae	<i>Rhea americana</i>	—	—
Casuariiformes	Dromaiidae	<i>Dromaius novaehollandiae</i>	—	—
Apterygiformes	Apterygidae	<i>Apteryx australis</i>	—	+
Tinamiformes	Tinamidae	<i>Tinamus major</i>	—	+
Sphenisciformes	Spheniscidae	<i>Pygoscelis antarctica</i>	—	—
		<i>Spheniscus magellanicus</i>	—	+
Gaviiformes	Gaviidae	<i>Gavia immer</i>	+	—
Podicipediformes	Podicipedidae	<i>Podilymbus podiceps</i>	—	—
		<i>Podiceps cristatus</i>	—	+
		<i>Podiceps auritus</i>	—	—
		<i>Aechmophorus occidentalis</i> ^a	—	—
Procellariiformes	Diomedidae	<i>Diomedea nigripes</i>	+	—
	Procellariidae	<i>Pterodroma alba</i>	+	—
	Hydrobatidae	<i>Oceanodroma homochroa</i> ^a	+	—
	Pelecanoididae	<i>Pelecanoides urinatrix</i>	+	—
Pelecaniformes	Pelecanidae	<i>Pelecanus erythrorhynchos</i>	+	—
	Sulidae	<i>Sula sula</i>	+	—
	Phalacrocoracidae	<i>Phalacrocorax pelagicus</i>	+	—
	Anhingidae	<i>Anhinga anhinga</i> ^a	+	—
Ciconiiformes	Ardeidae	<i>Botaurus lentiginosus</i> ^a	+	—
		<i>Ardea herodias</i>	+	+
	Ciconiidae	<i>Ciconia ciconia</i>	+	—
		<i>Leptoptilos crumeniferus</i>	+	+
	Phoenicopteridae	<i>Phoenicopterus ruber</i>	—	+
		<i>Phoeniconaias minor</i>	—	—
Anseriformes	Anatidae	<i>Cygnus olor</i> ^b	+	+
		<i>Branta canadensis</i> ^b	+	—
		<i>Anas platyrhynchos</i> ^b	+	+
		<i>Mergus merganser</i> ^b	+	—
Falconiformes	Cathartidae	<i>Cathartes aura</i>	+	—
	Accipitridae	<i>Circus cyaneus</i>	+	+
		<i>Buteo lineatus</i>	+	—
		<i>Buteo jamaicensis</i> ^a	+	—
	Falconidae	<i>Falco peregrinus</i>	+	—
		<i>Falco sparverius</i> ^a	+	—
Galliformes	Phasianidae	<i>Meleagris gallopavo</i>	+	—
		<i>Bonasa umbellus</i> ^c	+	—
		<i>Colinus virginianus</i> ^a	+	—
		<i>Gallus gallus</i> ^b	+	+
Gruiformes	Opisthocomidae	<i>Opisthocomus hoazin</i>	+	—
	Gruidae	<i>Grus antigone</i>	+	—
	Rallidae	<i>Porzana carolina</i> ^a	+	—
		<i>Gallinula chloropus</i>	+	—
		<i>Fulica americana</i>	+	+
Charadriiformes	Otididae	<i>Eupodotis senegalensis</i>	+	—
	Jacaniidae	<i>Jacana jacana</i>	+	—
	Haematopodidae	<i>Haematopus bachmani</i>	—	—
	Recurvirostridae	<i>Himantopus himantopus</i>	—	—
		<i>Cladorhynchus leucocephalus</i>	—	+
	Charadriidae	<i>Charadrius vociferus</i> ^b	—	+
		<i>Vanellus vanellus</i> ^{b, c}	—	—
	Scolopacidae	<i>Numenius tahitiensis</i>	+	—
		<i>Phalaropus lobatus</i> ^a	+	—
		<i>Gallinago gallinago</i> ^b	+	—
		<i>Calidris pusilla</i> ^a	+	—
	Laridae	<i>Larus argentatus</i> ^b	+	—
		<i>Larus fuscus</i>	+	—
		<i>Gygis alba</i>	+	+
Columbiformes	Alcidae	<i>Uria lomvia</i>	+	—
	Raphidae	<i>Columba livia</i>	+	+
		<i>Zenaidura macroura</i> ^a	+	—
Psittaciformes	Psittacidae	<i>Ara chloroptera</i>	+	—
Cuculiformes	Cuculidae	<i>Coccyzus americanus</i> ^a	+	—
		<i>Geococcyx californiana</i>	+	—