

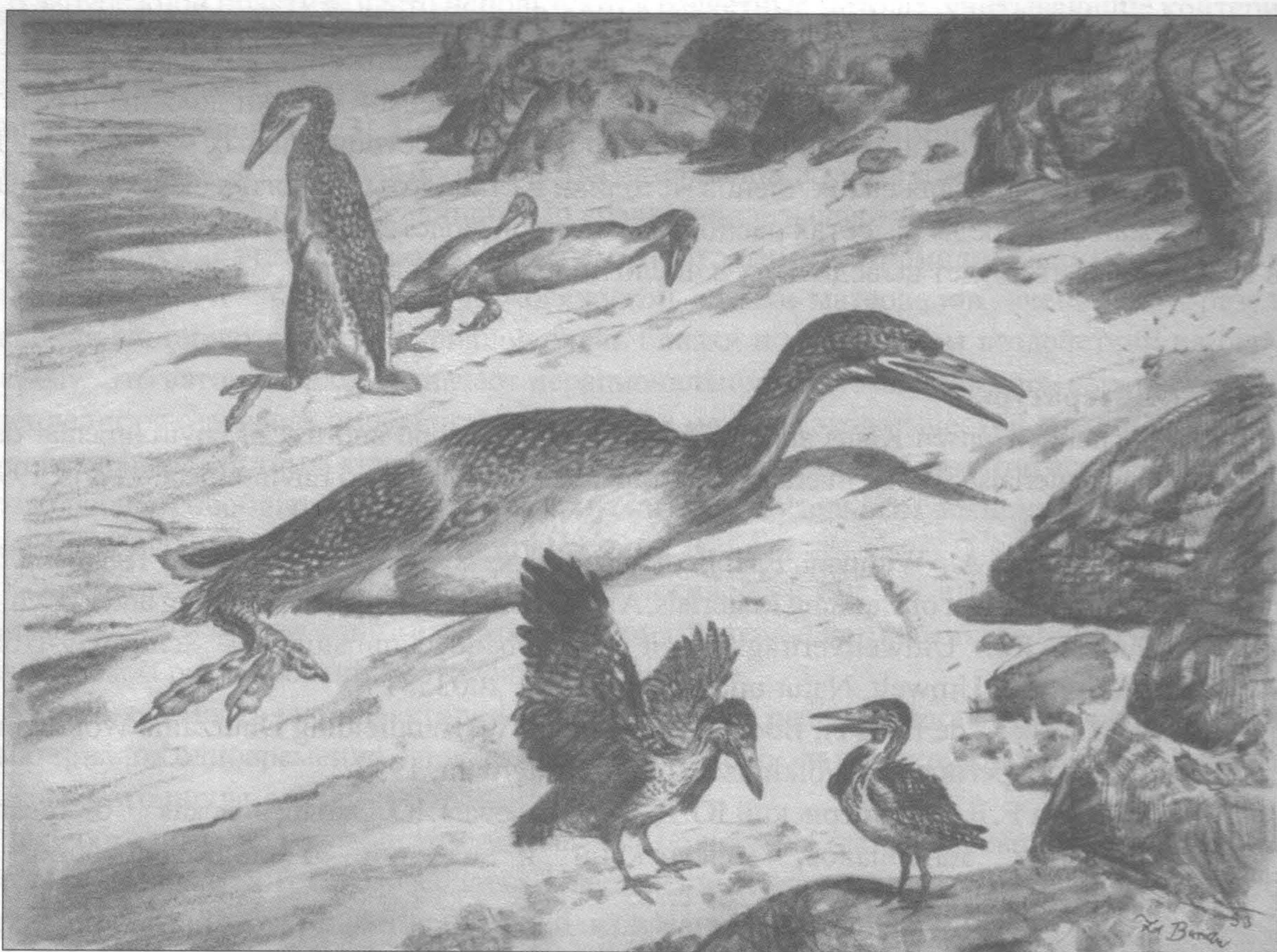


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## CRETACIOUS FOOT-PROPELLED BIRD HESPERORNIS: ITS OWN WAY

*Hesperornis regalis* belongs to the order Hesperornithiformes, which includes a small and restricted group of mid- to Late Cretaceous marine toothed, foot-propelled diving birds [1] (fig. 1). Since its discovery in Cretaceous shales of Kansas in 1870 [2, 3] *Hesperornis* has been treated in numerous publications.



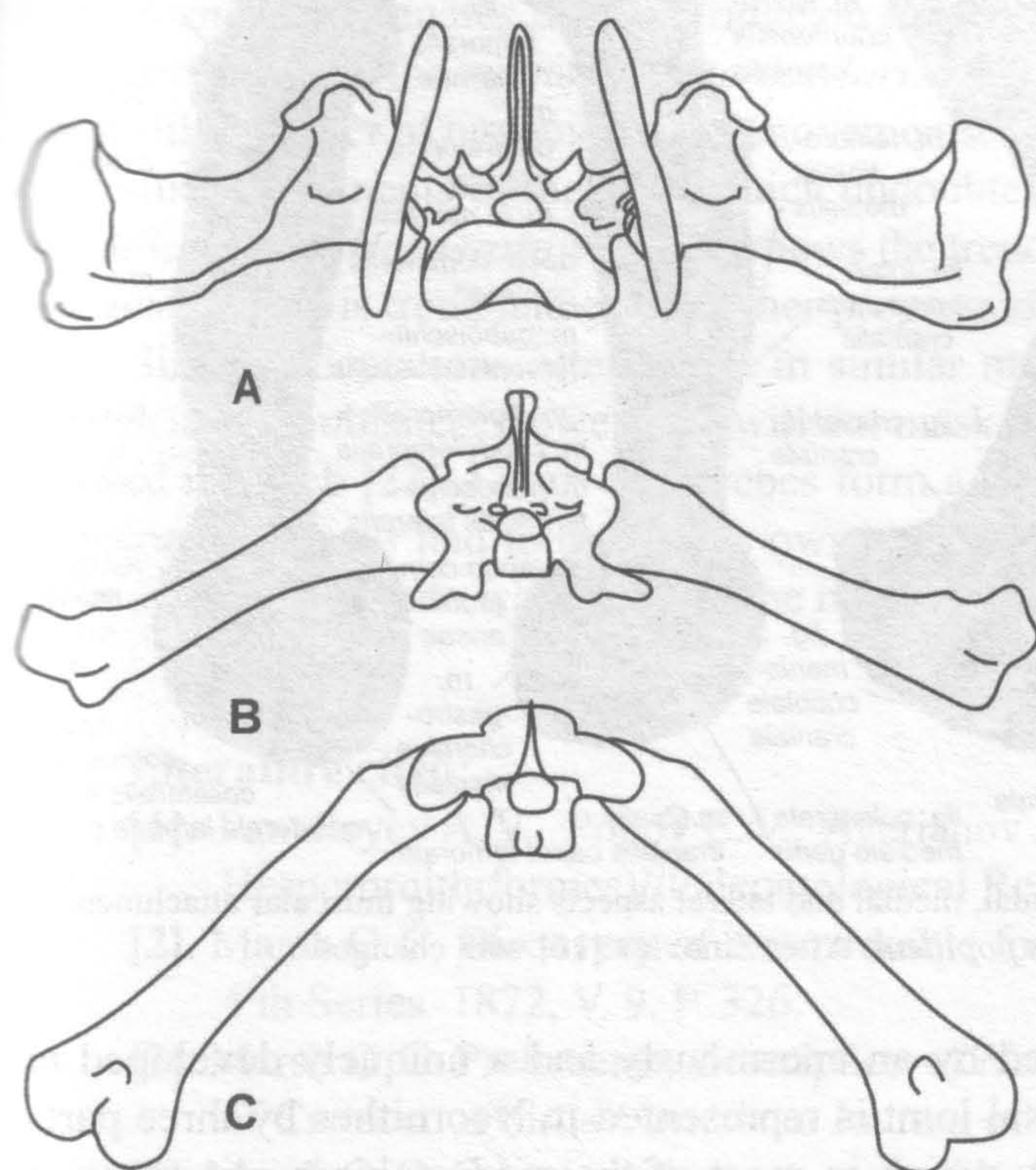
**Figure 1.** *Hesperornis* and *Ichthyornis* (two individuals on the foreground) on the beach of Late Cretaceous sea. After Augusta & Burian [23] with changes.

Marsh's monograph [4], preceded by several smaller papers by the same author [5–9] gave a comprehensive first description of its skeleton along with some functional interpretations. Marsh was the first to notice the resemblance of *Hesperornis*'s hindlimb skeleton to that of the grebe, supposing a similar pattern of foot-propelled diving in both birds. Although the foot-propelled diving by *Hesperornis* might have resembled that of grebes or loons, Marsh correctly noticed that the former was somewhat further on the way toward adaptations for diving. Besides losing the ability of flight, *Hesperornis* had only one (fourth) toe predominantly developed as “an example of the same kind of specialized modification which has prepared the foot of the Ostrich, among recent birds, and the Horse among mammals, for extreme speed on the land” [4: p. 95]. Finally, Marsh gave a reconstruction of the *Hesperornis*'s lifestyle which generally corresponds

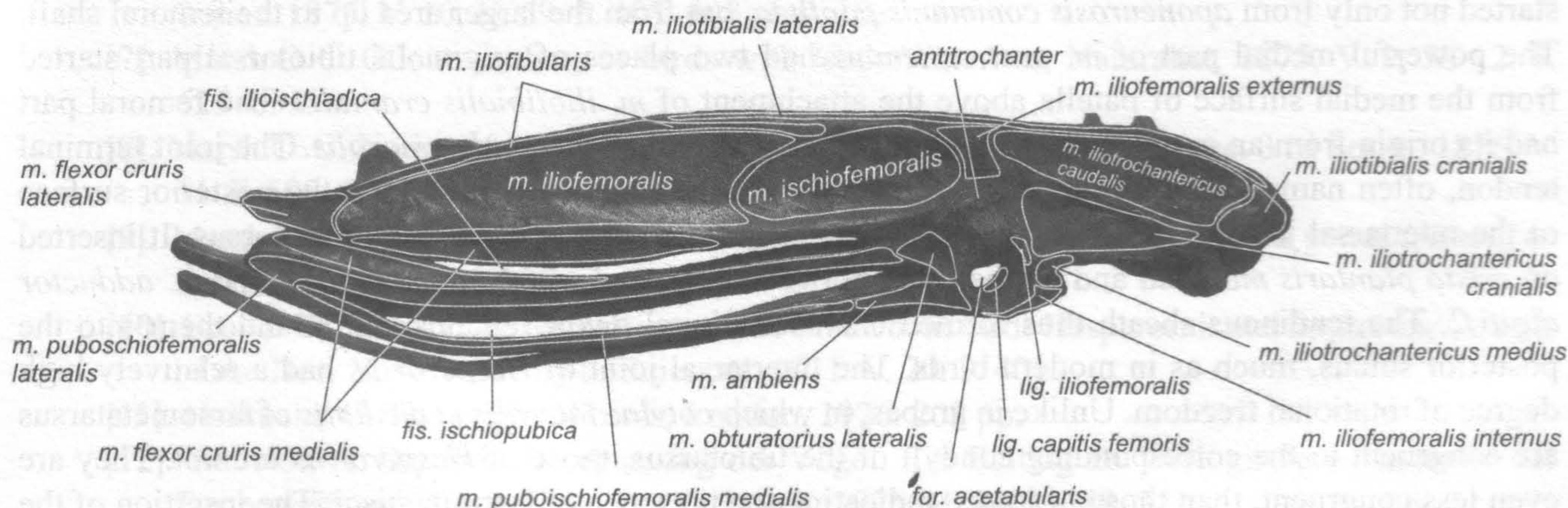
our modern understanding of this fossil bird. “*Hesperornis* was a typical aquatic bird, and in habit was doubtless very similar to the Loon, although, flight being impossible, its life was probably passed entirely upon the water, except when visiting the shore for the purpose of breeding... *Hesperornis*, as we have seen, was an admirable diver, while the long neck with its capabilities of rapid flexure, and the long slender jaws armed with sharp recurved teeth formed together a perfect instrument for the capture and retention of the most agile fish” [4: p. 112]. Most of the following authors agreed with Marsh’s reconstruction [10, 11]. Although hindlimb bones and those of the pelvic girdle of *Hesperornis* bear pronounced marks of muscular origins and insertions, nobody has ever attempted to reconstruct them. The majority of authors mention robust development of the muscles responsible for holding the femur and for extending and flexing the intertarsal joint [12, 13]. Stolpe [14] also discussed the development of femoral pronators and ligaments of the intertarsal joint. Only Martin and Tate [15], in their comparative treatment of *Baptornis*, made an attempt to reconstruct some of *Hesperornis*’s muscles. The following paragraphs summarize the more extensive treatment of hindlimb muscles and ligaments of *Hesperornis*, presented elsewhere [16].

It is of particular value for understanding the early adaptive evolution of birds.

Hindlimb myology and syndesmology of *Hesperornis regalis* shows a remarkable mixture of features, characteristic of modern foot-propelled divers, such as loons and grebes. Shortened and anteroposteriorly compressed femora were held in an extremely sprawling position, exceeding that of modern counterparts (fig. 2). Although fixed by tight ligaments, the hip joint of *Hesperornis* allowed a certain degree of craniocaudal movement, necessary for the propulsive and recovery strokes. The retraction of the femur was especially important owing to a high development of *mm. puboischiofemorales*, *m. iliofemoralis* and, probably, *m. caudofemoralis* (fig. 3). The latter was the principle femoral retractor of the archosaurian ancestors, and might have been still well-developed in *Hesperornis*, participating in movements of the relatively powerful tail. Well developed deep pelvic muscles such as *mm. iliotrochanterici*, *m. ischiofemoralis*, *m. iliofemorales externus et internus*, *mm.*

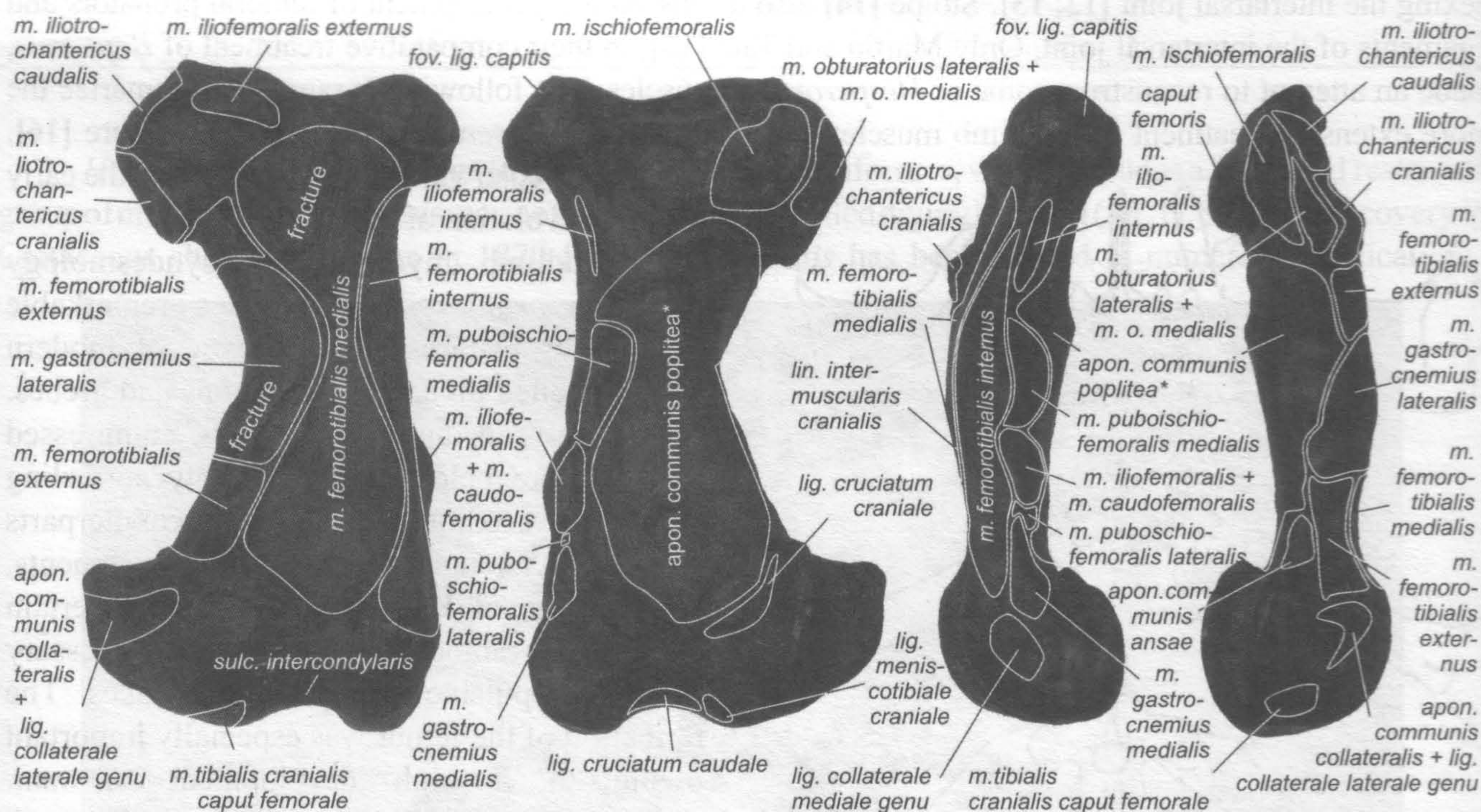


**Figure 2.** Anterior view of pelvi of *Hesperornis regalis* (A), Red-throated Loon *Gavia stellata* (B) and Great Crested Grebe *Podiceps cristatus* (C) showing the position of femora. B and C, after Kurochkin [18]. Not to the scale.



**Figure 3.** Pelvis of *Hesperornis regalis* showing muscular attachments. After Zinoviev [16] with changes.

*obturatores* controlled the hip joint, counteracting side-effects (inward and outward rotation) of the femoral protractors-retractors action (fig. 3). Ligaments of the knee joint of typical avian position and morphology allowed a high degree of inward-outward rotation of the tibiotarsus, which has been held close to the body and more likely, was enclosed in the thickly feathered skin of the body wall. Flexion-extension movements in the knee-joint were highly reduced, partially by well-developed *mm. flexores cruris*, *m. iliofibularis* and postacetabular portion of *m. iliotibialis lateralis*, and partially by *m. femorotibialis medialis*, which inserted onto almost entire posterior surface of enlarged patella (fig. 4). Enlargement and elongation of the patella allowed corresponding enlargement and elongations of extensors of the intertarsal joint. This increased the power and amplitude of propulsive and recovery



**Figure 4.** Right femur of *Hesperornis regalis* in cranial, caudal, medial and lateral aspects showing muscular attachments. indicates greatly expanded *apon. communis popliteus*. After Zinoviev [16] with changes.

strokes of feet, in which the main role was played by an enormously and a uniquely developed *m. gastrocnemius*. This powerful extensor of intertarsal joint is represented in Neornithes by three parts. The lateral part (*m. gastrocnemius pars lateralis*), which in most of the modern birds originates on the *aponeurosis communis ansae*, shows unique features in *Hesperornis*. Enormously developed, it expands proximally on the lateral and cranial surface of the femoral shaft. Its fleshy origin is marked by fine striations while the powerful tendinous origin is manifested by a large scar. The intermediate part (*m. gastrocnemius pars intermedia*), generally small in modern birds, was also unusually powerful. It started not only from *aponeurosis communis poplitea*, but from the larger area up to the femoral shaft. The powerful medial part of *m. gastrocnemius* had two places of origin. Its tibiotarsal part started from the medial surface of patella above the attachment of *m. iliotibialis cranialis*. The femoral part had its origin from an extensive tuberosity just distal to that of *m. caudofemoralis*. The joint terminal tendon, often named the Achilles tendon, passed over the tibial cartilage along the posterior surface of the intertarsal joint to insert on almost the entire plantar surface of the tarsometatarsus. It inserted on *crista plantaris mediana* and on the ridge between bellies of *m. abductor digiti 4* and *m. adductor digiti 2*. The tendinous sheath thus formed enclosed digital flexor tendons and bound them into the posterior sulcus, much as in modern birds. The intertarsal joint of *Hesperornis* had a relatively high degree of rotational freedom. Unlike in grebes, in which *cotylae lateralis et medialis* of tarsometatarsus are congruent to the corresponding condyli of the tibiotarsus, those of *Hesperornis* are not. They are even less congruent, than those of loons, indicating the presence of large menisci. The insertion of the *meniscus lateralis* is visible on the joint surface of *Hesperornis's* tibiotarsus (fig. 5). *Cornu caudale*

of the mentioned meniscus inserted in the pit posteromedial to *eminentia intercotylaris*. The medial meniscus did not leave any traces on the anterior rim of the *cotyla medialis*. The incongruence of bony surfaces of corresponding cotyla and condyle in *Hesperornis* makes the presence of *meniscus medialis* at least along the anterior rim of *cotyla medialis* highly desirable. The absence of bony congruence in the intertarsal joint and the presence of well-developed menisci are indicative of a relatively free intertarsal joint [17]. Such a joint in *Hesperornis* shows an importance of supination of the tarsometatarsus during underwater locomotion, like in modern loons [18]. The supination of the tarsometatarsus is achieved by the contraction of *m. fibularis brevis*, the presence of which in *Hesperornis* is thus proved on functional grounds. This relatively free joint should also be stabilized. This stabilization in extant birds is achieved through a peculiar morphology of *lig. anticum*, which shortens during the inward rotation of tarsometatarsus. This brings the joint surfaces closer to each other [17]. Modern grebes have a highly congruent and tight intertarsal joint, fixed by strong collateral ligaments and thus lacks *lig. anticum* [18, 19]. On the contrary, loons have this ligament [18–20] as does *Hesperornis*. It originates from the ridge on the proximal part of *sulcus intercondylaris* and inserted on the anterior rim of the *eminentia intercotylaris* (fig. 6). In this way it resembled that of loons, showing a loon-like manner of tarsometatarsal movements. This loon-like manner, however, was combined with grebe-like movements of the toes, which undoubtedly had asymmetrical lobes [19]. Unlike grebes or fossil *Baptornis*, *Hesperornis regalis* shows the trend to the enlargement of the fourth toe at the expense of the others. This trend had even further progression in *Hesperornis mengeli* [21] and *H. rossicus* [1].

Similar adaptations often result in similar morphological changes. These changes can result in superficial resemblance. However, it will not mask true affinities if the morphology is subjected to more detailed research [22]. Loons and grebes form a good example [12, 14, 19]. Present study shows that *Hesperornis regalis* had found yet its own – a third way [11, 13, 15], combining more loon- and less grebe-like features into what became the most specialized foot-propelled avian diver ever known.

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#### Figure captions

Figure 5. Right tibiotarsus and patella of *Hesperornis regalis* in medial, cranial, lateral and caudal aspects showing muscular attachments. After Zinoviev [16] with changes.

Figure 6. Proximal joint surface of right tarsometatarsus of After Zinoviev [16] with changes.