

THE RADIUS AND RELATIONSHIP OF OWLS¹

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WHILE skinning a specimen of *Ninox strenua*, Mr. Michael Traynor of the National Museum of Victoria noticed a "bony spur" on the wing near the wrist. Wing spurs in owls were unknown to Mr. Traynor, and hence he showed it to Allan McEvey. Further examination revealed that this spur lay beneath the skin and that it was attached to the radius, not to the carpometacarpus as is the usual position of the wing spur in birds (Jeffries, 1882*a*; Rand, 1954; only the spur-winged goose, *Plectropterus*, has a spur on the radiale). Initial study disclosed that this structure is not a wing spur, but an enlarged sesamoid bone. The presence of a sesamoid bone associated with the tendon of the *M. tensor patagii longus* where it bends around the distal end of the radius and its enlargement in some hawks has been known since the middle of the nineteenth century (Giebel, 1866:35; Milne-Edwards, 1867-8: Plate 10, Fig. 1; Alix, 1874:403; Plate 2, Fig. 1; reviewed in Gadow, 1891: 72, 256; Plate 20, Fig. 2). Little significance was given to the presence and configuration of this sesamoid. This radial sesamoid was described and discussed fully for the first time by Shufeldt in the owls (Shufeldt, 1881*a*:615; 1900:600, Fig. 5) and in the hawks (Shufeldt, 1881*b*). He designated it as the *os prominens*. Jeffries (1882*b*) pointed out that this structure had been described earlier by Milne-Edwards, Mivart and Alix. Both Shufeldt and Jeffries showed that the tendon of the *M. tensor patagii longus* inserts on the *os prominens* and discussed its possible functional significance. Lucas (1882*b*), in a brief but characteristically excellent note summarized the knowledge of the *os prominens* and associated tendons in the hawks and owls. To our knowledge, no significant advance over Lucas' discussion has appeared in the eighty years since his contribution. After the initial series of papers by Shufeldt, Jeffries and Lucas, only a few references to the presence of the *os prominens* have been published (Pycraft, 1903:32; Hudson and Lanzillotti, 1955:40, Fig. 33).

During the preliminary examination of the radius in owls, our attention was drawn to another peculiar feature of this bone; namely, a small bony arch on the inner side of the shaft. This structure was described as the osseous arch by Shufeldt (1900:679, 680; Fig. 5) very briefly and without additional comments. Pycraft (1903:43) mentioned the bony arch of the radius in passing. The osseous arch of the radius in the owls has again become all but forgotten in the subsequent literature. Nothing had been pub-

¹ We dedicate this paper to the late Dr. Tilly Edinger, who had a lifelong interest in heterotopic ossifications, in recognition of her achievements in vertebrate morphology and paleontology.

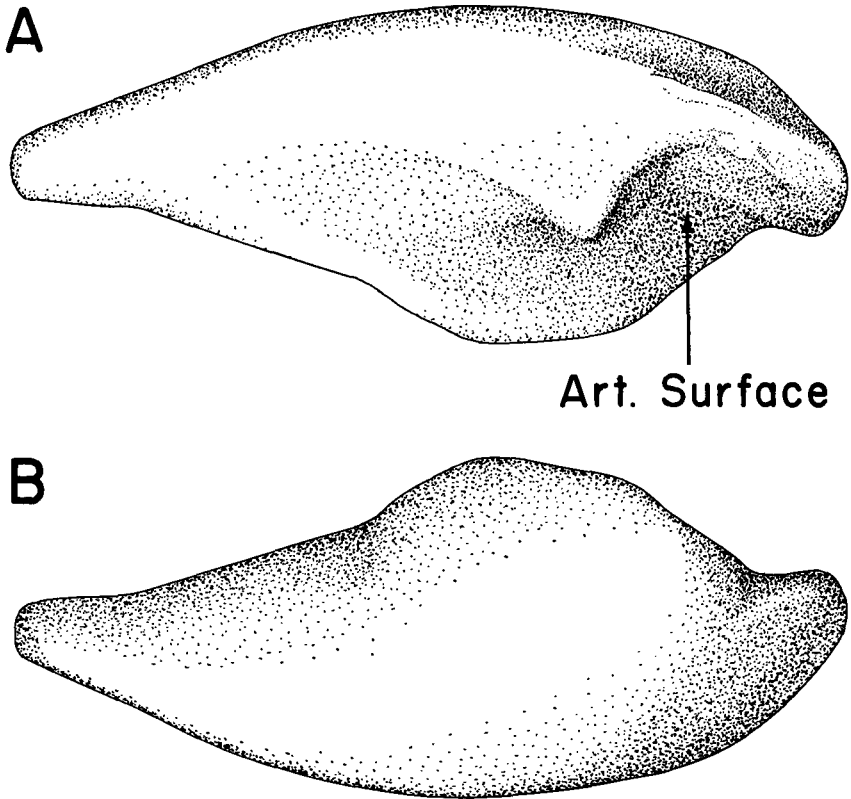


FIG. 1. An isolated os prominens from an immature *Ninox strenua* showing the dorsal surface (A) and the ventral surface (B). The articular surface can be seen on the dorsal surface.

lished on its interrelationships with surrounding soft tissues or on its possible functional significances.

In this paper, we would like to redescribe the os prominens and the osseous arch of the radius, to speculate on their possible functional significance, and to discuss the pertinence of these structures to the relationships of the owls.

DESCRIPTION

The os prominens in owls.—An isolated os prominens from an immature *Ninox strenua* is shown in Figure 1. This heterotopic bone is 20 mm long, 9 mm wide at its greatest width and 4 mm thick. This particular example of the os prominens is much wider than those usually seen in owls. In another specimen of *Ninox strenua* (Fig. 3B), the os prominens is more typical in shape and measures 23 mm long, 8 mm wide, and 7 mm thick. The bone tapers rapidly from its greatest width to a blunt point onto

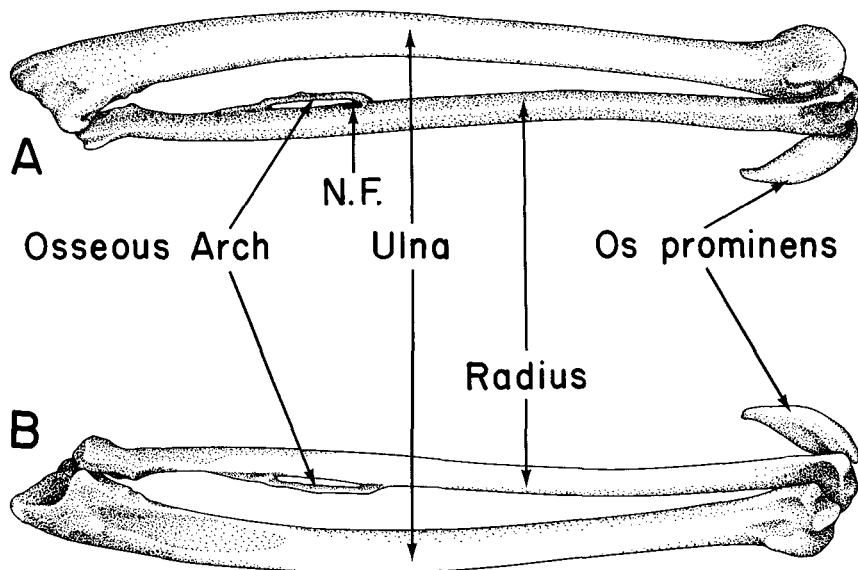


FIG. 2. The forearm of *Ninox strenua* (same specimen as in Figure 1) as seen from below (A) and above (B) to show the os prominens and the osseous arch. The nutrient foramen (N.F.) of the radius can be seen at the distal end of the osseous arch.

which the tendon of the *M. tensor patagii longus* inserts. Its ventral surface (Fig. 1B) is convex and smooth without any distinctive features, whereas its dorsal surface is concave with an articular surface at its distal end. A slight projection lies along part of the proximal border of the articular surface. The os prominens is attached to the anteroventral surface of the distal external radial condyle. The exact relationship in life of the sesamoid bone to the radius is not necessarily as shown in Figure 2. These bones meet in a moveable articulation, and the os prominens doubtlessly shifts in position with directional changes in the tendon of the tensor patagii.

The os prominens in *Pulsatrix perspicillata* (Fig. 3A), *Ninox strenua* (Fig. 3B, another specimen with the more typical form of the sesamoid), and *Ninox novaeseelandiae* (Fig. 3C) show the more typical configuration of this sesamoid—a hook-shaped bone. It is more elongated and slightly decurved, and in all examples it ends in a blunt point. A thorough survey of the occurrence and configuration of the os prominens in all genera of strigid owls is not meaningful at this time because this sesamoid bone could be easily detached and lost in many osteological specimens. A rough survey indicates that the os prominens is present throughout the strigid owls, even in the smaller species like the Screech Owl (*Otus asio*); its shape is always like that illustrated in Figures 1-3. However, the os prominens is lacking in all specimens of *Tyto* that we have examined. Shufeldt (1900:675) also reported the absence of the os prominens in *Tyto alba* (= *Strix pratincola*) as did Lucas (1882:87).

In strigid owls, such as *Ninox strenua* (Fig. 4B) and *Asio otus* (Fig. 4C), the tendon of the *M. tensor patagii longus* bifurcates at some point before the distal end of the radius. One branch of the tendon inserts onto the proximal tip of the os prominens.

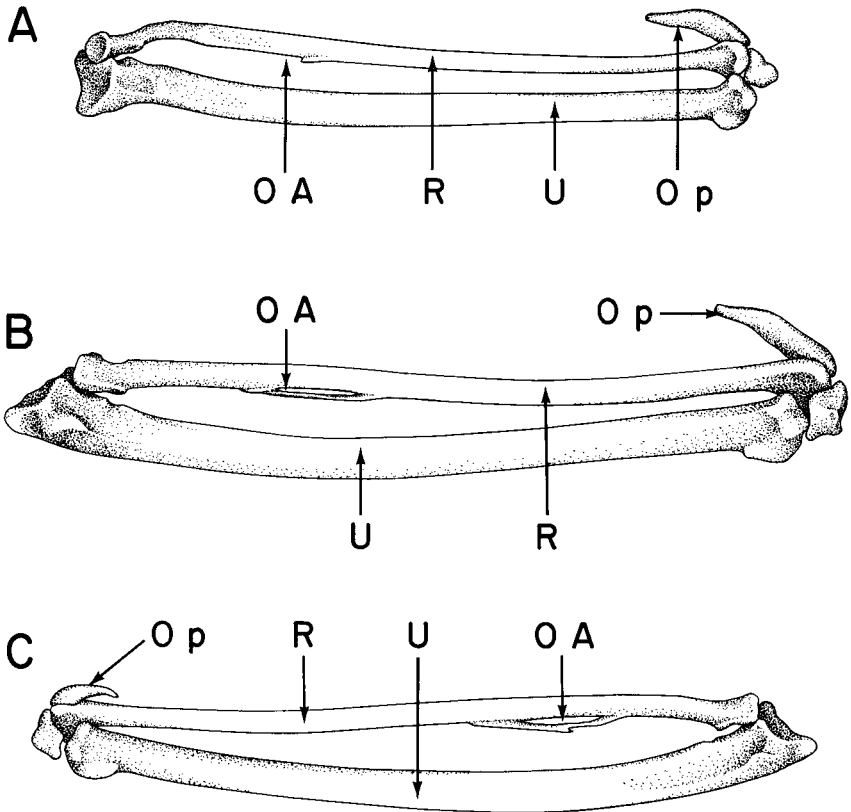
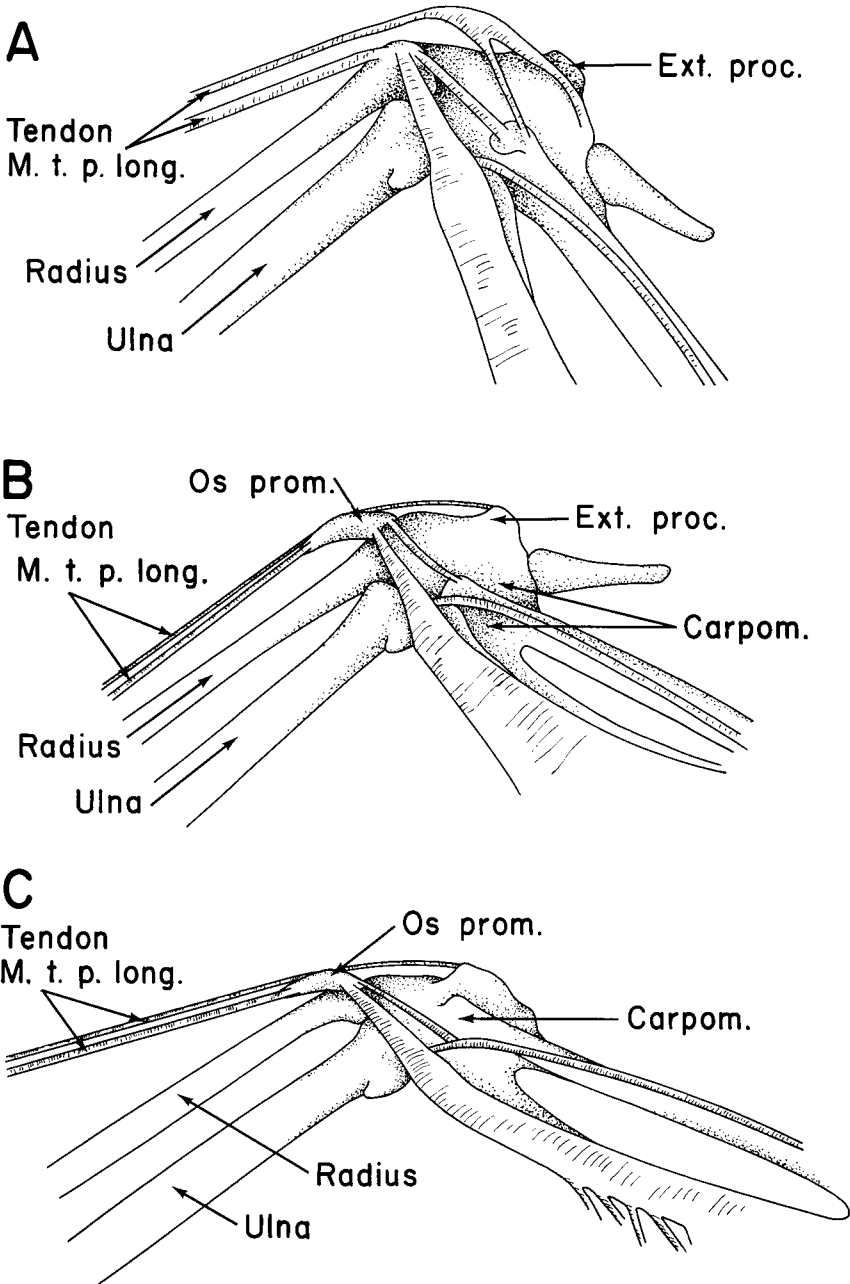


FIG. 3. The forearm of *Pulsatrix perspicillata* (A) *Ninox strenua* (B) and *Ninox novaeseelandiae* (C) as seen from above to show the os prominens (O p) and the osseous arch (O A). The arch is broken in *Pulsatrix perspicillata* with only one end remaining.

The other branch of the tendon passes dorsal to the os prominens and inserts on the extensor process of the carpometacarpus. Our dissections confirm the findings of Lucas (1882:87) who figured these tendons in *Bubo virginianus*. Two ligaments arise from the base of the os prominens. One runs a short distance before inserting on the main body of the carpometacarpus. The other ligament broadens into a flat sheet that runs along the posterior edge of the carpometacarpus and sends off small slips to the

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FIG. 4. The carpal joint in *Tyto alba* (A), *Ninox strenua* (B), and *Asio otus* (C), to show the attachment of the tendon of the M. tensor patagii longus. This tendon splits with one branch inserting onto the extensor process of the carpometacarpus and the other branch inserting onto the radius or the os prominens. Two ligaments arise from the radius or base of the os prominens and run to the carpometacarpus and the bases of the primaries.



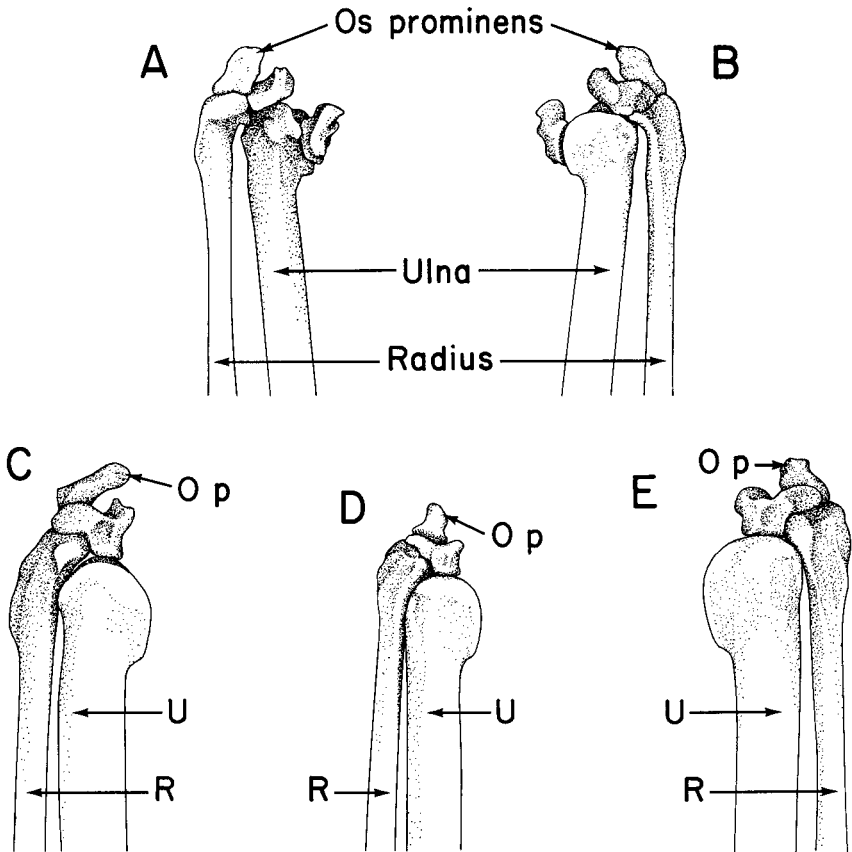


FIG. 5. The forearm of *Accipiter cooperii* (ventral, A and dorsal, B), *Circus cyaneus hudsonius* (C), *Buteo melanoleucus* (D), and *Aquila chrysaetos* (E) to show the os prominens (O p).

bases of the primary quills. These tendons and ligaments are quite similar in *Tyto alba* (Fig. 4A) except for the absence of the os prominens. The tendon of the M. tensor patagii longus splits in *Tyto*, one branch inserting onto the distal end of the radius and the other branch inserting on the extensor process of the carpometacarpus. Two ligaments arise from the radius close to the insertion of the tendon of the M. tensor patagii longus. The shorter ligament inserts on the main body of the carpometacarpus, while the other ligament broadens, runs along the posterior edge of the carpometacarpus and sends off short slips to the bases of the primary quills.

The large size of the os prominens as compared with the size of the M. tensor patagii longus and its tendon is of interest. We did not dissect this muscle in the owls studied, but referred to the description in George and Berger (1966:317-319). The muscle is small, and presumably produces little force compared to the size of the os prominens;

this discrepancy in size of the bone and the muscle is an anomaly and will be discussed below.

The os prominens in hawks.—The os prominens in hawks is a rectangular sesamoid articulating with the anterioventral surface of the external distal radial condyle. Moreover, this sesamoid articulates (probably) with the radiale although the exact relationships between these bones cannot be determined with certainty from dried skeletons. In *Accipiter cooperii* (Fig. 5A and 5B) the os prominens is 5 mm long, 3 mm wide, and 2 mm thick; in *Circus cyaneus hudsonius* (Fig. 5C) it is 8 mm long, 3 mm wide, and 3 mm thick; in *Buteo melanoleucus* (Fig. 5D) it is 8 mm long, 5 mm wide, and 5 mm thick; and in *Aquila chrysaetos* (Fig. 5E) it is 9 mm long, 7 mm wide, and 6 mm thick. The free end of the os prominens is blunt and rounded. In life, the os prominens apparently lies perpendicular to the longitudinal axis of the wrist joint; it is oblique to the longitudinal axis of the radius with its free end pointing toward the tip of the wing.

Again, a detailed survey of the occurrence and configuration of the os prominens in the hawks is not realistic at this time because the sesamoid could be lost in many specimens; alcoholic specimens or carefully prepared skeletons are needed. However, a rough survey was conducted and the results are as follows. This bone appears to be absent in the Cathartidae. A well-developed os prominens as described above was found in many genera of the Accipitridae such as *Accipiter*, *Heterospizas*, *Buteo*, *Circus*, *Aquila*, and *Haliaeetus*. It was not found (presumably absent) in many kites, Old World vultures, and many large hawks and eagles. Lucas (1882:87–88) reported a large, hook-shaped os prominens in *Otogyps (Torgos) calvus*, describing it as a simple sesamoid in the tendon of the M. tensor patagii longus; we were unable to confirm his report. The os prominens has been reported in *Pandion* (Shufeldt, 1881b:201), although we could not find it nor could Lucas (1882:88). It appears to be absent in the Falconidae as a well-developed heterotopic bone, although a small simple sesamoid is present in the tendon of the M. tensor patagii longus in *Falco* (Alix, 1874) and in *Falco mexicanus* (Hudson and Lanzillotti, 1955:40). Dr. George Hudson (pers. comm.) informs us that a simple sesamoid was present in 16 of the 18 genera of hawks dissected; it was absent in *Coragyps* and was only slightly ossified in *Sagittarius*.

Shufeldt (1881b:119) reported that the tendon of the M. tensor patagii longus (his extensor plicae alaris) inserts on the free end of the os prominens, as did Milne-Edwards (1867–68; see also Gadow, 1891: Plate 20, Fig. 2, who reproduced Milne-Edwards' figure). Dissection of a specimen of *Buteo swainsoni* (Fig. 6B) confirms these earlier findings. The tendon of the M. tensor patagii longus attaches onto the free tip of the os prominens, after which the tendon continues to the extensor process of the carpometacarpus where it inserts. A short extension of the tendon continues to the pollex. Two ligaments run from the distal end of the radius, one to the main body of the carpometacarpus and one to the bases of the primary quills; these ligaments are similar to those seen in the owls. In *Falco sparverius* (Fig. 6A), the tendon of the M. tensor patagii longus passes over the distal end of the radius to insert on the extensor process of the carpometacarpus. A slight thickening in the tendon may indicate the position of the sesamoid.

The osseous arch in owls.—A low thin bony arch is present on the posterior edge of the radius (facing the ulna) about one-third of the distance from the proximal end of the bone (Figs. 2 and 3). This arch has been described earlier by Shufeldt (1900:673; 680, Fig. 5). Except for a passing mention by Pycraft (1903:43), we have not been able to find any other reference to this feature. In *Ninox strenua*, the arch is 23 mm long (outer dimension), 3 mm high, and 1 mm thick on a radius 125 mm long. The

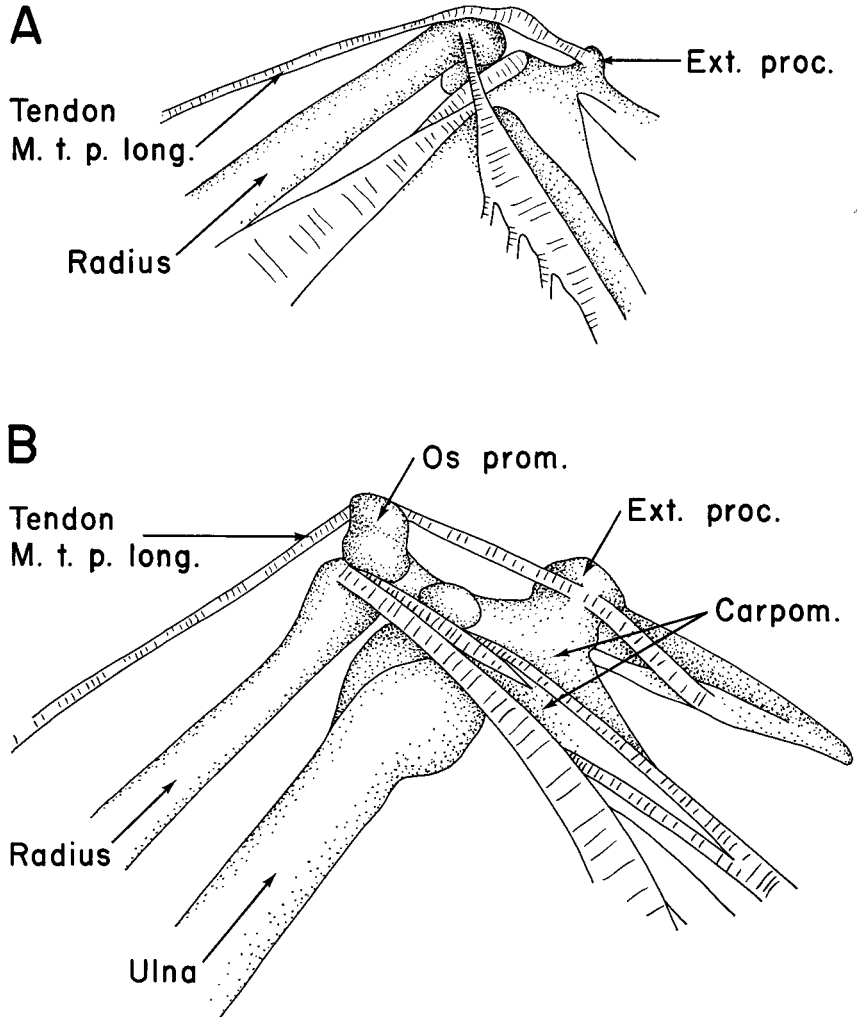


FIG. 6. The carpal joint of *Falco sparverius* (A) and *Buteo swainsoni* (B) to show the attachment of the tendon of the M. tensor patagii longus. In *Falco*, the tendon attaches directly to the extensor process of the carpometacarpus. A small sesamoid may be present in the swelling of the tendon. In *Buteo*, the tendon attaches to the free end of the os prominens before inserting on the extensor process.

inside dimensions of the arch are 9 mm long and 2 mm high. The nutrient foramen of the radius is located at the distal end of the arch; this foramen is very small and may be filled with dried tissue. The radius of some specimens had to be thoroughly cleaned by boiling before the nutrient foramen became visible. The arch is frequently broken

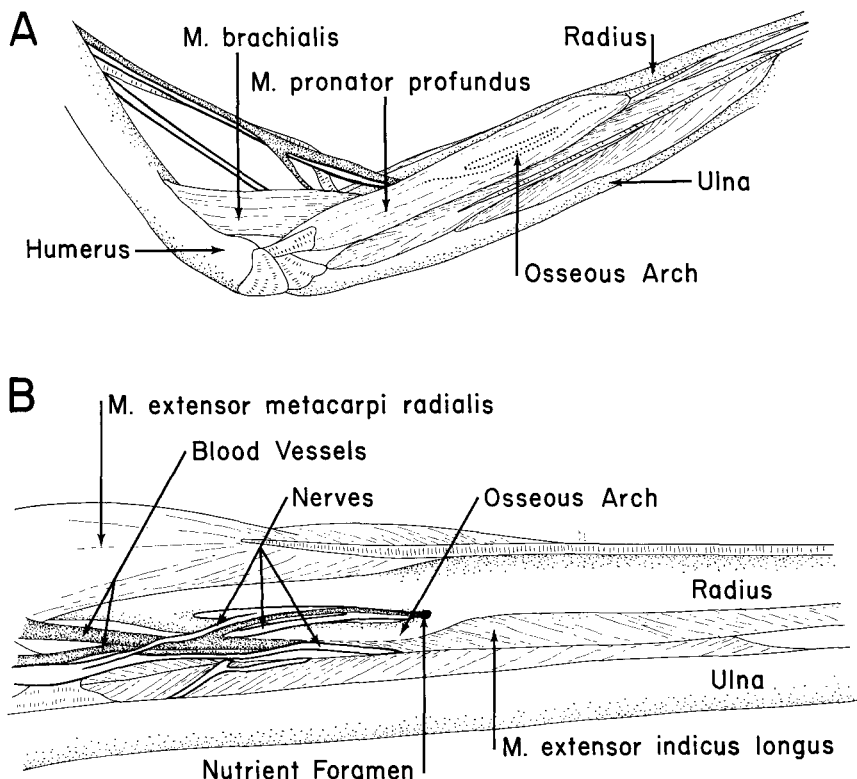


FIG. 7. The forearm of *Asio flammeus* to show the attachment of the M. pronator profundus (A) and of the M. extensor indicis longus (B) to the osseous arch. Nerves and blood vessels pass over the osseous arch to reach the space beneath it. A blood vessel passes through the nutrient foramen.

(as in Fig. 3A) with only the stump of one limb of the arch left; in almost all specimens, at least a remnant of the arch remains. The osseous arch of the radius is present in *Tyto* and in all genera of strigid owls examined. We have not seen a similar structure in any other group of birds, nor do we know of any references to such a structure.

Bony arches such as seen on the radius of owls may serve as the site of muscular attachment or as protection for some feature, such as a nerve or blood vessel, passing beneath it. The forearm of several specimens of Screech Owl (*Otus asio*) and two specimens of Short-eared Owl (*Asio flammeus*; Fig. 7) were dissected to ascertain the relationships of muscles and other structures to the osseous arch. The terminology for the muscles follows George and Berger (1966).

Two muscles attach to the osseous arch of the radius. The more superficial muscle, the M. pronator profundus, originates from the distal end of the humerus, passes over the M. brachialis and inserts on the shaft of the radius distal to the passage of the major nerve trunks and blood vessels from the upper arm to the forearm. The in-

sertion of the *M. pronator profundus* covers the ventral surface of the osseous arch (Fig. 7A). The deeper muscle, the *M. extensor indicis longus*, originates from the edge and dorsal surface of the distal limb of the osseous arch and from the inner surface of the radial shaft distal to the arch (Fig. 7B). The origin of this muscle may be slightly ossified resulting in a small keel on the osseous arch. A series of nerves and blood vessels runs over the ventral surface of the osseous arch to reach the space beneath it (Fig. 7B). Most of the space beneath the arch is filled with a whitish tissue continuous with and similar to the nerves. An elongated tissue, presumably a blood vessel could be traced through the nutrient foramen into the marrow cavity of the radius. However, it was not possible to trace any nerves through the arch to the muscles on the dorsal side of the radius. A more detailed analysis of the tissues within the osseous arch must await histological study.

DISCUSSION

The functional significance of the os prominens and the osseous arch remains as poorly known as in Shufeldt's day. Although the osseous arch functions as part of the site of attachment for the *M. pronator profundus* and the *M. extensor indicis longus*, it is doubtful that this function is associated with the adaptive reasons underlying its evolution. Both of these muscles could attach to the shaft of the radius as they do in all other birds. The intervention of the osseous arch appears to be completely nonessential for the proper attachment of these muscles in the owls. The configuration of blood vessels and nerves at the osseous arch suggests the best possible hypothesis for the adaptive reason for its evolution. The arch could serve as protection for these structures from the forces developed by the surrounding muscles. Our "educated" guess is that protection for the nerves and nerve-like tissues is the main adaptive significance of the osseous arch.

Shufeldt (1881*b*), Jeffries (1882*b*), and Lucas (1882) discussed several possible functions of the os prominens in hawks. We agree in general with their conclusions; namely, that the os prominens displaces the tendon of the *M. tensor patagii longus* from the surface of the carpus and thereby: (a) increases the moment arm of the force of the *M. tensor patagii longus* and hence increases the torque of this muscle on the carpometacarpus; (b) increases slightly the surface area of the wing and hence its lifting force; (c) possibly removes some of the force of the *M. tensor patagii longus* from the carpal bones and thereby protects the carpal bones (we doubt whether friction plays an important role because tendons are usually encased in sheaths with low friction surfaces). The first of these possible functions appears to be the most important and may be associated with adaptive reasons for the evolution of the os prominens in hawks. We have excluded consideration of the small sesamoid in the tendon of the *M. tensor patagii longus* in this discussion. This sesamoid appears to serve the usual functions of a sesamoid lying in the bend of a tendon around the end of a long bone.

Neither Shufeldt nor Jeffries discussed the function of the os prominens in owls; Lucas alludes briefly to the owls in his discussion. In the owls, one branch of the *M. tensor patagii longus* runs directly to and inserts on the extensor process of the carpometacarpus. The other branch of the tendon attaches directly to the distal end of the radius (*Tyto*) or indirectly to the distal end of the radius via the os prominens (strigid owls). In *Tyto*, two ligaments run from the distal end of the radius to the body of the carpometacarpus and to the bases of the primary quills. In strigid owls, these ligaments originate from the base of the os prominens. From a consideration of these tendons and ligaments, the major functions of the os prominens in owls appear to be: (a) to displace the tendon of the *M. tensor patagii longus* from the radius and therefore increase the moment arm of the muscular force; and (b) to couple the action of the *M. tensor patagii longus* and the ligaments to the carpometacarpus and primary quills directly and independently (or semi-independently) of the action of the radius. Most peculiar is the large size of the os prominens relative to the size of the radius and the size of the *M. tensor patagii longus*. Quite possibly, this bone experiences substantial bending forces; consequently, it must be large to resist them. Large bending forces would be associated with both possible functions mentioned above. We would suggest that both functions proposed for the os prominens in owls are associated with the adaptive reasons for its evolution in this group.

Shufeldt (1900; 1909:75) and Lucas (1882) imply that the os prominens of the hawks and of the owls is the same feature; *i.e.*, that they are homologous, although neither author makes a definite statement. Because of the continued discussion of the relationships between hawks and owls (Starck and Barnikol, 1954:58-59; Starck, 1959; Vopio, 1955:128; Sibley¹, 1960; 1965:117), the exact homology of this structure is an important question. We will follow the definition of homology given by Bock (1963) and would like to divide the question of homology into two parts: (A) Is the os prominens in the hawks and in the owls homologous as a sesamoid bone in the tendon of the *M. tensor patagii longus*? and; (B) Is the detailed configuration of the os prominens in the hawks homologous to the detailed configuration of the os prominens in the owls?

¹ Professor Sibley very kindly made available to us the most recent data and interpretations from his work on the electrophoretic patterns of the egg-white proteins and hemoglobins of hawks and owls for which we are most grateful. Both the egg-white proteins and the hemoglobins show differences between *Tyto* and the strigid owls, indicating a separation between these groups of owls, although nothing can be said about degree of relationship. The egg-white patterns of *Tyto* and *Falco* are different, but the hemoglobins of both genera show two components with similar mobilities in starch gel. These results say that these two groups could be related, but they prove nothing one way or the other. Sibley's general conclusions that *Tyto* and the strigid owls are distinct groups, and that the similarities between *Tyto* and *Falco* must be looked upon as of unknown and uncertain significance are in close agreement with our general conclusions (see below).

The answer to the first question is probably "yes" because of the tendency of sesamoid bones to develop in tendons where they curve around the end of a bone and because of the frequent and widespread presence of a small sesamoid in this tendon at the carpal joint, as seen in many hawks and other birds (see Gadow, 1891:72; 256; George and Berger, 1966:318; Hudson, pers. comm.). But the homology of the os prominens in hawks and owls as a sesamoid in the tendon of the *M. tensor patagii longus* means only that a sesamoid found in this position in any bird would be homologous. This conclusion is of no value in ascertaining the relationships of hawks and owls.

The answer to the second question is clearly "no"; the detailed configuration of the os prominens in these groups is not homologous. We base our decision on the markedly different shape of this bone in the two groups and on the different relationships between the bone and the attached tendons and ligaments. Hence we would conclude that the os prominens in hawks and the os prominens in owls had separate evolutionary histories (evolved from a rudimentary sesamoid in the tendon of the *M. tensor patagii longus* independently and under the action of different selection forces). Consequently, the presence of this enlarged heterotopic bone in the two groups does not imply affinity. The use of the same name for these two non-homologous bones is confusing, and we would suggest that some descriptive adjective such as strigid and accipitrid be used to distinguish between them.

The presence of an osseous arch of the radius and the arrangement of the tendon of the *M. tensor patagii longus* argue against the hypothesis that *Tyto* is related to any group within the falconiformes (e.g., the Falconidae). These features provide strong support for the existing classifications that place *Tyto* in the same order as the strigid owls. Although the insertion of the tendon of the *M. tensor patagii longus* on the distal end of the radius (directly or indirectly via the os prominens) is not unique to owls, it is unusual for birds and is either unknown or very rare in birds believed to be close relatives of owls. The osseous arch is, to our knowledge, unique to owls and argues strongly for a monophyletic origin of all owls. Sufficient evidence is available to separate *Tyto* from strigid owls no matter what taxonomic rank is assigned to this separation. The absence of the os prominens in *Tyto* provides another bit of evidence supporting this separation as Lucas had mentioned as long ago as 1882.

SUMMARY

1. The os prominens is a large, hook-shaped sesamoid bone in the tendon of the *M. tensor patagii longus* of strigid owls; it is absent in *Tyto*. A low rectangular os prominens is present in many hawks. The relationships of tendons and ligaments to the os prominens differ in owls and hawks. The functional and adaptive significances of the os prominens could only be suggested.

2. The osseous arch of the radius is a bony arch on the shaft of the radius; it is found in all owls. The *M. pronator profundus* and the *M. extensor indicis* attach to the osseous arch. Several nerves and blood vessels run into the cavity beneath the arch, and a whitish tissue (nervous?) fills the cavity beneath the arch.

3. The *os prominens* in hawks and owls is homologous only as a sesamoid in the tendon of the *M. tensor patagii longus*. The detailed configuration of this enlarged heterotopic bone in hawks and owls is not homologous and hence does not imply affinity. The presence of the osseous arch and arrangement of the tendons of the *M. tensor patagii longus* support placing *Tyto* in the same order as other owls. These features do not support relationship between *Tyto* and any hawk.

ACKNOWLEDGMENTS

Above all, we would like to express our appreciation and thanks to Mr. Michael Traynor, preparator at the National Museum of Victoria, for calling our attention to the *os prominens*. Without his careful surveillance for new and peculiar structures in the material being handled, we would still be ignorant of this feature of owls and could not have done this study. Dr. Tilly Edinger has kindly made available her notes on heterotopic bones in vertebrates for which we are most grateful. We would also like to thank Mrs. Frances Jewel who devoted her usual skill and care in drawing the figures that accompany the text. The officials of the Bird Room, British Museum (Natural History) made available to us several specimens under their care for which we wish to express our appreciation. Special mention and thanks must be given to Major Harold Hall, O.B.E., M.C. and to the Myer Foundation, the Ian Potter Foundation, and the M.A. Ingram Trust, for generously enabling Allan McEvey to spend a month in New York in order to take part in this research. This study was supported by grant N.S.F. GB-3802 from the National Science Foundation to Walter Bock.

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