/LATE CRETACEOUS (CENOMANIAN)
HESPERORNITHIFORMES FROM THE PASQUIA HILLS,
SASKATCHEWAN, CANADA/

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ABSTRACT

A large assemblage of fossil bird bones, collected over several field seasons from marine deposits at a locality in the Pasquia Hills, Saskatchewan, Canada, has revealed new information on the order Hesperornithiformes. The fossils were discovered in the Belle Fourche Member of the Ashville Formation, a mid Cenomanian (~95 Ma) deposit which outcrops along the eastern margin of the Western Interior Basin. Over 250 disarticulated and non-associated fossil bird bones were discovered along with fossil remains of sharks, bony fishes and tetrapods in a bonebed associated with the *Ostrea beloiti* layer, a regional stratigraphic marker. Two species of the hesperornithiform genus *Pasquiaornis* previously described from a locality on the Carrot River, 100 km to the SE and of similar age have now been identified at the Pasquia Hills locality. These two localities have produced the oldest diverse avifauna found to date in North America, including Ichthyornithiformes and Enantiornithes, as well as the oldest Hesperornithiformes known from North America.

The fauna from the Pasquia Hills bonebed includes a possible new species of *Pasquiaornis* as well as a possible new unknown hesperornithiform species. The original description of *Pasquiaornis* included the quadrate, humerus, femur and tarsometatarsus. This study adds descriptions of new elements such as the cranial and mandibular elements, teeth, vertebrae, scapula, coracoid, ulna, radius, carpometacarpus, pelvis, tibiotarsus, fibula and phalanges as well as a more complete description of previously described *Pasquiaornis* elements. The new pectoral and wing elements of *Pasquiaornis* add new information on the evolution of flightlessness in Hesperornithiformes. Comparisons are made with several other genera of Hesperornithiformes, including

Enaliornis from the late Albian of England, the oldest known. The new discoveries of hesperornithiform material from the Pasquia Hills locality add considerably to interpretations of the early evolution and diversification of these marine toothed birds in the Late Cretaceous Western Interior Seaway.

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INTRODUCTION

A marine bonebed from the Late Cretaceous (Cenomanian) was discovered in 1994 by a joint team from the Canadian Museum of Nature (CMN) and the Royal Saskatchewan Museum (RSM) in eastern Saskatchewan, along the northern portion of the Manitoba Escarpment. This bonebed, located along the Bainbridge River in the Pasquia Hills (Figure 1), has already received abundant scientific attention and is part of a more extensive stratigraphic section that has been studied to advance our understanding of the evolution of the northeastern portion of the Western Interior Seaway (WIS). Several studies have addressed paleoenvironments, stratigraphy and overall faunal composition (Cumbaa and Tokaryk, 1999; Cumbaa and Bryant, 2001; Schröder-Adams et al., 2001; Cumbaa et al., 2006).

The faunal assemblage of the bioclastic conglomerate is diverse and contains abundant fossil shark teeth as well as teeth, scales and bone fragments from bony fish, turtle bone, plesiosaur bone, and bird bones and teeth (Cumbaa et al., 2006). The fossil group that has not yet received detailed study are the abundant bird bones and teeth known from the locality.

The bonebed contains the largest accumulation of bird bones known from the Cretaceous of North America, and along with those found in the Carrot River locality, 100 km southwest of the Bainbridge River (Figure 1), the oldest known bird bones in North America (Cumbaa and Tokaryk, 1999). The majority of the bird bones from the Bainbridge River site were tentatively described as *Hesperornithiformes*.

Hesperornithiformes are known from the Late Cretaceous and were loon-like birds, using foot-propelled diving as their primary locomotion (Figure 2). Marsh (1880)

Figure 1. Map of North America focusing on the Manitoba escarpment, which forms the eastern erosional edge of the Cretaceous Western Interior Sea. 1, Pasquia Hills; ●, Bainbridge River locality; ■, Carrot River locality. Modified from Schröder-Adams et al. (2001).

Figure 2. Skeleton of *Baptornis advensus* showing the general body plan of a hesperornithiform (Martin and Tate, 1976). Scale bar equals 5 cm.

was the first to discover and describe the Hesperornithiformes, using the lower end of a tibiotarsus discovered by him in 1870 near the Smoky Hills River in western Kansas. His expedition to the area was cut short by local threats from Native American tribes and extreme weather (Marsh, 1880). The following year, with a larger group and an escort of troops, Marsh returned and discovered the rest of the skeleton of the species he named *Hesperornis regalis* (Marsh, 1880). From these and subsequent expeditions, Marsh discovered about nine genera and twenty species of birds (Marsh, 1880). *Hesperornis* and *Ichthyornis* were two of the more unusual birds, as they both had teeth (Gingerich, 1976). Marsh's results were published in his book "*Odontornithes: A monograph on the extinct toothed birds of North America*" in 1880.

Hesperornithiformes have now been found globally, but appear mainly in the northern hemisphere. Localities include parts of the United States, such as Alaska (Bryant, 1983), Montana (Shufeldt, 1915), Wyoming (Bryant, 1983), South Dakota (Martin and Cordes-Person, 2007), Nebraska (Bryant, 1983) and Kansas (Marsh, 1880); parts of Canada, such as Saskatchewan (Tokaryk et al., 1997; Tokaryk and Harrington, 1992), Alberta (Bryant, 1983), Manitoba (Martin and Lim, 2002), Ellesmere Island (Hills et al., 1999) and Bylot Island (Hou, 1999); England (Seeley, 1876), Sweden (Rees and Lindgren, 2005), Russia (Penteleyev et al., 2004), Ukraine, Mongolia (Nessov and Borkin, 1983), and northern Kazakhstan (Dyke et al., 2006). A hesperornithiform has been said to be found in the southern hemisphere in Chile (Chiappe, 1991), although this claim has been disputed (Olson, 1992).

Five genera are described from North America; *Hesperornis* (Marsh, 1880), *Baptornis* (Martin and Tate, 1976), *Paraheperornis* (Martin, 1984), *Pasquiaornis* (Tokaryk et al., 1997) and *Canadaga* (Hou, 1999) and four are known from Europe and

Asia; *Hesperornis* (Panteleyev et al., 2004), *Enaliornis* (Seeley, 1876; Elzanowski and Galton, 1991; Galton and Martin, 2002), *Judinornis* (Nesov and Borkin, 1983) and *Asiahesperornis* (Rees and Lindgren, 2005). The majority of hesperornithiform bones were discovered in marine deposits; however, they are also known from freshwater deposits (Fox, 1974). Hesperornithiformes are known from the Albian (*Enaliornis* in England) to Maastrichtian (*Judinornis* from Mongolia and *Canadaga* from Bylot Island, Nunavut) aged strata (Galton and Martin, 2002; Hou, 1999; Panteleyev et al., 2004) of the Cretaceous. Specimens can range to well over a meter in size, resembling a loon in shape, but with a toothed beak and smaller (reduced) wings.

The Carrot River hesperornithiform fauna (Tokaryk et al., 1997) offers important comparative material for the Bainbridge River avian fauna of this study as it is of similar age and of close proximity. Fossils at the Carrot River locality, located 100 km from the Bainbridge River site in Saskatchewan were collected by Dickson Hardie for many years. Hardie's site (SMNH locality 63E03-0001) was excavated in 1992 and 1993 by the Royal Saskatchewan Museum and the Canadian Museum of Nature (Tokaryk et al., 1997). From this locality two species of the new genus *Pasquiaornis* (Tokaryk et al., 1997) were described.

This study will focus on the description of the Bainbridge River site hesperornithiform birds, with comments on taphonomy and paleoenvironments. Since the Bainbridge River fossils and those from the Carrot River locality are the oldest known hesperornithiform bones in North America (slightly older than a baptornithid known from the Greenhorn Formation in north central Kansas (Everhart and Bell, 2009), as well as constituting the largest known accumulation of bird bones in the Mesozoic of North America, the descriptions of these bones will contribute greatly to the knowledge of the

early evolution of hesperornithiforms and to fossil birds in general. The study of these birds will also contribute to our understanding of the early Late Cretaceous ecosystem and its vertebrate fauna that characterized the eastern shore of the Western Interior Seaway.

GEOLOGICAL SETTING

Western Canadian Sedimentary Basin

The Western Canadian Sedimentary Basin, a foreland basin, formed in correlation with the Cordillera Orogeny during the mid-Jurassic to Eocene (Kauffman and Caldwell, 1993). During the mid-Jurassic, the North American plate was migrating west as a result of rapid sea-floor spreading forming the early North Atlantic basin (Kauffman and Caldwell, 1993). The proto-Cordillera was created from the compression caused by the subduction of the Farallon plates underneath the western margin of the North American plate (Kauffman and Caldwell, 1993). During the mid-Jurassic to Eocene, the Western Canadian Sedimentary Basin evolved through the flexural downwarping of the lithosphere beneath the load of accreting terranes and developing fold and thrust belt (Beaumont et al, 1993). The Western Canadian Sedimentary Basin was a north-south trending basin, oriented parallel to the eastern margin of the Cordillera (Kauffman and Caldwell, 1993). The deepest part of the Western Canadian Sedimentary Basin was to the west, associated with the foredeep, and shallowing to the east onto the forebulge and stable eastern platform (Leckie and Smith, 1992).

Sedimentation into the Western Canadian Sedimentary Basin was controlled by many factors, including tectonics in the west and eustatic sea level fluctuations (Schröder-Adams et al., 2001). Erosion of the orogenic belt served as a source of fine-grained and

coarse-grained sediments filling the basin during the Mesozoic and Cenozoic, resulting in an eastward thinning wedge (McNeil and Caldwell, 1981; Kauffman and Caldwell, 1993; Kreitner and Plint, 2006).

The Late Cretaceous Western Interior Seaway

During the middle to Late Cretaceous (Albian age at about 110 - 100 Ma to the end of the Maastrichtian age at 65 Ma) an interior sea flooded much of the western interior of North America due to basin subsidence, tectonic uplift and generally high eustatic sea level (Hancock and Kauffman, 1979; Schröder-Adams et al., 2001). Shorelines moved dramatically and at highest sea levels, the seaway spanned 45° of latitude filling the mid-continent between the Cordillera and the Canadian Shield, connecting the Boreal Ocean to the north with the Tethyan Ocean to the south, and attained a width between 1200 and 2000 km (Kauffman, 1975; Williams and Stelck, 1975; Schröder-Adams et al., 2001). This seaway, known as the Western Interior Seaway (WIS), formed in the elongated Western Canadian Sedimentary Basin in the west and spilled over the Canadian Shield to the east (Schröder-Adams et al., 2001). Several transgressions and regressions occurred during the lifespan of the WIS (Figure 3). The end of the Maastrichtian was marked by rapid draining of the Western Canadian Sedimentary Basin, resulting in the retreat of the sea and a change from marine to terrestrial sedimentation (Cvancara and Hoganson, 1993).

The Cenomanian of the Late Cretaceous was affected by the Greenhorn transgressive – recessive cycles (Figure 3). Several sea-level lowstands affected the Cenomanian seaway. These are indicated by bioclastic conglomerates occurring at the

Figure 3. Global transgressive-regressive cycles of the Western Cretaceous Sedimentary Basin during the Cretaceous (Aptian to Santonian) and radiometric ages at the stage boundaries. Original global T-R cycle modified after Kauffman (1977). The lowstand at the Albian-Cenomanian boundary after Leckie et al. (2000); the mid-Cenomanian lowstand after Bhattacharya and Walker (1991); and the lowstand at the Cenomanian-Turonian boundary after Schröder-Adams et al. (1996). Absolute ages after Obradovich (1993).

Albian/ Cenomanian boundary (Leckie et al., 2000), in the mid-Cenomanian (Bhattacharya and Walker, 1991), and at the Cenomanian/ Turonian boundary (Schröder-Adams et al., 1996).

Relatively long periods of episodic water mass density stratification occurred throughout the history of the basin due to sluggish oceanic circulation and the interaction of northerly and southerly derived water masses (Kauffman, 1988; Hay, 1989; Hay et al., 1993). Thermal and salinity stratification is thought to have played a large role within the WIS during the Late Cenomanian to Santonian, by the mixing of cool, slightly brackish, Boreally derived waters and warm, normal salinity Tethys-derived waters (Kauffman, 1988; Hay, 1989; Caldwell et al., 1993; Glancy et al. 1993; Hay et al., 1993; Kyser et al., 1993; Schröder-Adams et al., 1996). These conditions, combined with possible northward incursions of expanded oxygen minimum zones into the bottom waters of the WIS from the Tethys Sea during peak transgression periods, all contributed to the density stratification, reduced downward mixing of oxygenated surface waters, reduced benthic oxygenation and increased organic-carbon accumulation during the late Cretaceous (Kauffman, 1988; Hay, 1989; Caldwell et al., 1993; Glancy et al., 1993; Hay et al., 1993; Kyser et al., 1993; Schröder-Adams et al., 1996; Leckie et al., 1998). Bottom waters in the mid-late Cenomanian on the eastern margin of the WIS would have been inhospitable for many benthic life forms.

The Manitoba Escarpment

The Manitoba Escarpment represents the eastern erosional margin of the Western Canadian Sedimentary Basin and the WIS. The escarpment trends southeast to northwest and is a series of uplands extending from south-central Manitoba and north-central North

Dakota to east-central Saskatchewan. From north to south, the Manitoba Escarpment is made up of the Pasquia Hills, the Porcupine Hills, Duck Mountain, Riding Mountain, and Pembina Mountain (Figure 1) (McNeil and Caldwell, 1981) and extends over 675 km (Cumbaa and Tokaryk, 1999).

The Manitoba Escarpment represents sedimentation that occurred along the eastern shore of the WIS, with significantly reduced sedimentation rates as compared to the western foredeep. Cretaceous strata along the Manitoba Escarpment are of Albian to Santonian age (McNeil and Caldwell, 1981; Cumbaa et al, 2006). These include, in ascending order, the Swan River Formation, Ashville Formation, Favel Formation, Morden Shale, Niobrara Formation, Pierre Formation and the Boissevain Formation (Figure 4) (Cumbaa et al, 2006; McNeil and Caldwell, 1981).

Cretaceous strata in the Pasquia Hills, the northernmost part of the Manitoba Escarpment, are characterized by marine sediments that were deposited during the upper Greenhorn and Niobrara eustatic cycles, which occurred in the Cenomanian to Campanian (McNeil and Caldwell, 1981; Kauffman and Caldwell, 1993; Schröder-Adams et al., 2001). The Greenhorn and Niobrara cycles are second-order cycles of the global sea-level scale (Haq et al., 1987; Schröder-Adams et al., 2001). Lithologies are dominated by siltstones, mudstones and calcareous mudstones (Bloch et al., 1999; Schröder-Adams et al., 2001).

Bainbridge River Locality

The Bainbridge River locality containing the bonebed is located on the northern slope of the Pasquia Hills, 100 km northeast of the Carrot River locality (Cumbaa and Bryant, 2001). The Pasquia Hills are located in east-central Saskatchewan, Canada and

Bainbridge River

Figure 4. Regional stratigraphic nomenclature with lithostratigraphy, relative abundances of planktic and agglutinated foraminifera and calcareous nannofossils and sea-level interpretation at the Bainbridge River locality. ♦ marks the stratigraphic position of the bird-rich bonebed (modified from Cumbaa et al., 2006). Note the two bentonites in stratigraphic vicinity of the *Ostrea beloti* bed possibly representing the 'X' bentonite (lower) and 'red' bentonite (upper) described by Tyagi et al. (2007).

constitute the northernmost of the five uplands that make up the Manitoba Escarpment (Figure 1) (Cumbaa et al., 2006). The Bainbridge River outcrop with field number BR-3 (Figure 5 and Figure 6) (RSM locality number 63E09-0003), is Cenomanian to Coniacian in age and is comprised of, in ascending order, the Belle Fourche Member of the Ashville Formation, the Keld and Assiniboine members of the Favel Formation and the Morden Shale (McNeil and Caldwell, 1981; Cumbaa et al., 2006).

Two vertebrate-rich horizons are known from the Belle Fourche Member at this locality which was deposited during the Greenhorn Cyclothem (Figure 4) (Schröder-Adams et al., 2001; Cumbaa et al., 2006). The upper vertebrate-rich horizon, a bonebed that occurs in lenses, is the source of the fossil bird material that will form the basis of this study and is stratigraphically constrained by three marker beds. Immediately below the bonebed is the *Ostrea beloiti* bed, which is a widely recognized marker bed of middle Cenomanian age throughout the Western Interior (Hattin, 1965; McNeil and Caldwell, 1981; Collom, 2000; Cumbaa et al., 2006).

The *Ostrea beloiti* bed is associated with the ‘X’ bentonite (McNeil and Caldwell, 1981), which was designated in previous studies of this outcrop as the bentonite occurring two meters above the shell bed (Cumbaa and Bryant, 2001; Schröder-Adams et al., 2001; Cumbaa et al., 2006). However, a second bentonite also occurs below the shell bed (Figure 4) at the Bainbridge River locality. In Alberta, Tyagi et al. (2007) regionally correlated on well logs the ‘X’ bentonite (94.93 Ma) within the Belle Fourche Formation (equivalent to the Belle Fourche Member of the Ashville Formation) and mapped a regionally extensive bentonite known as the “red” bentonite (93.5 Ma) at the base of the Second White Specks Formation (subsurface equivalent of the Favel Formation). As this is the approximate position of what has been termed the ‘X’ bentonite at the Bainbridge

Figure 5. BR-3 outcrop along the Bainbridge River in Saskatchewan, Canada. The lower white line indicates the proximate position of the boundary between the Ashville Formation and the Favel Formation. The upper white line marks the boundary between the Favel Formation and the Morden Shale (Photo courtesy of Dr. Steve Cumbaa).

Figure 6. Bonebed in situ at the BR-3 site along the Bainbridge River. This bonebed is the source of the fossil bird material for this study. The *Ostrea beloiti* layer is a 2.5 to 5 cm resistant layer just below the bonebed, in the bottom third of the photo. The black arrow indicates the bonebed and the red arrow indicates the *Ostrea beloiti* layer. Scale bar equals 5 cm (Photo courtesy of Dr. Steve Cumbaa).

River locality, it has become apparent that new dates are necessary in order to clarify the correct position and designation of these two important marker bentonites, a study that is in progress. The 'X' bentonite marker bed gives published $^{40}\text{Ar}/^{39}\text{Ar}$ ages ranging from 93.3 Ma to 94.93 Ma (Cadrin, 1992; Obradovich, 1993; Tyagi et al., 2007), placing the bonebed chronostratigraphically between the middle Cenomanian and the early Turonian (Cumbaa et al., 2006).

The middle to late Cenomanian age is also supported by the presence of Foraminifera characteristic of the *Verneuilinoides perplexus* Zone (Schröder-Adams et al., 2001). In addition, the vertebrate fauna confirms a Cenomanian age assignment. Primarily, shark teeth of species known from Albian and Cenomanian age strata, like *Ptychodus decurrens* and *P. occidentalis* (Cenomanian), *Squalicorax curvatus* and *S. 'volgensis'* (Cenomanian), *Cretodus semiplicatus* (Cenomanian), *Carcharias amonensis* (Cenomanian), and *Cenocarcharias tenuiplicatus* (Cenomanian) support a Cenomanian age for the fauna (Cumbaa et al., 2006).

Origin and composition of the Bainbridge River bonebed

The bonebed is identified as a bioclastic conglomerate with large bone and teeth inclusions, randomly oriented, with abundant disarticulated bird, plesiosaur, shark and bony fish remains and abundant coprolites (Figure 7) (Cumbaa and Tokaryk, 1999). The bonebed is characterized by occasional calcite vugs, which range up to several centimetres in dimension (Cumbaa and Tokaryk, 1999). These vugs are the result of diagenetic changes in rip-up clasts of bentonite (Cumbaa and Tokaryk, 1999). Chunks of compacted and degraded volcanic ash were incorporated into the bioclastic material,

Figure 7. Samples of bonebed blocks from the Bainbridge River locality after initial acid preparation. Notice the abundance of fossil material. Bonebed contains shark teeth (1), bony fish teeth (2) and bones (3), bird teeth and bones (4), turtle bones, and plesiosaur and other reptile bones (5) and teeth. Lower photo courtesy of Dr. Charlie Underwood.

apparently before consolidation of the sediment as the enclosing matrix is frequently deformed around the clast (Cumbaa and Bryant, 2001).

Cretaceous strata at the Bainbridge River and Carrot River localities reflect several lowstand events that occurred throughout the overall Greenhorn transgression (Schröder-Adams et al., 2001). Schröder-Adams et al. (2001) suggest the presence of two facies in the Belle Fourche Member at this locality. Facies 1 is a black, non-calcareous shale that was most likely deposited in a shallow and quiet water environment below tidal influence where algal cysts could settle. Excellent preservation of algal cysts, a low diversity of benthic foraminiferal assemblage, lack of bioturbation and the presence of isorenieratane indicates depleted oxygen conditions in a restricted basin which may be suggestive of a lagoonal setting (Schröder-Adams et al., 2001).

The Cenomanian bonebeds that are located on top of facies 1 in the Bainbridge River and Carrot River sections are interpreted as being the result of a sea-level fall and subsequent transgression causing reworking and seafloor winnowing on the clastic sediment-starved eastern margin of the WIS, resulting in high accumulation of vertebrate debris (Schröder-Adams et al., 2001). Facies 2 of the Belle Fourche Member is found at the Bainbridge River section, but not the Carrot River section, and represents an early transgressive deposit that is characterized by numerous fine sandstone interbeds and increased oxygen, allowing bioturbation and oyster beds to develop, which were frequently reworked by currents and waves as indicated by hummocky cross stratification (Schröder-Adams et al., 2001). This explains why algal cysts became rare and foraminiferal assemblages were still unable to establish (Schröder-Adams et al., 2001). This interval is marked by a lag of bivalve shell debris (*Ostrea beloiti*) overlain by a lens-

shaped bonebed (Schröder-Adams et al., 2001) that was interpreted as a result of a major marine erosion event of short duration.

The coarser clastic intervals found within the Belle Fourche Formation in the foredeep regions of the WIS reflect periods of sea-level lowstand and increased sediment input during orogenesis to the west (Cumbaa et al., 2006). Along the eastern margin of the seaway where only minor coarse clastic sediment is available, seafloor winnowing and reworking resulted in rich bonebeds (Cumbaa et al., 2006).

Cumbaa et al. (2006) created a comprehensive list of the vertebrate fauna found in the Bainbridge River site. This list of taxa contains few, if any, species that are obligate offshore forms. Rather, the species list suggests a nearshore environment, such as the lagoonal environment suggested by Schröder-Adams et al. (2001).

Schröder-Adams et al. (2001) studied the taphonomy of the bonebed for clues to its origin. The presence of numerous and well preserved coprolites suggests a continuous accumulation of biotic sediment in quiet water (Schröder-Adams et al., 2001). The lack of siliclastic components and the high concentration of bones and teeth (48% to 70%) indicate a relatively long period of deposition with little terrigenous sedimentation (Schröder-Adams et al., 2001). Some of the larger and heavier fossil elements, like plesiosaur vertebrae, are worn and rounded, while the lighter fossil elements, like shark teeth and bird bones, are well preserved. Taphonomic indicators of the bonebed suggest a process of continual accumulation in a sediment starved environment. Water depths would have been shallow enough that winnowing by waves could occur, which would cause the lighter elements to drift and then be redeposited while the heavier elements would be abraded (Schröder-Adams et al., 2001).

The bioclastic conglomerate is classified as a bone-biospharenite that had coarse grainstone to rudstone texture (Phillips, 2008). The rock was relatively well sorted and consisted of 39.4% calcite cement, with phosphatic clasts tabular, spindle and ovoid in shape. It also contained fossils, accounting for 57.4 % of the rock (Phillips, 2008). The BR-3 locality contained trace siliclastic grains (quartz) and common inoceramid-derived prismatic calcite. Euhedral and framboidal pyrite, though rare, sometimes occurs around inoceramid-derived calcite crystals and coprolites. Significantly pyritized grains were rare. Randomly oriented, “floating” grains were abundant, with point contacts between grains. Grain size of the BR-3 bonebed was large (1-3mm) (Phillips, 2008). Bone preservation is generally excellent, and the bird bones, while sometimes abraded and incomplete, show little if any distortion.

MATERIAL AND METHODS

Fossil material used in this study was collected from the Bainbridge River locality in Saskatchewan during multiple field seasons between 1994 and 2009 by a joint field project of the Royal Saskatchewan Museum (RSM) and the Canadian Museum of Nature (CMN). The fossil bird bones are part of one bonebed as described above. A significant amount of preparation was required to free the bones from the sedimentary matrix to make them available for study.

Preparation

Over 300 bird bones were prepared from the bonebed blocks. The blocks were carefully prepared by using an airtscribe, pin vise, dental pick, and scalpel. An airtscribe was used for the removal of the surrounding matrix that was not in direct contact with the

bone. Once preparation was close to the bone surface, a pin vise dental pick, and scalpel were used to remove the matrix so as to minimize bone damage. A 5% acryloid B-72/acetone mixture was used to consolidate the bone material by brushing the glue gently on to newly exposed bone surfaces to fill in any cracks and porous areas.

A solution of 5% acetic acid (CH_3COOH) buffered with a calcium orthophosphate [$\text{Ca}_3(\text{PO}_4)_2$] was used to loosen the sediment by dissolving the calcium carbonate cement on some of the more fragile specimens as to avoid damage by the pin vise or air scribe. Bones prepared in this fashion were rinsed in water for 24 hours to remove any residual acid. This type of preparation was also used in order to retrieve all shark teeth, bony fish teeth, scales and bone, and other fossil material from the bonebed blocks. Many bird bones obtained from previous acid preparations were highly fragmented. These bones were still used for analysis when identification was possible. Appendix I shows a list of all the fossil bird material prepared from the Bainbridge River bonebed blocks.

Comparative Study

Once the bones were fully prepared catalogue numbers were received from the Royal Saskatchewan Museum. Bones were identified using both literature (Gilbert et al., 1981; Gregory, 1951; Marsh, 1880; Martin and Tate, 1976) and fossil and modern comparative skeletal material. Anatomical nomenclature used to describe bones was from Baumel et al. (1993) and Gilbert et al. (1981). Collections of hesperornithiform material were examined during visits to the Royal Saskatchewan Museum and its research station in Eastend (Saskatchewan), the Royal Tyrrell Museum in Drumheller (Alberta), the University of Kansas in Lawrence (Kansas) and the Peabody Museum at Yale University

in New Haven (Connecticut) to compare with fossil material from the Bainbridge River. Comparisons made with *Ichthyornis* and *Gansus* can be found in Appendices III and IV.

Measurements of bone material were made using sliding calipers that are accurate to 0.1 mm. Bone measurements were made using the standard measurement technique outlined in von den Driesch (1976). Appendix II shows all the bone measurements made from the Bainbridge River birds.

Bone Images, Scanning Electron Microscope and X-rays

Photos of the bones were taken using a Canon Power Shot S5IS digital camera. In order to obtain depth of field and sharp images, multiple photos were taken of the bone at different depths of focus and then put together using Auto Montage-Pro. A Philips XL30 Environmental Scanning Electron Microscope (ESEM) was used at the CMN to take high resolution images of hesperornithiform teeth in aid of detailed descriptions. Several bones were also x-rayed at the CMN to observe any internal structures.

Regularized Discriminant Analysis

The main purpose of Regularized Discriminant Analyses (RDA) is to assign objects to one of several groups based on a set of measurements obtained from the objects (Friedman, 1989). This statistical method was successfully used by Hinić-Frlog and Motani (*in press*) who categorized 245 species of extant birds into six swimming styles or categories based on RDA of 32 different skeletal measurements. This method is used here to reconstruct, by comparison, the style of swimming of *Pasquiaornis tankei* and *Pasquiaornis hardiei*.

The data was log transformed prior to the RDA. The first RDA was performed on *P. tankei* using the following measurements for analysis: humerus length, humerus mid-shaft transverse diameter, humerus mid-shaft medial-lateral diameter, carpometacarpus length, coracoid length, scapula length, femoral length, femoral mid-shaft transverse diameter, femoral mid-shaft medial-lateral diameter, cnemial crest length, tarsometatarsus length, tarsometatarsus mid-shaft transverse diameter, and tarsometatarsus mid-shaft medial-lateral diameter. *P. hardiei* was not included in the first RDA, as many of the measurements were not available. The second RDA addressed both *P. tankei* and *P. hardiei* using the following measurements for analysis: femoral length, femoral mid-shaft transverse diameter, femoral mid-shaft medial-lateral diameter, cnemial crest length, tarsometatarsus length, tarsometatarsus mid-shaft transverse diameter, and tarsometatarsus mid-shaft medial-lateral diameter. The analyses were performed using the program JMP 7.

Institutional Abbreviations Used:

AMNH, American Museum of Natural History, New York, New York, USA; **BMNH**, The Natural History Museum, London, UK; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **KUVP**, University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **PU**, Princeton University (collections now housed in Yale Peabody Museum), New Haven, Connecticut, USA; **RSM (SMNH)**, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **SDSM**, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **SMC**, Sedgwick Museum of Earth Sciences, The University of Cambridge, Cambridge, UK; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska, USA; **USNM**, Smithsonian National Museum of Natural History, Washington, D.C., USA; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA; **ZIN PO**, Paleornithological Collection of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

RESULTS

Systematic Palaeontology

Class AVES Linnaeus. 1758

Subclass ODONTOHOLCAE Stejneger, 1885

Subclass ORNITHURAE Haeckel, 1866

Order HESPERORNITHIFORMES Fürbringer, 1888

Diagnosis – Foot-propelled diving birds with fusion of cranial bones caudal to frontoparietal suture, palate with short broad pterygoids and long narrow palatines, quadrate pneumaticity reduced or absent, small prementary bone, intramandibular articulation between angular and splenial bones, all dorsal vertebrae heterocoelous, sternum unkeeled, long bones non-pneumatic, reduction of wing, humerus lacks distinct distal condyles, acetabulum partly closed, postacetabular pelvis greatly elongated, femur relatively short and broad, tibiotarsus with large cnemial crest shaped like an isosceles triangle in cranial view, large trihedral patella with foramen for ambiens tendon, tarsometatarsus transversely compressed with distinct craniolateral ridge leading distally to lateral trochlea (IV), distal lateral trochlea at least as large and distally extending as the middle trochlea (III), feet lobed with fourth toe the longest (Galton and Martin, 2002).

Family BAPTORNITHIDAE American

Ornithologist's Union, 1910

Diagnosis – Foot-propelled diving birds with fully heterocoelous vertebrae; uncinate processes turned dorsally (straight in *Hesperornis*); coracoid more slender than hesperornithids; pelvis with preacetabular portion of the ilium relatively longer than in hesperornithids; patella pyramidal in shape (much more laterally compressed in

Hesperornis); intracentral bones not fused to caudal vertebrae; pygostyle long and laterally compressed; outer trochlea of tarsometatarsus an open groove; toe rotation not well developed (Martin and Tate, 1976).

Genus PASQUIAORNIS Tokaryk et al., 1997

Diagnosis – Differs from the other member of the family, *Baptornis*, in: the trochanteric ridge of the femur is closer to the shaft of the femur; proximal end relatively less expanded lateromedially; the intercotylar prominence of the tarsometatarsus is anterior, overhanging the shaft; and trochlea for digit 2 posterior and close to the base of trochlea for digit 3 (Tokaryk et al., 1997).

Revised Diagnosis – Glenoid and scapular facet located farther sternally on the coracoid than in other Hesperornithiformes; less reduced humerus compared to other Hesperornithiformes, with distinctive condyles distally; less reduced ulna; presence of a carpometacarpus; dorsal vertebrae are amphicoelous; the acetabulum of the pelvis is open; the trochanteric ridge of the femur is closer to the shaft; proximal end relatively less expanded lateromedially; femur slender compared to other hesperornithiforms; the neck of the femur is short; the proximal articular surface of tibiotarsus is perpendicular; the intercotylar prominence of the tarsometatarsus is anterior, overhanging the shaft, and; trochlea for digit 2 posterior and close to the base of trochlea for digit 3; the anterior ridge along metatarsal 3 dissipates half way down the shaft.

Pasquiaornis hardiei Tokaryk et al., 1997

Diagnosis – Internal cotyle of the tarsometatarsi deflected toward shaft; neck of 3rd trochlea higher anteriorly than 4th; femur small, distal rim of head perpendicular to shaft.

Referred specimens from the Bainbridge River locality - RSM P2957.12, left frontal; RSM P2997.36, right frontal; RSM P2526.4, partial right dentary; RSM P2831.6, rostral tip of the left dentary; RSM P2831.21, right splenial; RSM P2985.9, right splenial; RSM P2988.27, right splenial; RSM P2831.18, right angular; RSM P2988.19, left angular; RSM P2989.37, right angular; RSM P2997.76, right angular; RSM P2989.19, left lower jaw; RSM P2831.8, cervical vertebra; RSM P2831.7, left half of a dorsal vertebra; RSM P2985.2, dorsal vertebra; RSM P2626.18, cranial end of a synsacrum; RSM P2831.12, ventral half of a synsacrum; RSM P2989.25, cranial portion of the synsacrum; RSM P2831.54, left coracoid; RSM P2985.8, proximal left scapula; RSM P2987.21, proximal right scapula; RSM P2989.15, distal right humerus; RSM P2995.3, proximal left ulna; RSM P2997.27, proximal left ulna; RSM P2997.28, proximal ulna; RSM P2997.29, distal left ulna; RSM P2987.26, proximal left radius; RSM P2997.74, right radius; RSM P2997.75, shaft of a radius; RSM P3015.10, proximal right radius; RSM P2997.46, proximal right tibiotarsus; RSM P2957.29, partial right pelvis; RSM P2988.17, partial right pelvis; RSM P2989.39, left pelvis; RSM P2997.62, right pelvis; RSM P2997.63, left antitrochanter of the pelvis; RSM P2626.35, distal right femur; RSM P2626.37, distal left femur; RSM P2831.1, proximal left femur; RSM P2988.1, proximal right femur; RSM P2997.4, right femur; RSM P2997.9, distal right femur; RSM P2997.10, right femur; RSM P2997.12, right femur; RSM P2997.14, distal left femur; RSM P2997.79, proximal right femur; RSM P3015.1, proximal right femur; RSM P3015.2, proximal right femur; RSM P3015.3, proximal right femur; RSM P2626.20, distal left tibiotarsus; RSM P2626.40, distal left tibiotarsus; RSM P2830.4, proximal right tibiotarsus; RSM P2957.13, distal left tibiotarsus; RSM P2957.14, distal right tibiotarsus; RSM P2995.7, proximal right tibiotarsus; RSM P2997.40, distal left tibiotarsus; RSM P2997.41, distal left tibiotarsus; RSM P2997.42, distal right tibiotarsus; RSM P2997.47, distal right tibiotarsus; RSM P2997.48, distal right tibiotarsus; RSM P2626.41; proximal right fibula; RSM P2988.21, proximal left fibula; RSM P2626.31, distal left tarsometatarsus; RSM P2626.33, distal left tarsometatarsus; RSM P2830.1, proximal left tarsometatarsus; RSM P2830.2, distal left tarsometatarsus; RSM P2957.6, distal right tarsometatarsus; RSM P2985.6, distal left tarsometatarsus; RSM P2987.1, left tarsometatarsus; RSM P2988.3, distal right tarsometatarsus; RSM P2989.2, proximal right tarsometatarsus; RSM P2989.3, distal right tarsometatarsus; RSM P2989.4, distal right tarsometatarsus; RSM P2989.6, distal left tarsometatarsus; RSM P2989.8, proximal right tarsometatarsus; RSM P2989.9, proximal left tarsometatarsus; RSM P2997.15, right tarsometatarsus; RSM P2997.16, proximal right tarsometatarsus; RSM P2997.18, left tarsometatarsus; RSM P2997.19, proximal left tarsometatarsus; RSM P2997.20, distal left tarsometatarsus; RSM P2997.22, proximal right tarsometatarsus; RSM P2997.81, proximal left tarsometatarsus; RSM P2997.83, proximal right tarsometatarsus; RSM P3015.18, distal right tarsometatarsus; RSM P2831.15, phalanx from the left foot; RSM P2831.16, phalanx from the left foot; RSM P2985.5, phalanx from the left foot; RSM

P2989.40, phalanx; RSM P2997.69, phalanx from the right foot; RSM P3015.14, distal phalanx from the right foot.

Pasquiaornis tankei Tokaryk et al., 1997

Diagnosis – Internal cotyla of tarsometatarsi nearly anterior-posterior, neck of 4th trochlea higher anteriorly than 3rd; femur large, distal rim of head slanted toward shaft.

Referred specimens from the Bainbridge River locality - RSM P2988.22, left maxilla; RSM P2995.5, left maxilla; RSM P2626.12, right frontal; RSM P2831.55, left frontal; RSM P2989.20, right frontal; RSM P2989.38, right frontal; RSM P2995.4, right frontal; RSM P2997.38, left frontal; RSM P2997.85, left frontal; RSM P2831.52, left quadrate; RSM P2988.25, right quadrate; RSM P2831.5, left dentary; RSM P2985.10, right dentary; RSM P2988.11, rostral tip of the left dentary; RSM P2989.193, right splenial; RSM P2989.194, right splenial; RSM P2986.2, left angular; RSM P2989.36, right angular; RSM P2626.42, right lower jaw; RSM P2957.23, left lower jaw; RSM P2988.10, left lower jaw; RSM P2989.21, left lower jaw; RSM P2997.35, right lower jaw; RSM P2626.15, cervical vertebra; RSM P2626.16, cervical vertebra; RSM P2831.9, ventral half of a cervical vertebra; RSM P2957.16, cranial portion of a cervical vertebra; RSM P2957.17, cervical vertebra; RSM P2987.13, cervical vertebra; RSM P2987.14, cervical vertebra; RSM P2987.15, cervical vertebra; RSM P2987.16, cervical vertebra; RSM P2987.17, cervical vertebra; RSM P2988.12 first dorsal or last cervical vertebra; RSM P2988.13, cervical vertebra; RSM P2988.14, cervical vertebra; RSM P2989.24, cervical vertebra; RSM P2997.52, cervical vertebra; RSM P2997.53, cervical vertebra; RSM P2997.54, cervical vertebra; RSM P2997.55 cervical vertebra; RSM P3015.6, cervical vertebra; RSM P3015.7, cervical vertebra; RSM P3015.20, cervical vertebra; RSM P2626.39, dorsal vertebra; RSM P2831.10, ventral half of a dorsal vertebra; RSM P2831.11, dorsal vertebra; RSM P2957.15, dorsal vertebra; RSM P2985.1, dorsal vertebra; RSM P2985.3, dorsal vertebra; RSM P2985.4, dorsal vertebra; RSM P2987.18, ventral half of a dorsal vertebra; RSM P2989.22; dorsal vertebra; RSM P2989.23, dorsal vertebra; RSM P2997.50, dorsal vertebra; RSM P2997.51; dorsal vertebra; RSM P2987.20, ventral half of the cranial end of the synsacrum; RSM P2988.16, synsacrum; RSM P2997.56, cranial end of the synsacrum; RSM P2997.84, caudal vertebra; RSM P2626.10, left coracoid; RSM P2626.11, distal right coracoid; RSM P2626.30, left coracoid; RSM P2957.2, right coracoid; RSM P2957.9, proximal right coracoid; RSM P2957.10, proximal right coracoid; RSM P2985.7, proximal right coracoid; RSM P2987.5, right coracoid; RSM P2987.6, distal left coracoid; RSM P2987.7, proximal coracoid; RSM P2988.9, left coracoid; RSM P2997.31, proximal left coracoid; RSM P2830.3, proximal right scapula; RSM P2831.56, proximal left scapula; RSM P2957.19, proximal left scapula; RSM P2997.58, proximal right scapula; RSM P2997.59, right proximal scapula; RSM P2997.60, left proximal scapula; RSM P2997.82, proximal right scapula; RSM 3015.8, proximal left scapula; RSM P3015.16, proximal left scapula; RSM P3015.17, proximal right scapula; RSM P2831.2, proximal left humerus; RSM P2957.7, proximal humerus; RSM P2957.24, distal right humerus; RSM P2957.25, distal left humerus; RSM P2957.26, distal right humerus; RSM P2987.2, distal right humerus; RSM P2987.3, distal right humerus; RSM P2987.4, proximal left humerus; RSM P2988.5, right

humerus; RSM P2988.6, proximal left humerus; RSM P2988.7, proximal right humerus; RSM P2989.10, distal left humerus; RSM P2989.11, proximal left humerus; RSM P2989.12, proximal left humerus; RSM P2989.13, proximal left humerus; RSM P2989.14, proximal right humerus; RSM P2995.1, left humerus; RSM P2997.24, distal right humerus; RSM P2997.25, distal left humerus; RSM P2989.16, distal left ulna; RSM P2989.17, proximal right ulna; RSM P2997.30, distal left ulna; RSM P3015.5, distal right ulna; RSM P2526.2, proximal left radius; RSM P2526.3, proximal left radius; RSM P2831.20, proximal right radius; RSM P2831.57, left radius; RSM P2987.25, proximal radius; RSM P2988.18, proximal right radius; RSM P2988.26 proximal left radius; RSM P2989.30, proximal right radius; RSM P2831.4, proximal left carpometacarpus; RSM P2987.8, proximal left carpometacarpus; RSM P2989.18, proximal right carpometacarpus; RSM P2989.34, distal left carpometacarpus; RSM P2997.32, proximal right carpometacarpus; RSM P2997.33, proximal left carpometacarpus; RSM P2997.34, proximal right carpometacarpus; RSM P2997.78, distal right carpometacarpus; RSM P3015.11, proximal left carpometacarpus; RSM P2626.6, partial right pelvis; RSM P2626.27, right pelvis; RSM P2626.29, left pelvis; RSM P2831.53, right pelvis; RSM P2997.64, antitrochanter from the right pelvis; RSM P2626.34, distal left femur; RSM P2626.36, proximal left femur; RSM P2957.5, proximal right femur; RSM P2988.2, distal left femur; RSM P2988.20, distal left femur; RSM P2989.1, left femur; RSM P2997.2, right femur; RSM P2997.3, left femur; RSM P2997.5, distal right femur; RSM P2997.6, right femur; RSM P2997.7, left femur; RSM P2997.8, proximal right femur and shaft; RSM P2997.11, distal right femur and shaft; RSM P2997.13, right femur; RSM P2997.77, proximal right femur; RSM P3015.12, shaft of left femur; RSM P2957.21, distal left tibiotarsus; RSM P2957.22, proximal left tibiotarsus; RSM P2987.10, proximal right tibiotarsus; RSM P2997.43, proximal left tibiotarsus; RSM P2997.44, proximal right tibiotarsus; RSM P2997.45, shaft of the right tibiotarsus; RSM P2989.35, proximal right fibula; RSM P2995.9, proximal left fibula; RSM P2997.80, proximal right fibula; RSM P2957.27, left tarsometatarsus; RSM P2997.21, proximal right tarsometatarsus; RSM P2997.23, distal right tarsometatarsus; RSM P3015.4, proximal right tarsometatarsus; RSM P3015.19, left tarsometatarsus; RSM P2626.19, phalanx from the left foot; RSM P2626.31, phalanx from left foot; RSM P2987.24, phalanx from the left foot; RSM P2988.23, proximal phalanx from the left foot; RSM P2988.24, distal phalanx from the right foot. RSM P2989.27, phalanx from the left foot; RSM P2989.28, phalanx from the left foot; RSM P2989.29, proximal phalanx from the right foot; RSM P2989.41, phalanx; RSM P2995.8, proximal phalanx from the right foot; RSM P2997.65, phalanx from the left foot; RSM P2997.66, phalanx from the right foot; RSM P2997.67, phalanx from the right foot; RSM P2997.68, phalanx from the left foot; RSM P2997.70, proximal phalanx from the right foot; RSM P2997.71, phalanx from the right foot; RSM P2997.72, proximal phalanx from the right foot; RSM P2997.73, proximal phalanx from the left foot; RSM P3015.9, phalanx from the right foot; RSM P3015.15, distal phalanx from the right foot.

Pasquiaornis sp. A

Diagnosis – 2nd trochlea of tarsometatarsus expanded; tarsometatarsus more

robust than *P. hardiei* and smaller than *P. tankei*.

Referred specimens from the Bainbridge River locality - RSM P2989.5, distal right tarsometatarsus; RSM P2989.7, right tarsometatarsus; RSM P2997.17, proximal left tarsometatarsus.

Hesperornithiformes incertae sedis

Diagnosis - Known from only a humerus; the humerus is extremely reduced and curves ventrally about halfway along the shaft, with the proximal end still showing bicipital and deltopectoral crests separated by a distinctive midline ridge on the caudal surface.

Referred specimens from the Bainbridge River locality - RSM P2626.43, highly reduced right humerus; RSM P2986.1, highly reduced left humerus; RSM P2997.26, highly reduced right humerus; RSM P3015.13, reduced distal left humerus.

Bone Descriptions

Over 300 bird elements were prepared from the Bainbridge River blocks and used for description and classification. The majority of elements discovered were vertebrae and limb bones (Figure 8). Two humeri were identified as belonging to *Ichthyornis*. One possible Enantiornithes scapula was recovered as well as several unidentified Aves bones. The following are descriptions of those elements belonging to the order Hesperornithiformes, mainly the genus *Pasquiaornis*.

Maxilla

This is the first description of the maxilla of *Pasquiaornis*. No complete maxilla is known from the Bainbridge River locality. No rostral or caudal ends are preserved.

Pasquiaornis tankei: RSM P2988.22/ RSM P2995.5

Figure 8. Abundances of elements found in the Bainbridge River locality sorted by element type. Teeth are not included here, although over 30 possible *Pasquiaornis* teeth are recovered. These elements are those only believed to belong to the genus *Pasquiaornis*. TMT = tarsometatarsi, CMC = carpometacarpi and Crania = all skull elements.

Plate I

The most complete maxilla specimen preserves eight fully enclosed alveoli. The bone is thinnest dorsally and expands ventrally towards the alveoli. On the lateral surface, there is a ridge that runs along the length of the dorsal half of the bone. Preserved in the caudal most part of the preserved bone is a foramen just ventral to the ridge. On the medial surface of the bone, there are two preserved grooves running along the length of the bone on a slight angle dipping ventrally as they go to the rostral end. The more dorsal of the two grooves reaches the dorsal edge of the preserved bone just before the caudal end. Along the more ventral groove are six foramina following the same angle as the grooves.

Frontal

This is the first description of the frontal of *Pasquiaornis*. The frontals preserved from the Bainbridge River locality are all partial and no left and right frontal pairs were found articulated.

***Pasquiaornis tankei*:** RSM P2626.12/ RSM P2831.55/ RSM P2989.20/ RSM P2989.38/
RSM P2995.4/ RSM P2997.38/ RSM P2997.85

Plate II

Overall the frontal is concave on the ventral side. The widest portion of the frontal is the caudal portion, thinning rostrally. The lateral portion of the bone is straight at the rostral end and then curves out laterally as it goes caudal. The lateral edge outlines the dorsal part of the orbit. The lateral side has a thin ventrally protruding segment of bone that extends furthest ventrally in the caudal part and gradually lessens in extent toward the rostral end. The dorsal surface of the frontal has a prominent ridge that runs rostral

caudally down the middle of the bone. At the caudal end the ridge forks medially and laterally. The rostral end of the frontal bends laterally. The medial surface of the frontal is relatively straight with a slight bend laterally towards the rostral end. The medial surface sutures with the opposite frontal from the caudal end towards the rostral end just before the bone bends laterally. The rostral surface preserves the contact with the nasal bone.

Pasquiaornis hardiei: RSM P2957.12/ RSM P2997.36

Plate II

The frontal of *P. hardiei* is approximately half the size of that of *P. tankei*. Overall the frontal is concave on the ventral side. The widest portion of the frontal is the caudal portion, thinning rostrally. The lateral portion of the bone curves out laterally, while the medial portion is relatively straight. The lateral surface is wide dorso-ventrally and quickly thins as it goes medially. There is a prominent dorsal ridge as in *P. tankei*, but it is much closer to the lateral edge and branches off medially toward the caudal end. However the ridge does not extend all the way medially on the caudal end. The caudal portion of the ridge is much more prominent extending further dorsally than the rest of the bone around it. The rostral portion of the ridge is much less prominent than in *P. tankei*.

Quadrate

The quadrate of *Pasquiaornis* was first described by Tokaryk et al. (1997). Here is a further description based on the specimens from the Bainbridge River locality. No complete quadrate was found from the Bainbridge River locality.

Pasquiaornis tankei: RSM P2831.52/ RSM P2988.25

Plate III

On the ventral surface there is a medial and lateral condyle. The medial condyle is elongated to articulate with the medial cotyla of the articular. The medial condyle slightly overlaps the lateral condyle caudally. The lateral end of the medial condyle rises dorsally to the lateral condyle on the caudal side. A groove running rostral medially to caudal lateral separates the two condyles. The lateral condyle is relatively square in shape and articulates with the lateral cotyla of the articular. On the caudal surface, just dorsal to the medial condyle is a large oval depression. On the medial edge dorsal to the medial condyle is a small process (pterygoid condyle). The pterygoid condyle is flush with the medial edge of the medial condyle. Dorsal to the pterygoid condyle, the rest of the preserved bone becomes more slender. On the medial side of the bone just dorsal to the pterygoid condyle the medial edge splits in two, creating a large oval opening (*fossa basiorbitalis*) into the bone. This opening is enclosed with bone except for the medial side. The opening proceeds into the bone leading laterally to a point creating a cone shape. On the caudal surface just lateral to the medial edge is a small shallow oval depression. The lateral edge of the bone slightly curved just dorsal to the lateral condyle. The curve is concave in shape.

Dentary

This is the first description of the partial dentary of *Pasquiaornis*. There are no complete dentaries preserved from the Bainbridge River specimens. There are specimens that preserve the rostral end and some which preserve neither of the ends. There are also two different size ranges of dentaries, the smaller being approximately half the size of the larger, but other than size, no differences are noticeable.

Pasquiaornis tankei RSM P2831.5/ RSM P2985.10/ RSM P2988.11

Plate IV

The rostral end of the dentary is made up of two circular bumps, with one situated above the other so that there is a small notch between them. The ventral side of the rostral end extends furthest rostrally. This terminal facet on the rostral end would be the articulating point with the prementary bone. The most complete specimen (RSM P2985.10) preserves at 8 alveoli. The teeth of *Pasquiaornis* seem to have been arranged in an open alveolar groove with slight indication of incomplete sockets. The alveoli are distinguishable on the medial surface along the groove and are each made up of short parallel ridges running perpendicular to the length of the bone.

On the more ventral side of the medial surface is a shallow groove running lengthwise and terminating rostrally at a foramen just before the terminal facet. On the lateral surface there are two parallel grooves running along the length of the bone, both of which terminate before the terminal facet. There is a small foramen on the rostral end between the facets on the lateral side at the level of the more dorsal of the two grooves. This foramen is in line with the more ventral of the two parallel grooves. Along the more ventral groove further caudally than the first foramen is another small foramen.

Another specimen (RSM P2831.5) preserves bone that is closer to the caudal end of the dentary. On the lateral surface towards the caudal end there are no apparent grooves. On the medial surface towards the caudal end there is a large groove running along the length of the bone approximately in the middle. The beginning of the alveolar groove is preserved in the specimen and it shows the shallow groove becoming deeper as it goes rostrally.

Pasquiaornis hardiei RSM P2526.4/ RSM P2831.6

Pasquiaornis hardiei has a lot less of the dentary preserved. No alveoli are preserved in this group. What is preserved is very similar to that of *P. tankei* except that *P. hardiei* is approximately half the size.

Dentition

Thirty teeth have been catalogued from the Bainbridge River site, however more than three times this amount have already been prepared from the Bainbridge River blocks and more are likely to come. There are two different tooth morphologies among the Bainbridge River specimens.

Tooth type A:

Plates V, VI and VII

The teeth from the Bainbridge River locality have an unserrated crown which terminates at a point. From the tip of the crown, the tooth broadens until it reaches its maximum width approximately four fifths from the top of the crown. The base of the crown is narrower than the top of the root. The crown is curved lingually and caudally. The lingual curvature differs slightly from tooth to tooth with some teeth curving more than others. This may be due to individual variation or position of the tooth in the jaw. Along the caudal and cranial surfaces of the crown, the rounded crown becomes a thin blade-like edge called the carinae that spans the length of the crown before it tapers to a waist. There are no denticles present along the carinae. The maximum width of the root is slightly greater in the cranial-caudal direction than that of the maximum width of the crown.

The root maintains an even width throughout its length. The root is slightly longer than the crown. In the upper two thirds of the root, there is an oval resorption pit on the

lingual side. The resorption pit is enclosed at the bottom of the root. Tooth type A varies in size and this may be due to differences between the species *P. hardiei* and *P. tankei*, which differ in size. Lingually the root is almost planar, not counting the resorption pit. Laterally the root slants lingually towards the base of the crown.

Tooth type B:

Plate VII (fig. 2)

Tooth type B is approximately half the size as tooth type A. Many characteristics are shared between the two tooth types with the following differences. The crown of tooth Type B is curved much more lingually than Type A, making an almost hooked shape. The crown curves slightly rostrally just after the waist, before curving back caudally. The waist between the root and crown is less prominent.

Splénial

This is the first description of the splénial of *Pasquiaornis*. No complete splénial is known from the Bainbridge River locality. The splénial was found disarticulated from the rest of the mandible.

Pasquiaornis hardiei RSM P2831.21/ RSM P2985.9/ RSM P2988.27

Plate VIII

The caudal surface is preserved where the bone would articulate with the angular. The caudal articulating surface is smooth and is at a 45 degree angle. The most caudal point of the bone is on the ventral surface. The ventral edge of the bone is straight and continuous with the ventral edge of the dentary. From the tip of the caudal end, as the bone rises dorsally at 45 degrees, approximately a third the way along the preserved bone, a medial ridge develops and becomes parallel to the ventral edge. From this point the

dorsal surface of the bone continues to rise anteriorly at a slightly shallower angle. The medial ridge is slightly concave dorsally. This area is most likely where the dentary would articulate with the splenial.

Pasquiaornis tankei: RSM P2989.193/ RSM P2989.194

The splenial of *P. tankei* is very similar to that of *P. hardiei*. It is about twice the size of *P. hardiei*. The medial ridge in *P. tankei* dips slightly more ventrally than it does in *P. hardiei*.

Angular

This is the first description of the angular of *Pasquiaornis*.

Pasquiaornis tankei RSMP2986.2/ RSM P2989.36

Plate VIII

The angular sits rostral to the prearticular. The rostral portion is the broadest part of the angular with the dorsal surface extending farthest cranially. The rostral edge of the angular articulates with the splenial forming an angle of 45 degrees. The ventral margin of the angular is relatively horizontal compared to the dorsal margin. The dorsal edge of the angular is highest rostrally where it meets the splenial, and then dips caudally at approximately a 30 degree angle. Approximately halfway along the bone caudally a medial shelf develops. From this point the lateral surface rises slightly dorsally. The prearticular articulates along the medial shelf of the angular.

Pasquiaornis hardiei RSM P2831.18/ RSM P2988.19/ RSM P2989.37/ RSM P2997.76

Plate VIII

The angular of *P. hardiei* is very similar to that of *P. tankei*. The only noticeable difference is that *P. tankei* is about twice the size as *P. hardiei*.

Articular/Prearticular/Surangular

This is the first description of the articular, prearticular, and surangular of *Pasquiaornis*.

Pasquiaornis tankei RSM P2626.42/ RSM P2957.23/RSM P2997.35/RSM P2989.21/
RSM P2988.10

Plate IX

The surangular, articular and prearticular are tightly fused. The most caudal portion of the mandible of *Pasquiaornis tankei* is the articular. The caudal portion of the articular is a large flattened surface and rounded at the end. The edges of this portion are broadly rounded edges. On the ventral surface of this portion there is a distinct lip around the edge. The centre of this ventral surface is concave. The rostral portion of the articular has the medial and lateral cotyla on the dorsal surface. The medial cotyla is elongated and caudal to the lateral cotyla and is angled from a caudal position laterally to rostral position medially. The lateral cotyla is roughly circular in shape and is rostral to the lateral portion of the medial cotyla. The medial and lateral cotyla are separated by a low ridge. On the medial side of the articular, slightly caudal to the medial cotyla there is a triangular portion of bone projecting medially, which contains the articular foramen.

The surangular and prearticular are positioned just rostral to the articular. The articular is fused to the surangular and prearticular with a large, slightly sinuous sinusoidal groove on the lateral side between them, trending from a ventral position caudally to a dorsal position rostrally. The surangular lies dorsal to the prearticular. The medial portion of these bones is concave where the prearticular and surangular meet. The ventral portion of this area (the prearticular) is broader in a medial-lateral direction than

the dorsal portion (the surangular), creating a shelf between the two bones. This shelf angles ventrally as it trends rostrally.

Pasquiaornis hardiei RSMP2989.19

Plate IX

P. hardiei differs from *P. tankei* by being much smaller. Relatively speaking, the caudal end does not extend as far out laterally as in *P. tankei*. The ventral surface of the caudal end of the articular is not as concave as in *P. tankei*.

Cervical vertebrae

This is the first description of the cervical vertebrae of *Pasquiaornis*.

Pasquiaornis tankei RSM P2626.15/ RSM P2626.16/ RSM P2831.9/ RSM P2957.16/
RSM P2957.17/ RSM P2987.13/ RSM P2987.14/ RSM P2987.15/ RSM P2987.16/ RSM
P2987.17/ RSM P2988.13/ RSM P2988.14/ RSM P2989.24/ RSM P2997.52/ RSM
P2997.53/ RSM P2997.54/ RSM P2997.55/ RSM P3015.6/ RSM P3015.7/ RSM
P3015.20

Plate X and XII

The cervical vertebrae are heterocoelous. For the anterior most cervical vertebrae, the cranial end of the centrum is saddle shaped, with the lateral edges of the articular surfaces projecting furthest cranially. Dorsal to the centrum is the vertebral foramen. Lateral and slightly dorsal to the vertebral foramen are the cranial zygapophyses which have their articular faces on the dorsal side slanted slightly toward the center axis of the vertebra. Ventral and lateral to the cranial zygapophyses are the *ansa costotransversariae* which extend ventrally to attach to the ventro-lateral edge of the centrum, creating an oval foramen known as the *foramen transversarium*. The *ansa costotransversariae* are a very

thin bone, extending caudally to the caudal portion of the cranial zygapophyses. The ventral portion of the cranial face of the vertebra is an inverted “u” shape, created by the paired, incurved carotid processes on the ventral surface of the centrum. These processes form the *sulcus caroticus*.

The *sulcus caroticus* becomes more prominent in the more posterior cervical vertebrae. The width of the ventral surface of the centrum decreases caudally, and then widens again at the caudal end. The caudal end of the centrum is approximately half the width of the cranial end. The caudal end of the C3 and C4 vertebrae is even thinner along the ventral surface, creating a slight ridge in the center. The dorsal surface is much wider than the ventral surface overall. Running longitudinally down the centre of the dorsal surface of the bone is a small ridge. The caudal face of the centrum is saddle-shaped with the furthest projecting ends being the dorsal and ventral edges. Dorsal to the centrum is the vertebral foramen which is wider than the face of the centrum on the caudal end. Dorsal and lateral to the centrum and vertebral foramen on the caudal end of the vertebra are the caudal zygapophyses. The articulating face is on the ventral side of the caudal zygapophyses and is slanted slightly away from the center axis of the vertebra.

The most posterior cervical vertebrae differ from the more anterior cervical vertebrae (Plate XII, fig. 1 and 2). The posterior cervicals lack the *foramen transversarium*. The bone does not extend from the ventral lateral surface of the cranial zygapophyses on the diapophyses to the ventral lateral surface of the centrum. The cranial zygapophyses are projected further laterally in the more posterior cervicals than in the more anterior cervical vertebrae. The diapophyses ventral to the cranial zygapophyses are much more prominent. The *sulcus caroticus* is also very prominent in these cervical vertebrae. At approximately the 15th cervical vertebra, the *sulcus caroticus* turns into a

ventral spine or hypapophysis. A slight depression is also seen in the middle portion of the lateral surfaces of these vertebrae just above the ventral side.

***Pasquiaornis hardiei* RSM P2831.8**

Plate XI

The cervical vertebrae of *P. hardiei* are very similar to those of *P. tankei*. However the vertebrae are about a third the size of *P. tankei* and are much less robust. The cervical vertebrae of *P. hardiei* have very thin bone compared to *P. tankei*. The cranial face of the centrum of the 6th to 9th cervical vertebra in *P. hardiei* wraps around further caudally into the neural foramen than that of *P. tankei*. This difference may also be due to slight differences in which cervical vertebrae are being compared. In *P. hardiei*, on the dorsal surface of the caudal zygapophyses there are dorsal laterally projecting ridges that are not seen in *P. tankei*. The caudal zygapophyses of *P. hardiei* are more elongate than those of *P. tankei* which are sub-rounded.

Dorsal vertebrae

This is the first description of the dorsal vertebrae of *Pasquiaornis*. The dorsal vertebrae of *Pasquiaornis* are amphicoelous.

***Pasquiaornis tankei* RSM P2626.39/ RSM P2831.10/ RSM P2831.11/ RSM P2957.15/ RSM P2985.1/ RSM P2985.3/ RSM P2985.4/ RSM P2987.18/ RSM P2988.12/ RSM P2989.22/ RSM P 2989.23/ RSM P2997.50/ RSM P2997.51**

Plate XII, fig. 3 and Plate XIII

The dorsal vertebrae of *Pasquiaornis* are amphicoelous. The cranial face of the centrum is concave, and diamond to oval in shape with the widest axis oriented laterally. The lateral edges of the centrum come to a gentle point and are directed cranially. The

width across the cranial zygapophyses ranges from 80 to 90% of the width of the cranial face of the centrum. The cranial zygapophyses articular surface, which faces dorsally, slants approximately 45 degrees toward the central axis of the vertebra. Just ventral and caudal to the cranial zygapophyses are the facets for the ribs. The facets are roughly oval in shape and vary in orientation, depending on position in vertebral column. In ventral view the centrum as a whole has an hour glass shape, with the caudal end approximately two thirds the width of the cranial end. The transverse processes are situated above the centrum just caudal to the cranial zygapophyses and are directed away from the vertebra caudally. Just ventral to the transverse processes is a small, distinct, pit like depression. Ventral to this is a much larger and deeper depression that is oval in shape running most of the length of the centrum. Cranial to the transverse process and caudal to the cranial zygapophyses is a triangular depression created by a ridge running along the dorsal lateral edge of the cranial zygapophyses to the transverse process and another ridge running from the rib facet to the ventral cranial edge of the transverse processes.

The caudal face of the centrum is roughly square-shaped and slightly concave, with the right and left dorsal corners directed caudally. The caudal zygapophyses are slightly more dorsal than the cranial zygapophyses and are spread apart approximately the width of the caudal face of the centrum. The articular surface of the caudal zygapophyses is ventral and slanted approximately 45 degrees away from the centre axis of the bone. The caudal zygapophyses are the caudalmost part of the vertebra. The spinal process is the most dorsal part of the bone and runs along the length of the vertebral foramen between both pairs of zygapophyses. The longest dorsally extended part of the spinous process is the cranial end; it tapers slightly caudally.

The first dorsal vertebra differs slightly from the rest (Plate XII, fig. 3). It is a transitional form from the cervical vertebrae. The cranial and caudal ends of the centrum are more saddle-shaped than the rest of the dorsal vertebrae. Along the ventral surface, close to the cranial edge of the centrum, is a ventral process or hypapophysis, which is directed cranially.

Pasquiaornis hardiei RSM P2831.7/ RSM P2985.2

The dorsal vertebrae of *P. hardiei* are very similar to those of *P. tankei*. Two differences were noted. First, the dorsal vertebrae of *P. hardiei* are approximately half the size of those of *P. tankei*. Second, the large concave depressions on the lateral sides of the vertebrae in *P. hardiei* are larger relative to the size of the centrum than in *P. tankei*. This could be due to inadvertent comparison of vertebrae from different positions along the trunk, but since these are disarticulated specimens and there are many fewer *P. hardiei* dorsal vertebrae, vertebral position is hard to determine.

Synsacra

This is the first description of the synsacrum of *Pasquiaornis*. No *Pasquiaornis* synsacrum from the Bainbridge River assemblage is complete.

Pasquiaornis tankei: RSM P2987.20/ RSM P2988.16/ RSM P2997.56

Plate XIV

The synsacra of the *Pasquiaornis* are compressed transversely, indicative of diving birds. The synsacrum is almost completely straight with a slight bend dorso-ventrally. The most complete synsacrum preserves six fused vertebrae. The width of the synsacrum is broadest cranially and thins caudally. The most cranial end is preserved in some specimens. The first fused sacral vertebra has a broad, slightly concave cranial

centrum. The transverse processes of the first fused sacral vertebrae are relatively small. All the following fused sacral vertebrae have their transverse processes laterally compressed against each vertebra. The second fused sacral vertebra transverse processes are laterally compressed, but not as much as the more caudal sacral vertebra. The transverse processes of the second fused sacral vertebra are directed cranially. Part of the neural spine is preserved in one of the specimens (RSM P2988.16). The more cranial part of the synsacrum seems to have had a neural spine while the smaller caudal part of the synsacrum may not have. Large intervertebral foramina are present just above the height of the centrum along the whole of the synsacrum. In ventral view the centrum of the fused vertebrae are hourglass shaped.

***Pasquiaornis hardiei*:** RSM P2626.18/ RSM P2831.12/ RSM P2989.25

Plate XV

These synsacra are approximately half the size as the synsacra of *P. tankei*, but are very similar in shape. A difference is that in *P. hardiei*, the width of the centrum of the first fused vertebra narrows to some what more than half the width of the cranial surface width, while in *P. tankei*, it only narrows slightly.

***Unknown hesperornithiform synsacrum*:** RSM P2957.18/ RSM P2987.19/ RSM P2997.57

Plate XIV

This hesperornithiform synsacrum is much smaller than that of *P. tankei* and more similar in size to *P. hardiei*. The most complete of these hesperornithiform synsacra has eleven preserved fused vertebrae. These hesperornithiform synsacra are somewhat similar to that of the *Pasquiaornis* synsacra except that the broadest portion seems to be in the middle sacral vertebrae instead of the more anterior end. The first fused sacral vertebra is

relatively smaller than the sacral vertebra caudal to it, compared with *Pasquiaornis* specimens. Overall the synsacrum is much more compressed than the *Pasquiaornis* synsacra.

Caudal Vertebrae

This is the first description of the caudal vertebrae of *Pasquiaornis*.

***Pasquiaornis*:** RSM P2997.84

Figure 9

Only one caudal vertebra is known from the Bainbridge River locality. The vertebra is small and compact and cylindrical in shape. The cranial face of the centrum is laterally oval and slightly concave. The preserved ventral surface is planar, although the lateral edges are eroded. These eroded edges hint that the bone continued dorsally. The transverse processes are fused to the centrum and are directed cranially and ventrally. The ventral surface of the vertebra is hourglass shaped. The transverse processes extend slightly further ventrally than the lateral portions of the ventral surface, creating small grooves. The caudal surface of the centrum is oval in shape and more planar.

Ribs

This is the first description of the ribs of *Pasquiaornis*.

***Pasquiaornis*:** RSM P2957.28/ RSM P2997.51

Figure 10

There is no complete rib known from the Bainbridge River locality. Parts of the shaft and proximal end are known. The proximal end of the rib has a well developed capitulum and tuberculum. The capitulum is approximately twice the width of the

Figure 9. Caudal vertebra of *Pasquiaornis* (RSM P2997.84). A, cranial view; B, lateral view; C, caudal view; D, dorsal view; E, ventral view. Scale bar equals 1 cm.

Figure 10. Ribs of *Pasquiaornis*. A, proximal rib (RSM P2997.61); B-C, rib shaft (RSM P2957.8); B, anterior view; C, posterior view. Scale bar equals 1 cm.

tuberculum and over twice the length. Proximally the shaft is robust and oval in cross-section. The preserved shaft has a gradual curve. Along the more distal part the shaft becomes more triangular in cross-section. Along this portion there is a thin lateral flange that extends slightly out from the rest of the bone.

Coracoid

This is the first description of the coracoids of *Pasquiaornis*. There are two different size ranges of coracoids found from the Bainbridge River locality. The smaller group has no complete specimens.

Pasquiaornis tankei: RSM P2626.10/ RSM P2626.11/ RSM P2626.30/ RSM P2957.2/
RSM P2957.9/ RSM P2957.10/ RSM P2985.7/ RSM P2987.5/ RSM P2987.6/ RSM
P2987.7/ RSM P2988.9/ RSM P2997.31

Plate XVI, fig. 1

The sternal (posterior) end of the coracoid is triangular in shape. Extending most cranially on the scapular (anterior) end is the brachial tuberosity. On the lateral edge of the dorsal side toward the cranial end is an ovoid shaped glenoid facet, which is slightly concave. The glenoid facet is longest along the cranial-caudal axis. Just medial and caudal to the glenoid facet towards its caudal end is the scapular facet. The scapular facet is round in shape and forms a deeper depression than the glenoid facet. Caudal and medial to the scapular facet is the coracoidal foramen. Medial to the scapular facet is the procoracoid which extends out medially and slightly cranially. The extending procoracoid helps shape the triosseal canal on the medial ventral side of the bone. Located in the triosseal canal is a pneumatic foramen. On the ventral edge of the scapular end is the

furcular facet. The furcular facet is not completely preserved in any of the specimens, but it appears low on the scapular end and creates a very shallow depression.

As the bone extends caudally it starts to broaden in the medial-lateral axis. On the dorsal surface of the coracoid there is a broad shallow depression, which starts just as the bone broadens from the neck and ends just before the ridge that outlines the sterno-coracoidal fossa. The caudal-lateral edge is not preserved on any of the specimens. On the caudal end there is a ridge that outlines the sterno-coracoidal fossa. On the tip of the medial caudal end is the sternal facet.

Pasquiaornis hardiei: RSM P2831.54

Plate XVI, fig. 2

Only the mid part of the coracoid is known from *P. hardiei*. The portion that is known is approximately half the size as the *P. tankei* coracoids and is less robust. The part that is preserved shows a similar triangular depression that starts at the distal end of the neck on its dorsal surface that is seen in *P. tankei*. On the ventral surface there is a faint muscle scar running anterior to posterior near the medial edge.

Scapula

This is the first description of the scapula of *Pasquiaornis*. The scapulas vary in size with the largest approximately twice as big as the smallest; however, they are very similar in shape and features. No complete scapula is known from the Bainbridge River locality.

Pasquiaornis tankei: RSM P2830.3/ RSM P2831.56/ RSM P2957.19/ RSM P2997.58/
RSM P2997.59/ RSM P2997.60/ RSM P2997.82/ RSM P3015.8/ RSM P3015.16/ RSM
P3015.17

Plate XVII

The distal ends are not preserved in any of the specimens. The most cranial portion of the scapula is the well projected acromion process, which extends out cranially beyond the glenoid facet. The furcular articulation is visible in dorsal view along the most dorsal portion of the acromion process. Just caudal and ventral to the furcular articulation and acromion process is a bulbous coracoidal articulation. The coracoidal articulation and the furcular articulation and acromion process create a slight “c” shape on the cranial end of the scapula. Just caudal to the coracoidal articulation is the glenoid facet, which is set at a slight angle dipping medially.

The glenoid facet is ovoid in shape with its long axis in a cranial-caudal direction; its interior forming a slight depression. The glenoid facet is in contact with the most caudal portion of the coracoidal articulation. At the cranial end of the scapular blade, the shaft forms a thin edge on the dorsal side and thickens slightly ventrally. As the scapula extends caudally it curves medially towards the body. The ventral-dorsal width of the scapular blade tapers caudally. The medial-lateral width of the scapular blade narrows slightly cranial to caudal.

Pasquiaornis hardiei: RSM P2985.8/ RSM P2987.21

Plate XVII, fig. 3

The scapula of *P. hardiei* is very similar to that of *P. tankei*. They differ in that *P. hardiei* is approximately 15% smaller and is much more transversely compressed.

Humerus

The distal end of the humerus was first described by Tokaryk et al. (1997). The first complete description of the humeri of *Pasquiaornis* is given here from the specimens

found at the Bainbridge River locality. There are two distinct looking humeri from the Bainbridge River locality. One is reduced much like that of the classic hesperornithiform taxa such as *Hesperornis*. The other is much less reduced, resembling a more typical avian humerus. The first humerus that will be described is the less reduced humerus.

***Pasquiaornis tankei*:** RSM P2831.2/ RSM P2957.7/ RSM P2957.24/ RSM P2957.25/ RSM P2957.26/ RSM P2987.2/ RSM P2987.3/ RSM P2987.4/ RSM P2988.5/ RSM P2988.6/ RSM P2988.7/ RSM P2989.10/ RSM P2989.11/ RSM P2989.12/ RSM P2989.13/ RSM P2989.14/ RSM P2995.1/ RSM P2997.24/ RSM P2997.25

Plate XVIII and Figure 11 (A and B)

The proximal portion of the humerus is the broadest area of the bone. The proximal end curves slightly toward the body. The *caput humeri* (head) is the most proximal portion of the bone and is thick and rounded. On the cranial surface of the proximal end, just ventral to the *caput humeri* is a slight circular depression, the *sulcus ligamentus transversus*. Extending distally along the dorsal edge of the bone is a long thin curving deltoid (deltopectoral) crest which extends approximately a third the way down the shaft. The deltopectoral crest slants cranially. On the ventral edge of the proximal side is the bicipital crest. The bicipital crest is less than half the length of the deltopectoral crest.

The shaft of the humerus is long and is triangular in cross-section. The shaft is slightly twisted cranially. On the ventral-caudal side of the shaft just distal to the bicipital crest is a small foramen. The distal end has two very distinct condyles; the ventral and dorsal condyles. The dorsal condyle is larger than the ventral condyle, extending slightly further distally and proximally. Ventral to the ventral condyle is the ventral epicondyle. The epicondyle extends further caudally than the ventral and dorsal condyles, which

Figure 11. Humerus and ulna of *Pasquiaornis*. A, distal left humerus (RSM P2995.1) in anterior view; B, proximal left humerus (RSM P2989.11) in posterior view; C, proximal right ulna (RSM P2989.17) in anterior view; D, distal left ulna (RSM P2997.30) in ventral view. Abbreviations: bc, bicipital crest; bt, bicipital tubercle; dc, dorsal condyle; dco, dorsal cotyla; dpc, deltopectoral crest; h, head; iba, impression of *brachialis anticus*; ico, intercotyla; ics, intercotylar sulcus; ir, *incisura radialis*; m, *margo caudalis*; op, olecranon process; sp, styloid process; vc, ventral condyle; vco, ventral cotyla; vec, ventral epicondyle. Scale bar equals 1 cm.

oriented cranially. Proximal to the ventral epicondyle is the ventral *supracondylar tuberculum*, which is a small projection from the bone. Proximal to the distal condyles on the cranial surface is a triangular depression, with the long axis directed to the proximal end. This depression or fossa is the attachment for the *branchialis anticus* muscle.

Pasquiaornis hardiei RSM P2989.15

Plate XVIII, fig. 3

Only the distal end of the humerus is known from this species. It is similar to the distal end in *P. tankei*, except that the condyles are not as well developed. The ectepicondylar prominence is also not as well defined as in *P. tankei*.

Hesperornithiform species A: RSM P2626.43/ RSM P2986.1/ RSM P2997.26/ RSM P3015.13

Figure 12.1

The second type of humerus found in the Bainbridge River area is a strongly reduced humerus with a distinct, overall ventral bend. The proximal end is the broadest portion of the bone. The head of the proximal end is not preserved. The deltoid (deltopectoral) and bicipital crests are small, sharp-edged, and project very little from the shaft. The deltopectoral crest extends about 40% the length of the shaft and the bicipital crest extends approximately one third the length of the shaft. The deltopectoral crest projects toward the cranial side. A distinctive ridge (*Margo caudalis*) is a feature on the caudal surface, running from the head along the midline of proximal half of the shaft. The shaft is triangular in cross-section in this region, and ovoid in cross-section along the distal half. Approximately a third the way down the shaft from the proximal end is a large foramen on the ventral and caudal side. The distal end of the humerus is slightly oriented

Figure 12. Unknown hesperornithiform humerus from the Bainbridge River locality compared with other known hesperornithiform humeri. 1, reduced right humerus of unknown hesperornithiform (RSM P2986.1); 1a, posterior view; 1b, ventral view; 1c, anterior view; 1d, distal left humerus (RSM P3015.13); 2, right humerus from *Hesperornis regalis* (YPM1206) in posterior view; 3, left humerus from *Parahesperornis* (KU2287) in anterior view; 4, right humerus of *Baptornis advensus* (KU2290) in anterior view. Scale bar equals 1 cm.

cranially. The distal condyles are not prominent although they are slightly distinguishable from each other.

Ulna

This is the first description of the ulna of *Pasquiaornis*. No complete ulna was discovered in the Bainbridge River locality. Several proximal and distal ends were recovered.

***Pasquiaornis tankei*:** RSM P2989.16/ RSM P2989.17/ RSM P2997.30/ RSM P3015.5
Plate XIX and Figure 11 (C and D)

The articular face of the proximal end is triangular in shape. The most proximal point of the ulna is the olecranon process, which is on the caudal surface of the ulna. A small ridge runs from the olecranon process between the articular facets to the cranial surface of the proximal end. This ridge is the intercotyla. The intercotyla separates the dorsal and ventral cotylas. The dorsal cotyla is triangular in shape and slightly convex. The ventral cotyla is concave and circular in shape. Two separate, sharp-edged ridges on the ventral surface lead distally from the ventral cotyla. One ridge originates on the caudal border of the ventral cotyla and extends distally along the shaft slowly curving to the cranial edge of the ventral surface of the shaft. The second ridge originates from the cranial border of the ventral cotyla and extends distally for most of the preserved length of the shaft. There is a depression (*Impressio brachialis*) in the bone between the ridges. Distal to the *Impressio brachialis* along the cranial-ventral ridge is a nutrient foramen.

A small ridge originates from the cranial border of the dorsal cotyla and trends diagonally across the cranial surface of the shaft connecting with the long cranial-ventral ridge. This creates a small triangular depression known as the *incisura radialis*. The

incisura radialis is approximately a fifth the length of the *impressio brachialis*. At the distal tip of the *incisura radialis* is the bicipital tubercle, a muscle scar where the *m. biceps brachii* inserts.

The cross-section of the shaft becomes oval in shape distally. On the distal end there is a small projection on the cranial edge, the styloid process, which is directed distally. The rest of the distal end of the ulna is a broad articular surface for the carpometacarpus. The articular surface is comprised of the ventral and dorsal condyles. The intercondyle sulcus connecting them is smooth and curved, covering roughly half of the distal surface of the bone. On the ventral surface just proximal to the intercondyle sulcus is a slightly depressed area, the distal radial depression. No scars for follicular ligaments for the attachment of the secondary feathers were found on the ulna.

Pasquiaornis hardiei: RSM P2995.3/ RSM P2997.27/ RSM P2997.28/ RSM P2997.29

P. hardiei ulnae are very similar to those of *P. tankei* except that they are approximately a third smaller. The olecranon process is more pointed and more ventrally directed than in *P. tankei*.

Radius

This is the first description of the radius of *Pasquiaornis*. No complete radii were found at the Bainbridge River locality. Only the proximal end and a portion of the shaft are known.

Pasquiaornis tankei RSM P2526.2/ RSM P2526.3/ RSM P2831.20/ RSM P2831.57/
RSM P2987.25/ RSM P2988.18/ RSM P2988.26/ RSM P2989.30

Plate XX and Figure 13 (A and B)

Figure 13. Radius and carpometacarpus of *Pasquiaornis*. A-B, proximal right radius of *Pasquiaornis* (RSM P2831.20); A, lateral view; B, ventral view; C-D, proximal end of left carpometacarpus (RSM P2831.4); C, ventral view; D, medial view; E-F, distal end of left carpometacarpus (RSM P2989.34); E, dorsal view; F, distal view. Abbreviations: as, articular surface; ch, *cotyla humeralis*; etg, extensor groove; iml, intermuscular line; mcl, metacarpal I; mcll, metacarpal II; mclll, metacarpal III; mcp, metacarpal process; mct, metacarpal trochlea; pf, pollical facet; pp, pisiform process; rt, radial tuberosity. Scale bar equals 1 cm.

The top of the proximal end, the *cotyla humeralis* is oval in shape and slightly concave. On the ventral surface, just distal to the *cotyla humeralis*, is a shallow triangular depression with a small tubercle at its distal point. This is the radial bicipital tuberosity, the scar marking the insertion of *M. biceps brachii*. There is a faint intermuscular line leading distally from the radial bicipital tuberosity.

***Pasquiaornis hardiei*:** RSM P2987.26/ RSM P2997.74/ RSM P2997.75/ RSM P3015.10

The radius of *P. hardiei* is very similar to that of *P. tankei* except that *P. hardiei* is approximately half the size. The radial bicipital tuberosity in *P. hardiei* extends further down the shaft than in *P. tankei*, although it is narrower in width and less robust.

Carpometacarpus

This is the first description of the carpometacarpus of *Pasquiaornis*. No carpometacarpus has previously been identified as being from a hesperornithiform. This carpometacarpus is being referred to *Pasquiaornis* based on traits ascribed to modern diving birds (Longrich, 2006). First, the compact bone of the carpometacarpus is relatively thick, a characteristic often seen in diving and flightless birds and second, a distally placed extensor process. A distally placed extensor process is often seen in diving birds like Gaviformes, Alcidae, and Plotopteridae (Longrich, 2006).

***Pasquiaornis tankei*:** RSM P2626.28/ RSM P2831.4/ RSM P2987.8/ RSM P2989.18/
RSM P2989.34/ RSM P2997.32/ RSM P2997.33/ RSM P2997.34/ RSM P2997.78/ RSM
P3015.11

Plate XXI and Figure 13 (C-F)

No complete carpometacarpus was discovered at the Bainbridge River site. The proximal and distal ends were all found separately. These bones vary slightly in size. The most proximal portion of the carpometacarpus is the second metacarpal. The carpal trochlea from the dorsal side extends further proximally than the carpal trochlea on the ventral side. The first metacarpal is fused to the second metacarpal on the cranial side, distal to the carpal trochlea. The first metacarpal has a semi-circular shape and is slightly concave on its ventral surface. The proximal end of the first metacarpal is the metacarpal process for extensor muscle attachment. On the distal end of the first metacarpal is the pollical facet (alular process).

The third metacarpal is fused to the ventral side of the second metacarpal and extends proximally the same distance as the first metacarpal. The third and second metacarpals are subparallel to each other. The third metacarpal is less than half the diameter of the second metacarpal. The pisiform process is at the most proximal end of the third metacarpal where it is fused to the second metacarpal. The pisiform is aligned with the proximal point of the first metacarpal. There is a pit-like scar proximal to the pisiform.

The distal end is made up of the larger second metacarpal with the third metacarpal fused to the dorsal caudal portion of the second metacarpal. The distal edge of the second metacarpal shows a distinct articular surface. The extensor tendinal groove runs along the cranial edge of the second metacarpal on the distal end.

Pelvis

This is the first description of the pelvis of *Pasquiaornis*. From the known pelvis elements from the Bainbridge River locality there are two different size classes. Most of

the pelvis is known from the Bainbridge River specimens, although the pubis, ilium and ischium are not preserved in their entirety.

Pasquiaornis tankei: RSM P2626.6/ RSM P2626.27/ RSM P2626.29/ RSM P2831.53/
RSM P2997.64

Plate XXII, fig. 1

Overall, the pelvis is relatively robust. *P. tankei* has a long, slender, caudally-directed pubis, which narrows slightly the further caudally it goes. There is no indication of a prepubis bone, although this may be due to preservation. The ischium is approximately twice as broad as the pubis and narrows caudally. Laterally, the ischium is slightly convex in the preserved portion. The pubis and ischium are completely separated caudally in the elements preserved. The antitrochanter is a prominent feature of the ilium and situated dorsocranially to the ilium, extending out laterally. The articulating surface of the antitrochanter is broad and circular. The ilium is broad and lies dorsal to both the pubis and the ischium.

The pubis, ilium, and ischium all make up the rounded acetabulum. The antitrochanter makes up a significant portion of the acetabulum. The antitrochanter rises from the acetabulum at an approximate angle of 45 degrees. The pubis and ischium are fused to create the caudal portion of the acetabulum, but separate as they extend caudally. The ischium and ilium are fused together to create the dorsocaudal portion of the acetabulum. The pubis and ilium are fused to create the cranial portion of the acetabulum. The ilium forms the dorsal portion of the acetabulum. The pubis makes up most of the ventral portion of the acetabulum, with the ischium forming the rest. The acetabulum is open, expanding in diameter from the medial surface to its greatest diameter on the lateral surface.

***Pasquiaornis hardiei*:** RSM P2957.29/ RSM P2988.17/ RSM P2989.39/ RSM P2997.62/
RSM P2997.63

Plate XXII, fig. 2

The pelvis of *P. hardiei* is very similar to that of *P. tankei* except that it is half the size and less robust. The antitrochanter also rises from the acetabulum at a slightly steeper angle in *P. hardiei*. Anterior to the acetabulum where the ilium and pubis meet is a smooth curve while in *P. tankei*, the intersection is much more straight lined creating an angle of approximately 115 degrees.

Femur

The femur of *Pasquiaornis* was first described by Tokaryk et al. (1997). Here is a further description based on the new material from the Bainbridge River locality.

***Pasquiaornis tankei*:** RSM P2626.34/ RSM P2626.36/ RSM P2957.5/ RSM P2988.2/
RSM P2988.20/ RSM P2989.1/ RSM P2997.2/ RSM P2997.3/ RSM P2997.5/ RSM
P2997.6/ RSM P2997.7/ RSM P2997.8/ RSM P2997.11/ RSM P2997.13/ RSM P2997.77/
RSM P3015.12

Plate XXIII and Figure 14

The femur, as in most hesperornithiforms, is relatively short and broad. The proximal end of the femur has a slight medial-lateral incline with the greater trochanter higher than the head. On the lateral surface, the greater trochanter slants lateral-distal to medial-proximal. The distal edge of the greater trochanter is flush or nearly so with the axis of the shaft. Between the greater trochanter and head there is a small notch. On the cranial surface between the head and the greater trochanter there are small foramina grouped below the notch. The head is sub-rounded with a slight incline above the *Fovea*

Figure 14. Femur of *Pasquiaornis tankei*. A, left femur (RSM P2997.3) in lateral view; B – D, right femur; B, medial view; C, posterior view; D, anterior view. Abbreviations: as, articular surface; cfe, *m. caudifemoralis externus*; flc, *fovea ligamentous capitis*; ftm, *femorotibialis medius*; ftl, *femorotibialis lateralis*; gt, greater trochanter; h, head; itc, *ilio trochantericus cranialis*; lc, lateral condyle; mc, medial condyle; ms, muscle scar; nf, nutrient foramen; pg, patellar groove. Scale bar equals 1 cm.

ligamentus capitis on the medial surface. The cranial-caudal width of the head exceeds that of the greater trochanter. The medial distal rim of the head slants proximally at approximately a 30 degree angle. Just underneath the head on the medial cranial side is a small depression just below the rim of the head. On the lateral surface just below the greater trochanter is a visible muscle scar (insertion of the *m. iliotrochantericus cranialis*). When viewing the femur caudally, the lateral edge is relatively straight until at the distal end when the lateral condyle swings out laterally.

Starting on the caudal surface distal to the greater trochanter a muscle scar sweeps toward the lateral cranial surface of the bone and carries distally to the lateral condyle. On the medial surface, halfway up the shaft is a small muscle scar where *m. caudifemoralis externus* would insert. On the caudal surface of the mid-shaft there is a small foramen. On approximately the same level there is another foramen located on the lateral surface. The presence of these foramina is not visible in all specimens. At approximately mid shaft in cross section the diameter of the femur is on average about 50% cortical bone. On the cranial surface there is a faint intermuscular line that runs distally from the greater trochanter to the medial condyle. The attachment for the *femorotibialis lateralis* and *f. medialis* lie along this intermuscular line.

On the distal end, the lateral condyle is enlarged compared to the medial condyle. A large triangular patellar groove is found between the lateral and medial condyles and extends a third the way up the shaft. A large depression, the *fossa poplitea* is present between the lateral and medial condyles on the caudal surface. The lateral condyle extends further distally than the medial condyle. On the medial surface of the medial condyle there is a small depression for the origin of the *m. plantaris*. The *trochlea fibularis* on the lateral condyle is enlarged and angled laterally. The *trochlea fibularis*

articulates with the *caput fibulae* of the fibula. The intercondylar sulcus, which connects the medial and lateral condyles, is broad and rounded.

***Pasquiaornis hardiei*:** RSM P2626.35/ RSM P2626.37/ RSM P2831.1/ RSM P2988.1/ RSM P2997.4/ RSM P2997.9/ RSM P2997.10/ RSM P2997.12/ RSM P2997.14/ RSM P2997.79/ RSM P3015.1/ RSM P3015.2/ RSM P3015.3

Plate XXIII

The above description of *P. tankei* femora applies to those of *P. hardiei* with the following differences. The femur of *P. hardiei* is much smaller in size than that of *P. tankei*. The largest femur of *P. tankei* is approximately 23% larger than the largest femur of *P. hardiei*. The muscle scars on the femurs of *P. hardiei* are much less prominent than in *P. tankei*. The medial distal rim of the head slants proximally at angles varying from 30 to 60 degrees. At approximately midshaft in cross section the diameter of the femur is on average about 40% cortical bone.

Tibiotarsus

This is the first description of the tibiotarsus of *Pasquiaornis*. The tibiotarsus is the largest bone in Hesperornithiformes. From the Bainbridge River specimens, there is no fully complete example of the tibiotarsus, only distal and proximal ends and shafts.

***Pasquiaornis tankei*:** RSM P2957.21/ RSM P2957.22/ RSM P2987.10/ RSM P2997.43/ RSM P2997.44/ RSM P2997.45

Plate XXIV and Figure 15

The most proximal portion of the bone is the large triangular cnemial crest. The top of the cnemial crest is pointed in the most complete specimen. The cnemial crest projects from the cranial side, flaring out laterally. Caudal to the cnemial crest is the

Figure 15. Tibiotarsus of *Pasquiaornis tankei*. A-B, proximal left tibiotarsus (RSM P2957.22); A, anterior view; B, posterior view; C-D, distal left tibiotarsus (RSM P2957.21); C, anterior view; D, posterior view. Abbreviations: cc, cnemial crest; fc, fibular crest; ics, intercondylar sulcus; , lateral articular surface; lc, lateral condyle; lcc, lateral cnemial crest; mas, medial articular surface; mc, medial condyle; mcc, medial cnemial crest; tg, tendinal groove. Scale bar equals 1 cm.

proximal articular surface. The articular surface is almost horizontal, dipping slightly on the cranial lateral edge and the caudal medial edge. The medial articular facet is slightly concave and projects further caudally than the lateral articular facet, which is slightly convex. The lateral articular facet hangs slightly over the shaft caudal laterally.

A crest begins to form just distal to the lateral caudal edge of the lateral articular facet. This is the fibular crest and it becomes more prominent as it goes distally. The lateral edge of the cnemial crest, which protrudes in a slightly lateral cranial direction, extends below the articular surfaces and dissipates into the shaft. The medial edge of the cnemial crest extends distally down the shaft and disappears before the distal end.

The distal end of the bone has two prominent condyles; the lateral and medial condyles which protrude cranially. The cranial side of the distal end is concave on the medial half with ridges along the lateral and medial edges. There is a thick triangular section of bone just proximal to the lateral condyle on the cranial surface with the widest portion starting just proximal to the lateral condyle then tapering out approximately a quarter of the way up the shaft. This may be the fused pretibial bone. Along the lateral side on the distal end leading to the lateral condyle, the bone is relatively straight while on the medial side leading to the medial condyle the bone slightly swings out medially just before the medial condyle. On the caudal surface of the distal end there is a smooth sulcus between the condyles which wraps around to the cranial portion of the distal end. As in most other Hesperornithiformes the supratendinal bridge is not present. The tendinal groove runs along from the medial edge of the lateral condyle and then curves toward the lateral edge as it extends proximally up approximately a quarter of the shaft.

***Pasquiaornis hardiei*:** RSM P2626.20/ RSM P2626.40/ RSM P2830.4/ RSM P2957.13/
RSM P2957.14/ RSM P2995.7/ RSM P2997.40/ RSM P2997.41/ RSM P2997.42/ RSM
P2997.46/ RSM P2997.47/ RSM P2997.48

Plate XXIV, fig. 4 and Figure 16

The tibiotarsi of *P. hardiei* are similar to those of *P. tankei* except that *P. tankei* is over twice as large. The medial cotyla of *P. hardiei* is less concave than that of *P. tankei*. The lateral cotyla in *P. tankei* is also more bulbous than that in *P. hardiei*. Distally, the two *Pasquiaornis* species are very similar, except that in *P. tankei* is larger and more robust than *P. hardiei*. The large triangular section of bone above the lateral condyle on the cranial surface is relatively much larger in *P. tankei*.

Fibula

This is the first description of the fibula of *Pasquiaornis*. Only the proximal ends of the fibula were discovered at the Bainbridge River locality.

***Pasquiaornis tankei*:** RSM P2989.35/ RSM P2995.9/ RSM P2997.80

Plate XXV, fig. 1

The most proximal portion of the fibula is the *caput fibulae*. The *caput fibulae* is widest in the cranial caudal axis. Along its long axis, the *caput fibulae* is curved, with its center the lowest point, rising as it goes cranial and caudal. The caudal edge of the proximal end hangs over the shaft, while the cranial edge is almost flush with the shaft. On the medial surface, just distal to the *caput fibulae* is a triangular depression, with the flat edge along the proximal end, and the point directed distally. The preserved portion of the lateral surface is relatively flat. The medial surface is slanted following the caudal edge of the triangular depression.

Figure 16. Proximal tibiotarsus of *P. hardiei*. 1, proximal right tibiotarsus (RSM P2995.1); 1a, anterior view; 1b, lateral view; 1c, medial view; 1d, posterior view; 2, proximal right tibiotarsus (RSM P2997.46); 2a, posterior view; 2b, anterior view. Scale bar equals 1 cm.

Pasquiaornis hardiei: RSM P2626.41/ RSM P2988.21

Plate XXV, fig. 2

The fibula of *P. hardiei* is similar to that of *P. tankei* except that it is approximately half the size.

Tarsometatarsus

The tarsometatarsus of *Pasquiaornis* was first described by Tokaryk et al. (1997). Here is a further description based off the new material from the Bainbridge River locality.

Pasquiaornis hardiei: RSM P2626.32/ RSM P2626.33/ RSM P2830.1/ RSM P2830.2/ RSM P2957.6/ RSM P2985.6/ RSM P2987.1/ RSM P2988.3/ RSM P2989.2/ RSM P2989.3/ RSM P2989.4/ RSM P2989.6/ RSM P2989.8/ RSM P2989.9/ RSM P2997.15/ RSM P2997.16/ RSM P2997.18/ RSM P2997.19/ RSM P2997.20/ RSM P2997.22/ RSM P2997.81/ RSM P2997.83/ RSM P3015.18

Plate XXVI and Figure 17

Overall, the tarsometatarsi of *P. hardiei* are slender, elongated and transversely compressed. Proximally, the lateral (IV) metatarsal is the largest, followed by the middle (III) metatarsal and the medial (II) metatarsal, which is the smallest in a cranial-caudal direction. On the proximal end there are medial and lateral cotylae separated in the middle by an intercotylar prominence, which are all grouped toward the cranial half of the proximal end. The medial cotyla is circular, concave and dips slightly cranially and medially. The very cranial tip of the medial cotyla has a proximally directed lip. The intercondylar prominence is relatively small and rounded. The lateral cotyla is relatively flat compared to the medial cotyla and the cranial lip dips distally. The cranial edge of the

Figure 17. Tarsometatarsus of *Pasquiaornis*. A, *P. tankei* left tarsometatarsus (RSM P2957.27) in anterior view; B-C, *P. hardiei* left tarsometatarsus (RSM P2997.18); B, medial view; C, anterior view; D-E, *P. hardiei* proximal left tarsometatarsus (RSM P2997.81); D, posterior view; E, anterior view. Abbreviations: II, second metatarsal trochlea; III, third metatarsal trochlea; IV, fourth metatarsal trochlea; apf, anterior proximal foramina; clr, craniolateral ridge; df, distal foramen; icp, intercondylar prominence; lc, lateral cotyla; mc, medial cotyla; ppf, posterior proximal foramina. Scale bar equals 1 cm.

proximal end overhangs the shaft of the bone. Below the overhanging proximal end, just distal to the intercotylar prominence there are two proximal cranial foramina and the caudal surface two proximal caudal foramina. One specimen shows the foramina penetrating all the way through the bone, although this may be due to erosion. No hypotarsal is present on the caudal surface. Slight grooves are visible on the caudal surface leading distally. These outline the shafts of the fused metatarsals.

A prominent ridge leading from the cranial lateral edge of the lateral cotyla extends halfway down the shaft towards the metatarsal IV trochlea. The ridge becomes less prominent as it goes distally. This prominent ridge on the lateral edge extends much further cranially than the medial edge of the bone. The lateral surface of the bone is relatively broad and flat compared to the more slender and curving medial surface. On the lateral surface, just distal to the lateral cotyla is a scar where the *lig. Collateralis lateralis* would insert.

The trochleae of metatarsals III and IV on the distal end extend approximately the same distance distally. The trochlea of metatarsal II does not extend as far distally as the trochleae of metatarsals III and IV. The lateral edge of the trochlea of metatarsal IV extends further caudally than its medial edge but extend as far cranially as the lateral edge. The medial edge of the trochlea of metatarsal IV extends slightly more distally than the lateral edge. The medial and lateral edges of the trochlea of metatarsal III are similar, with the medial edge extending slightly further distally. The medial edge of the trochlea of metatarsal IV extends slightly further cranially than the trochlea of metatarsal III. The trochlea of metatarsal II is located medial and caudal to the trochlea of metatarsal III. The trochlea of metatarsal II only extends half way down the trochlea of metatarsal III distally. Part of the trochlea of metatarsal II overlaps the trochlea of metatarsal III

caudally. The trochlea of metatarsal trochlea is larger in cranial caudal dimension compared to metatarsals III and IV. The neck of the trochlea of metatarsal IV extends slightly further cranially than the neck of the trochlea of metatarsal III. Located between the trochlea of metatarsals III and IV is a distal foramen. Overall the metatarsal trochleas are closely compressed together.

Pasquiaornis tankei: RSM P2626.38/ RSM P2957.27/ RSM P2997.21/ RSM P2997.23/
RSM P3015.4/ RSM P3015.19

Plate XXVI and Figure 17

The tarsometatarsi of *P. tankei* are very similar to those of *P. hardiei* and differ only on a few characteristics. The tarsometatarsi of *P. tankei* are much larger. The largest tarsometatarsus of *P. tankei* is 25% larger than that of the largest tarsometatarsus of *P. hardiei*. The proximal foramina in *P. tankei* do not seem to penetrate to the caudal side as they do in *P. hardiei*, but this may be due to preservation. The trochlea of metatarsals III and IV of *P. tankei* are relatively farther apart compared to *P. hardiei*, which are compressed together. Located between the trochlea of metatarsals III and IV there is a distal foramen in *P. hardiei* that is not seen in *P. tankei*. This may be due to preservation. The neck of the trochlea of metatarsal III extends slightly more cranially than that of the trochlea of metatarsal IV. The trochlea of metatarsal II is not preserved in the tarsometatarsus of *P. tankei* in the Bainbridge River locality, however, when compared to those known from the Carrot River locality the trochlea of metatarsal II of *P. tankei* and *P. hardiei* are very similar.

Pasquiaornis species A: RSM P2985.5/ RSM P2989.7/ RSM P2997.17

Figure 18

Figure 18. Tarsometatarsus (RSM P2989.7) of possible new species of *Pasquiaornis*. A, anterior view; B, medial view; C, posterior to lateral view; D, posterior view. Scale bar equals 1 cm.

Pasquiaornis species A is less compressed transversely than the tarsometatarsi of *P. tankei* and *P. hardiei*. *Pasquiaornis* species A is the smallest of the three *Pasquiaornis* species, although more robust than *P. hardiei*. *P. tankei* is 30% larger than *Pasquiaornis* species A, while *P. hardiei* is 6% larger than *Pasquiaornis* species A. In *Pasquiaornis* species A, on the caudal surface of the tarsometatarsus towards the proximal end, there are two foramina, one of which is medial and the other lateral, both at the same height. These foramina are not visible in the tarsometatarsi of *P. tankei*. The trochlea of metatarsal II of *Pasquiaornis* species A is slightly larger and more flared than that of *P. hardiei*. The trochlea of the metatarsal II in *P. hardiei* is located further behind the trochlea of metatarsal III than is the case in *Pasquiaornis* species A.

Phalanges

This is the first description of the phalanges of *Pasquiaornis*. In Hesperornithiformes the fourth toe is the largest and most elongated.

***Pasquiaornis tankei*:** RSM P2626.19/ RSM P2626.31/ RSM P2987.24/ RSM P2988.23/
RSM P2988.24/ RSM P2989.27/ RSM P2989.28/ RSM P2989.29/ RSM P2995.8/ RSM
P2997.65/ RSM P2997.66/ RSM P2997.67/ RSM P2997.68/ RSM P2997.70/ RSM
P2997.71/ RSM P2997.72/ RSM P2997.73/ RSM P3015.9/ RSM P3015.15

Plate XXVII and XXVIII

The first digit of the fourth toe is slightly compressed medial-laterally. The proximal articular end is triangular in shape. There are two cotyla on the proximal end, separated by a ridge that runs from the dorsal lateral edge to the ventral medial edge. The more ventral cotyla is the largest. The ventral medial tip extends out further proximally. The dorsal surface of the bone is rounded. The ventral surface is flattened. The distal

articular end has two condyles. The two condyles are not parallel. The lateral condyle is slanted with the dorsal end closest to the medial condyle. The condyles are approximately the same size; however, the medial condyle is slightly more dorsal than the lateral condyle. The length of the lateral surface is slanted in a similar way to the lateral condyle. On the medial surface of the medial condyle there is a shallow rounded indentation. This is also found on the lateral surface of the lateral condyle except it is slightly shallower than that of the medial condyle.

RSM P2988.24/ RSM P3015.9 (possible first digit of 3rd toe) Plate XXVII, fig. 1: in general these phalanges match the above description except they are slightly longer and more slender. The distal condyles are also more parallel to each other, with the dorsal ends slanted laterally.

RSM P2989.27/ RSM P2989.28/ RSM P2997.67/ RSM P3015.15 (more distal digits) Plate XXVIII, fig. 1: Another group of phalanges were smaller and less compressed. The condyles on the distal end are both at an angle, creating a pyramidal shape. The medial condyle overlaps the lateral condyle dorsally. The proximal articulation is similar to other phalanges except it is slanted toward the medial side.

RSM P2997.71 (possible first digit of 2nd toe): This phalanx is much more elongated and slender than the other phalanges. The distal end has two condyles that are not parallel. The lateral condyle is slanted with the dorsal end closest to the medial condyle. The condyles are approximately the same size; however, the medial condyle is slightly more dorsal than the lateral condyle. The proximal articular end is roughly triangular in shape, but is eroded, so the features on it cannot be described in detail.

RSM P2989.41 (distal toe) Plate XXVIII, fig. 2: This phalanx is much thinner, although just as long as the other phalanges. The phalanx arcs slightly in a dorsal lateral

direction. The proximal end is the broadest end and is triangular in shape. There are two cotyla on the proximal end with a small ridge running down the middle separating the two. The medial surface of the bone is very concave until a third the way distally along the bone and then becomes planar. The lateral surface is planar. The dorsal surface has a groove running the length of the bone separating the distal condyles. The distal condyles are very small and even in size, each slanted lateral ventrally to dorsal medially.

RSM P2831.14 (terminal phalanx) Plate XXVIII, fig. 3: The proximal end is triangular in shape with a lateral and medial cotyla split down the middle by a ridge. The phalanx is thin transversely, with the thickest part being the proximal end. On the ventral surface, just distal to the proximal end is a prominent rounded flexor tuberculum. The distal portion ends in a broad point. Along the medial and lateral surfaces there is a midline groove which extends from the distal end nearly to the proximal end before it drops down to the ventral surface proximal to the flexor tuberculum. Overall, the phalanx bends slightly ventrally.

Pasquiaornis hardiei: RSM P2831.15/ RSM P2831.16/ RSM P2985.5/ RSM P2989.40/
RSM P2997.69/ RSM P3015.14

This group of phalanges is similar to those of *P. tankei* except they are approximately half the size.

Bone comparisons with other Hesperornithiformes

Comparisons of the Bainbridge River Hesperornithiformes are made here with other previously described taxa in the order, with the exception of the carpometacarpus, which is unknown in Hesperornithiformes. Comparisons of this element are also made

with *Ichthyornis*, also a member of Ornithurae, and Enantiornithes, other taxa found at the Bainbridge River site. Further comparisons are made with *Ichthyornis* and can be found in Appendix III. *Gansus yumenensis*, another Ornithurae (You et al., 2006), also was used for comparison as it also shows traits for aquatic life. These comparisons can be found in Appendix IV. All measurements used for size comparison are found in Appendix II.

Maxilla

Like all other hesperornithiforms, the maxilla of *Pasquiaornis* contained teeth, although none were preserved in the Bainbridge River maxilla. The maxillae of *Pasquiaornis tankei* are approximately half the size of *Hesperornis regalis* (YPM1206). The complete maxilla of *P. tankei* is not known. A smooth groove is present above the tooth row on the dorsal surface of the maxilla of *Hesperornis* (Gingerich, 1973), and is also present in *Pasquiaornis*. In *Hesperornis*, the teeth in the maxilla are set in a deep continuous alveolar groove with only a faint indication of separate sockets (Marsh, 1880), which is also the case in *Paraesperornis*. In *Pasquiaornis* there are fully separate sockets for the teeth. On the medial side, distal the alveoli, there are several foramina in *Pasquiaornis* that are not seen in *Hesperornis*. In *Hesperornis*, the lateral surface extends farther ventrally than the medial surface; while in *Pasquiaornis* the medial and lateral surface extend the same length. On the lateral surface in *Pasquiaornis* there is a foramen on the central groove that is not seen in *Hesperornis*.

Frontal

The frontals of *Pasquiaornis* are very similar in shape to those of other known Hesperornithiformes frontals. Overall, the frontals of *Pasquiaornis* are smaller than those of any other known hesperornithiform. The frontals of *Pasquiaornis* are unfused at the midline of the skull; right and left frontals were found separately, while those of *Baptornis*, *Hesperornis*, and *Paraesperornis* are fused. The frontals of *P. tankei* are similar in size to those of *Baptornis advensus*, while those of *P. hardiei* are approximately half the size. The frontals of *P. hardiei* are about 66% smaller than *Hesperornis regalis* (YPM1206) and the frontals of *P. tankei* are about 50% smaller. The frontals of *P. tankei* are about two thirds the size of *Paraesperornis* and those of *P. hardiei* are approximately one third the size.

The dorsal side of the frontal of *Baptornis* bears a faint scroll-like pattern similar to that seen in extant grebes (Martin and Tate, 1976). The frontals of *Pasquiaornis* have a much more prominent ridge on the dorsal surface than those of *Baptornis*. The suture between the frontals and beak is open in *Hesperornis* (Marsh, 1880). The frontals also articulated with the lachrymal (Marsh, 1880). Since the frontals of the Bainbridge River *Pasquiaornis* specimens were not found in articulation with any other skull bones and the sutures are not preserved, it cannot be said if this characteristic applies to *Pasquiaornis*. The caudal end of the frontal in *Hesperornis*, *Baptornis*, and *Paraesperornis* is triangular in shape. This portion is not preserved in the *Pasquiaornis* specimens.

Quadrates

A single *Pasquiaornis* quadrate found from the Carrot River locality was mentioned in Tokaryk et al. (1997). Tokaryk et al. (1997) describe the quadrate of *Pasquiaornis* as being apneumatic and having a fossa near the angled base of the orbital

process, a characteristic seen in other hesperornithiforms (Witmer, 1990). The quadrates found at the Bainbridge River locality are very similar to the one found at the Carrot River site. Only the ventral half is known from the Bainbridge River locality; however both have similarly oriented condyles which articulate with the mandible on the ventral side. The Bainbridge River specimens have a large pocket, which open on the medial side that is not seen in the Carrot River specimen. This may be due to preservation as there is evidence of erosion around that area in the Carrot River specimen. Because of the close similarity, the Bainbridge River specimens are also designated as *Pasquiaornis*.

Elzanowski et al. (2000) include a supplementary diagnosis for Hesperornithiformes that discusses the quadrate. Elzanowski et al. (2000) state that a hesperornithiform quadrate is characterized by a head that is undivided or the division is only barely indicated; pterygoid condyle elongate, nearly continuous with the ventral margin of the orbital process and appressed on the medial mandibular condyle. Unfortunately, the condition of the head of the quadrate from the Bainbridge River material is unknown because it is not preserved. The pterygoid condyle in *Pasquiaornis* is slightly elongated, and close to being continuous with the ventral margin of the orbital process. The orbital process is not fully preserved in the *Pasquiaornis* specimens.

The shafts of the quadrate in both *Baptornis* and *Pasquiaornis* are proportionally broad. The orbital process of the *Baptornis* quadrate has a triangular base (Martin and Tate, 1976). In *Baptornis*, a prominent pit is present on the dorsomedial margin of the base of the orbital foramen (Martin and Tate, 1976). This portion of the quadrate is not preserved in the quadrate of *Pasquiaornis* from the Bainbridge River locality. The pterygoid condyle on *Baptornis* is rectangular, with the long axis dorsoventral (Martin

and Tate, 1976), while that of *Pasquiaornis* is triangular. Both *Baptornis* and *Pasquiaornis* have a shallow depression lateral to the pterygoid condyle.

The ventral articular portion of the quadrates of *Hesperornis* and *Pasquiaornis* are similar. The lateral condyle in *Hesperornis* is set back slightly more medially than that of *Pasquiaornis*. The medial and lateral condyles of *Hesperornis* have a larger gap between them than in *Pasquiaornis*. Along the medial side above the pterygoid and medial condyles in *Pasquiaornis* is a “pocket” that is not present in *Baptornis* and *Hesperornis*. *Hesperornis* has a large orbital process that is not present in *Pasquiaornis*. The pterygoid condyle in *Pasquiaornis* is more prominent than in *Hesperornis*. There is a deeper depression on the posterior surface above the medial condyle in *Pasquiaornis* than there is in *Hesperornis*.

Dentary

From what is preserved of the dentary of *P. tankei* the depth of the dentary is only slightly smaller than that of *Hesperornis regalis* and *Paraesperornis*, at least towards the rostral end. From what is preserved, the depth of the dentary of *P. hardiei* is approximately half the size of *H. regalis* and *Paraesperornis*. The rostral end of the dentary bone of *Hesperornis* is blunt like that of *Pasquiaornis* and has an articulation for the prementary bone. This is also seen in *Paraesperornis alexi*. The dorsal lateral surface of the dentary of *Hesperornis*, much like that of *Pasquiaornis* has a distinctive pit. In *Hesperornis*, the prementary has a matching pit where a ligament may have crossed the joint and tied the two bones together (Martin and Naples, 2008). It is unknown if this feature occurred in *Pasquiaornis* since no prementary bone has been found. In *Hesperornis regalis* it is also known that the two dentaries lay directly against each other

for most of their length (Martin and Naples, 2008). This would make for a very narrow mandible, and is a feature seen in many fish eating extant birds. This may have also been the case in the *Pasquiaornis*. The teeth in the dentary of *Hesperornis* and *Paraesperornis* were set in an open groove, with faint indication of sockets. The dentary of *Pasquiaornis* also shows indications of sockets.

Dentition

The Bainbridge River teeth have similar features found in all other hesperornithiform teeth as well as in bird teeth in general. In the teeth of the Bainbridge River birds, as in all other described hesperornithiform teeth, the crown and root meet at a waist, and there is a resorption pit on the lingual side of the root (Martin and Stewart, 1980; Martin and Stewart, 1999). The root is also rectangular in shape. As mentioned in Martin and Stewart (1980), teeth of birds are most like those of crocodiles in how they replace their teeth. The new tooth would develop on the lingual side of the root of the old tooth where the pit is found (Martin and Stewart, 1980; Martin and Stewart, 1999). The replacement tooth would enter the pulp cavity of the old tooth and eventually expel it (Martin and Stewart, 1980; Martin and Stewart, 1999).

The Bainbridge River assemblage of teeth has two morphologies as stated earlier. Tooth shape B from the Bainbridge River assemblage is hooked, and curved lingually; a shape not seen in other hesperornithiform teeth. There is a great variation in size which may be due to the size of different individuals, different sized species of *Pasquiaornis*, small teeth may be teeth that had not fully grown to replace the previous teeth. However, it is likely that some if not most of these teeth belong to the genus *Pasquiaornis*. Further

study needs to be done on the Bainbridge River teeth. With the high abundance of teeth from this locality, it could add greatly to the knowledge of teeth in birds.

Splenial

The splenials of *P. hardiei* are about a third the size of *Hesperornis regalis* (YPM1206) and *Paraesperornis*. From what is preserved of the *Pasquiaornis* splenials, they seem to be similar to that of *Hesperornis* and *Paraesperornis*, except the splenial of *Hesperornis* and *Paraesperornis* are much larger and slightly more robust. The caudal articular portion of the splenial in *Hesperornis* is relatively wider than that of *Pasquiaornis*.

Angular

The angular of *P. tankei* is slightly smaller than that of *Hesperornis regalis*, while that of *P. hardiei* is about half the size. The angular of *Hesperornis* is similar in shape to that of *Pasquiaornis*. The medial shelf for the prearticular on the angular of *Pasquiaornis* is more inclined than that of *Hesperornis*, which looks closer to horizontal. The lateral wall of the splenial in *Hesperornis* extends further rostrally than that of *Pasquiaornis*.

The angular of *P. tankei* is approximately the same size as that of *Paraesperornis*, while in *P. hardiei* it is about half the size. The rostral edge of the angular of *P. tankei* is longer dorsoventrally than that of *Paraesperornis*, however, the angular of *Paraesperornis* is longer in total rostral-caudally. The medial shelf for the prearticular on the angular in *Pasquiaornis* is more inclined than that of *Paraesperornis* which looks closer to horizontal.

Articular/Prearticular/Surangular

The surangular, articular and prearticular are tightly fused in *Pasquiaornis*, as seen in all other Hesperornithiformes. The surangular, articular and prearticular of *P. tankei* are similar in size to *Baptornis advensus*, while *P. hardiei* is about half the size. In *Baptornis*, the surangular is fused to the articular, with a groove that runs along the suture between the two bones (Martin and Tate, 1976). This is also the case in *Pasquiaornis*. The articular cotyla of *Baptornis* is divided into anterolateral and posteromedial sections, which are separated by a low ridge (Martin and Tate, 1976) similar to that in *Pasquiaornis*. However, the postero-medial cotyla in *Pasquiaornis* is narrower than that in *Baptornis*. In *Baptornis*, along the margin of the posterior cotyla, is a groove, running under the internal articular process (Martin and Tate, 1976). This groove also incorporates the articular foramen. In *Pasquiaornis* it is more of a ridge than a groove that incorporates the articular foramen. The junction of the surangular and the articular in *Baptornis* is formed by a wide depression and a wide, deep groove, found anterior to the posterior articular surface (Martin and Tate, 1976), which is similar to that in *Pasquiaornis*.

The surangular, articular and prearticular *P. tankei* and *P. hardiei* are about two thirds the size and a quarter the size of *Hesperornis*, respectively. In *Baptornis* and *Hesperornis* the articular surfaces are about the same shape and occupy the same position on the ramus (Martin and Tate, 1976) as is the case in *Pasquiaornis*. The mandibular articulation of *Baptornis*, *Hesperornis*, and *Pasquiaornis* are very similar (Martin and Tate, 1976). Like in *Hesperornis*, the angular is large, extending back to fuse with the articular to form a retroarticular process (articular process) (Gregory, 1952). The articular process in *H. regalis* is directed more dorsally, while that of *Pasquiaornis* is directed

more caudally. The articular process of *Pasquiaornis* also is directed more medially than in *H. regalis*, creating a shallow groove on the lateral surface. The ridge along the ventral portion of the most caudal portion of the articular in *Hesperornis* has a much more prominent than that of *Pasquiaornis*. The most caudal process of the ramus of *Hesperornis* is square shaped while that of *Pasquiaornis* is rounded.

The surangular, articular and prearticular *P. tankei* and *P. hardiei* are, respectively, about two thirds the size and a quarter the size of those elements in *Parahesperornis*. The *Hesperornis* lower jaw is similar to that of *Parahesperornis* in that there is a ridge underneath the articular, and the articular joint points away dorsally while in *Pasquiaornis* it curves back caudally.

Cervical Vertebrae

The cervical vertebrae of *Pasquiaornis* and all other hesperornithiforms are heterocoelous and similar in overall shape. The cervical vertebrae of *P. tankei* and *P. hardiei* are both smaller than those of *Baptornis advensus*. The cervical vertebrae of *P. tankei* and *P. hardiei* are, respectively, about 29% and 57% smaller than those of *Hesperornis regalis* (YPM 1200). Overall the cervical vertebrae of *Hesperornis* are slightly more robust than those of *Pasquiaornis*, especially *P. hardiei*. *Hesperornis regalis* cervicals 15 and 16 have hypophyses and vertebra 14 has large paired ventral processes which Marsh (1880) refers to as catapophyses which are not present in any of the preserved *Pasquiaornis* vertebrae.

The cervical vertebrae of *P. tankei* are about twice the size of *Enaliornis*, while those of *P. hardiei* are similar in size. The cervical vertebrae of *Enaliornis* were described as being similar to cervical 12 and 13 of *Hesperornis* (Galton and Martin, 2002). The

centra of *Enaliornis* cervical vertebrae are short, heterocoelous like those of *Pasquiaornis*, but are subtriangular in ventral view with a carotid sulcus that, cranially, is bordered by the bases of the incomplete carotid processes (Galton and Martin, 2002). *Pasquiaornis* is more hourglass-shaped in ventral view.

Dorsal Vertebrae

Unlike other Hesperornithiformes, the dorsal vertebrae of *Pasquiaornis* seem to be slightly amphicoelous instead of being heterocoelous. The dorsal vertebrae of *P. tankei* and *P. hardiei* are respectively about 13% and 33% smaller than those of *Baptornis advensus* (KUV 2290). *Baptornis* dorsal vertebrae are similar in shape to those of *Pasquiaornis*. The centrum is much broader in *Baptornis* than in *Pasquiaornis*.

The dorsal vertebrae of *P. tankei* and *P. hardiei* are respectively about 30% and 50% smaller than those of *Hesperornis regalis* (YPM 1200). Overall the dorsal vertebrae of *Hesperornis* are more robust than those of *Pasquiaornis*. The first five dorsal vertebrae of *Hesperornis* have a hypapophysis that may only be present on the first two dorsal vertebrae of *Pasquiaornis*. Only one known dorsal vertebrae from *Pasquiaornis* has a hypapophysis. The dorsal vertebrae of *Pasquiaornis* have larger and deeper lateral concavities in the centrum than those of *Hesperornis*.

The dorsal vertebrae of *P. tankei* and *Enaliornis* are similar in size, while those of *P. hardiei* are about 20% smaller than those of *Enaliornis*. The single described *Enaliornis* dorsal vertebra is strongly heterocoelous and is probably the first free vertebra cranial to the synsacrum. The preserved parts are similar to those of *Baptornis* and *Hesperornis*, in which the ventral process is also absent (Galton and Martin, 2002). The

Pasquiaornis vertebra that is most likely to be the first free vertebra cranial to the synsacrum is not strongly heterocoelous and has no ventral process.

Synsacra

The synsacra of *P. tankei*, *P. hardiei* and the unknown hesperornithiform species are, respectively, about 9%, 38% and 31% smaller than *Baptornis advensus* (UNSM 20030) (in greatest diameter). The synsacra of *P. tankei*, *P. hardiei* and the unknown hesperornithiform species are, respectively, about 58%, 71%, and 69% smaller than those of *Hesperornis regalis* (YPM 1207). The synsacra of *P. tankei*, *P. hardiei* and the unknown hesperornithiform species are, respectively, about 1.5%, 33%, and 26% smaller than *Enaliornis* (SMC B552828). The synsacrum of *Baptornis* (KUVP 2290) contains 10 fused vertebrae (Lucas, 1903). The complete synsacrum of *Enaliornis* probably consisted of 10 vertebrae, as in *Baptornis* (Martin and Tate, 1976; Galton and Martin, 2002), while the most complete *Pasquiaornis* synsacrum preserves six fused vertebrae and the most complete of the unknown hesperornithiform species specimens preserves eleven fused vertebrae.

The synsacrum of *Pasquiaornis* differs from other Hesperornithiformes in that the centra are slightly amphicoelous rather than being very heterocoelous like all other Hesperornithiformes. The synsacrum of *Pasquiaornis* is straighter overall than that of *Baptornis*, *Hesperornis*, and *Parahesperornis*. Overall, they are similar to other Hesperornithiformes by having transversely narrow synsacra (Martin and Tate, 1976; Marsh, 1880). This indicates an elongate, compressed pelvis, a common trait among foot propelled divers (Galton and Martin, 2002). The ventral surface of the synsacrum becomes progressively narrower in *Pasquiaornis* as it does in other Hesperornithiformes.

The synsacrum in *Hesperornis* becomes much narrower caudally. In both *Pasquiaornis* species and the unknown hesperornithiform species, this also occurs, but not to the same extent as in *Hesperornis*.

The first fused sacral vertebra in the unknown hesperornithiform species is proportionally much smaller and more dorso-ventrally compressed than in other Hesperornithiformes. The cranial portion of the centrum in the first fused sacral vertebra is proportionally much larger in *Hesperornis* than it is in any of the Bainbridge River species. The most cranial sacral vertebra of *Baptornis* has a high, posteriorly sloping neural spine (Martin and Tate, 1976). The neural spine is not fully preserved in the Bainbridge River specimens. In the Bainbridge River species and *Baptornis*, the transverse processes are tilted and flattened laterally to form a broad contact with the ilium (Martin and Tate, 1976). The transverse process of the 2nd sacral vertebra projects anteriorly in *Baptornis* (Martin and Tate, 1976), similar to the Bainbridge River species.

The centra are pinched much more in *Enaliornis* than in *Pasquiaornis* and the unknown hesperornithiform species, although the unknown hesperornithiform species is more pinched than in *Pasquiaornis*, to form a median longitudinal ridge (Galton and Martin, 2002). Large intervertebral foramina are present in *Enaliornis* (Galton and Martin, 2002) as well as *Pasquiaornis* and the unknown hesperornithiform synsacra. The cranial synsacral centra of the Bainbridge River species, as well as *Baptornis* and *Hesperornis*, are not pinched in as in *Enaliornis* (Galton and Martin, 2002).

Caudal vertebrae

All the dorsoventrally flattened caudal vertebrae have large transverse processes in *Enaliornis* (Galton and Martin, 2002), where as in *Pasquiaornis* are relatively smaller and compressed against the body of the vertebra.

Coracoid

The coracoids found in the Bainbridge River locality are almost identical to those found at the Carrot River locality. The coracoids found in the Carrot River locality (of similar age to the Bainbridge River locality) were originally identified as *Ichthyornis* on the basis of the scapular facet being nearly parallel to the sternal end of the glenoid facet (Tokaryk et al., 1997; Marsh 1880) and being very different to other known hesperornithiform coracoids (Tokaryk et al., 1997). Longrich (2009) stated that the coracoids referred to as *Ichthyornis* by Tokaryk et al. (1997) are more likely *Pasquiaornis*, as he believed they did not resemble those of *Ichthyornis*. Three reasons are given for Longrich' (2009) designation: first, the coracoids from the Carrot River locality both had large and small morphs, like other bones of *Pasquiaornis*; second, the coracoids exhibit pachyostosis, a diving adaptation (Longrich, 2006) seen in *Pasquiaornis*, but not known in *Ichthyornis*; and third, there are no coracoids of *Pasquiaornis* known and there is no other material of *Ichthyornis* known from the Carrot River locality except the disputed coracoids. There are two humeri of *Ichthyornis* identified from the Bainbridge River locality, which also produced abundant *Pasquiaornis* material. This would negate Longrich's (2009) third reason. However, the coracoids from the Carrot and Bainbridge River sites are much too large for the humeri of *Ichthyornis* found at the Bainbridge River site. This author agrees with Longrich (2009) on this designation and therefore refers both the Bainbridge and Carrot River specimens

to *Pasquiaornis*. Appendix III includes a more complete comparison of the bones of *Ichthyornis* and *Pasquiaornis*.

Overall, the coracoids of *P. tankei* are 15% smaller than those of *Hesperornis regalis* (YPM1207) and *Paraesperornis* and 12 % smaller than *Baptornis*. *P. hardiei* is about a half the size of *P. tankei*. The coracoid of *Pasquiaornis* is closest in shape to that of *Baptornis*. All coracoids so far described from Hesperornithiformes have a glenoid facet on the tip of the scapular end. This is unlike that of *Pasquiaornis* whose glenoid facet is further posterior on the scapular end, on the dorsal side. In *Baptornis* the glenoid facet is large, elliptical, and shallow (Martin and Tate, 1976), which is similar to *Pasquiaornis*, except in *Pasquiaornis* the glenoid facet is slightly deeper. The coracoids of *Baptornis*, *Paraesperornis* (Plate XVI, fig. 3) and *Hesperornis* broaden more abruptly toward the posterior end. However *Baptornis* does not broaden as quickly as *Hesperornis* and *Paraesperornis*. *Pasquiaornis* has a longer, slender neck and broadens more gradually.

The distal portion of the coracoid in *Pasquiaornis* is triangular in shape while those of *Hesperornis*, *Paraesperornis* and *Baptornis* are more rectangular. However, the coracoids of *Paraesperornis* and *Baptornis* are more elongate than that of *Hesperornis* (Martin, 1984) and also much less square-shaped on the distal portion. The procoracoid of *Pasquiaornis* is recurved toward the shaft and points medially, while that of *Baptornis*, which is also recurved toward the shaft, is directed toward the scapular end. The procoracoid of *Hesperornis* and *Paraesperornis* are not redirected toward the shaft. The sternal facet of Hesperornithiformes is described as perpendicular to the longitudinal axis of the coracoid. In *Pasquiaornis*, the sternal facet is slightly inclined. The distal end of the coracoid in *Baptornis* is slightly concave posteriorly and curved and convex anteriorly

(Martin and Tate, 1976), similar to that of *Pasquiaornis*. The sterno-coracoidal fossa in *Pasquiaornis* is slightly more concave than in *Baptornis*. The medial edge of the coracoid is slightly straighter in *Baptornis* than in *Hesperornis* (Martin and Tate, 1976) and in *Pasquiaornis* it is more curved.

Longrich (2009) described a right coracoid (TMP 1986.112.6), identified as an Ornithurine from the Dinosaur Park Formation in Alberta, as being very similar to the coracoids known from the Carrot River, referred to in this paper as *Pasquiaornis*. In general the bone looks very similar to the *Pasquiaornis* coracoids with a few differences. First, the Dinosaur Park Formation coracoid is approximately twice as large as the largest *Pasquiaornis* coracoids from the Bainbridge River or Carrot River localities. Secondly, the Dinosaur Park Formation coracoid has a much more prominent ridge on the medial edge of the glenoid facet, creating a deeper groove running cranio-caudally on the bone compared to the coracoids of *Pasquiaornis*. The procoracoid is not entirely preserved in the Dinosaur Park Formation, but what is preserved suggests that the procoracoid in the specimen was directed slightly more cranially than the *Pasquiaornis* coracoids. The characters of the Dinosaur Park Formation coracoid and *Pasquiaornis* coracoids that are similar according to Longrich (2009) are a shallow scapular cotyla; a massive coracoid shaft; and a dorsal bowing of the coracoid shaft in lateral view. The glenoid facet on both is also located antero-lateral to the scapular facet. If the Dinosaur Park Formation coracoid is closely related to *Pasquiaornis*, this would suggest a close relative of *Pasquiaornis* in the Campanian of what is today western Canada.

Scapula

The scapula of *Baptornis* is only known from the articular end of the scapula. The scapula of *P. tankei* is slightly smaller in size to that of *Baptornis advensus*, while that of *P. hardiei* is about half the size. The coracoidal articulation of the scapula of *Baptornis* is long, narrow, and slightly curved (Martin and Tate, 1976), while that of *Pasquiaornis* is bulbous and rounded. The anterodorsal margin of the *Baptornis* scapula does not show any articulation for the furcula on the proximal end (Martin and Tate, 1976), while that of *Pasquiaornis* does. The ventral border of the *Baptornis* scapula bears a long, shallow groove (Martin and Tate, 1976) not seen in *Pasquiaornis*. The neck of the scapula is wide and thick in *Baptornis* as well as in *Hesperornis* (Martin and Tate, 1976). The neck of *Pasquiaornis* is also wide and thin, but less so than that of *Baptornis* and *Hesperornis*. The glenoid facet is also located right at the end of the articular surface in *Baptornis*, *Hesperornis* and *Paraheperornis*, while in *Pasquiaornis* there is a large acromion process with the glenoid process more distal.

The proximal portion of the scapula of *P. tankei* is similar in size to that of *Hesperornis regalis*, while that of *P. hardiei* is about half the size. The scapula of *Pasquiaornis*, like that of *Hesperornis* is somewhat curved. The scapula of *Hesperornis* is relatively the same width throughout its length while that of *Pasquiaornis* gets slightly more narrow as it goes distal. Similar to *Hesperornis*, the scapula of *Pasquiaornis* is thickest proximally and then gets thinner as it goes distal. *Hesperornis* has no acromion process (Marsh, 1880), while *Pasquiaornis* does. The glenoid facet is more concave in *Pasquiaornis* compared to that of *Hesperornis* and the coracoidal articulation is more prominent in *Pasquiaornis* compared to that of *Hesperornis*.

The proximal portion of the scapula of *P. tankei* is similar in size to that of *Paraheperornis*, while that of *P. hardiei* is about half the size. The scapula of

Paraesperornis is dorsoventrally curved, while that of *Pasquiaornis* is curved medial-laterally, although it still may curve dorsoventrally, however the complete shaft is not known. The glenoid facet is more concave in *Pasquiaornis* compared to that of *Paraesperornis* and the coracoidal articulation is more prominent in *Pasquiaornis* compared to that of *Paraesperornis*.

Humerus

From the Carrot River locality, distal ends of the humerus (Figure 19.3 and 19.4) were found and designated as *Pasquiaornis*. The group of less reduced Bainbridge River humeri specimens are of similar sizes to those of the Carrot River *Pasquiaornis*. In the two *Pasquiaornis* species, *P. tankei* and *P. hardiei*, their humeri differ in that the ectepicondylar prominence on the distal end in *P. tankei* is a low ridge, parallel to the shaft and extending farther down the external condyle (Tokaryk et al., 1997). In *P. hardiei*, the external condyle and ectepicondylar prominence are less well defined (Tokaryk et al., 1997). This is also seen in two different groups of Bainbridge River humeri. The Carrot River specimens are very similar to those from the Bainbridge River which were also identified as *Pasquiaornis*. The other group of Bainbridge River hesperornithiform humeri are greatly reduced compared to the Carrot River *Pasquiaornis* humeri. *Pasquiaornis* has much more developed condyles on the distal end compared to the extremely reduced Bainbridge River humeri and are also larger.

The humerus of *Pasquiaornis* differs completely from that of other hesperornithiforms, whose humeri are much reduced. The humerus of *Pasquiaornis* has a prominent proximal end compared to other hesperornithiforms with many preserved features that are not found in these taxa, such as the presence of a large *caput humeri*,

Figure 19. *Pasquiaornis* bones from the Carrot River locality. 1, left tarsometatarsus and Holotype of *P. tankei* (RSM P2077.63); 1a, antero-medial view; 1b, postero-lateral view; 2, left tarsometatarsus and Holotype of *P. hardiei* (RSM P2077.117); 2a, medial view; 2b, anterior view; 3, shaft and distal end of left humerus of *P. tankei* in anterior view (RSM P2487.4); 4, shaft and distal end of right humerus of *P. hardiei* in anterior view (RSM P2487.3); 5, left femur of *P. hardiei* (RSM P2077.60); 5a, posterior view; 5b, anterior view; 6, right femur of *P. tankei* (RSM P2077.108); 6a, anterior view; 6b, posterior view. Scale bar equals 1 cm.

deltopectoral and bicipital crests, and other areas of muscle attachment seen on more typical bird humeri. The distal end of the *Pasquiaornis* humerus also has prominent condyles that are not seen in other hesperornithiforms. An interesting feature of the *Pasquiaornis* humerus is the anteriorly deflected deltopectoral crest. Clarke and Norell (2002) consider this an “advanced” avian feature, one that might not be expected in a hesperornithiform. The much more reduced Bainbridge River humeri are similar to the “classic” hesperornithiform humerus.

The reduced Bainbridge River humeri specimens (Figure 12.1) (RSM P2626.43/ RSM P2986.1/ RSM P2997.26/ RSM P3015.13) are about 37% smaller than *Baptornis advensus* (KUV2290) (Figure 12.4), 51% smaller than *Hesperornis regalis* (YPM1206) (Figure 12.2), and 32% smaller than *Parahesperornis* (KUV2287) (Figure 12.3). Marsh (1880) first described the humerus of *Hesperornis* as being rudimentary. The humerus of *Hesperornis* is even more reduced than that of *Baptornis* and the Bainbridge River reduced humeri. Overall, the humeri of Hesperornithiformes, excluding *Pasquiaornis*, are long and slender. The proximal end of the reduced Bainbridge River specimen is more broadened and flat than that of *Parahesperornis*, *Hesperornis* and *Baptornis* which are more rounded. The reduced Bainbridge River humeri have more distinct deltopectoral and bicipital crests than seen in other known Hesperornithiformes, excluding *Pasquiaornis*. The reduced Bainbridge River humerus has a midline ridge (*Margo caudalis*) on the posterior surface of the proximal end that is much more prominent than in other reduced hesperornithiform humeri.

The shaft of *Baptornis* curves downward then expands noticeably and is twisted posteromedially (Martin and Tate, 1976). The shafts of *Hesperornis* and *Parahesperornis* also curve downward slightly. The shaft of the reduced Bainbridge River specimen is

even more curved although it does not seem to be twisted as in *Baptornis*. There is a nutrient foramen situated in a groove on the shaft of the humerus of *Baptornis* similar to that of the reduced Bainbridge River specimens; however, a second foramen is situated distal to this one in *Baptornis* (Martin and Tate, 1976) that is not seen in the reduced Bainbridge River humerus. In both *Baptornis* and the Bainbridge River reduced specimens, the condyles on the distal end are barely developed. The humerus of *Hesperornis* has no articular facets on the distal end. The distal end of the Bainbridge River specimen has very reduced articular facets, but not as reduced as *Hesperornis*, *Paraesperornis*, and *Baptornis*.

Ulna

The only other known hesperornithiform ulna, other than *Pasquiaornis*, is that of *Baptornis*. The proximal end of the ulna of *P. tankei* and *P. hardiei* are about 47% and 33% larger than that of *Baptornis advensus* (KUV 2290). The *Baptornis* ulna is much shorter, stout and more robust compared to the more elongated and slender *Pasquiaornis* ulna. The intercotyla of *Baptornis* is small, making the inner and outer cotyla almost continuous (Martin and Tate, 1976). The intercotyla in *Pasquiaornis* is much more prominent. The *Baptornis* specimen has no nutrient foramina as seen along the shaft in *Pasquiaornis*. The shafts of both *Baptornis* (Martin and Tate, 1976) and *Pasquiaornis* have no noticeable scars for secondary feather attachment. In both *Baptornis* and *Pasquiaornis*, the distal radial depression is very shallow. The styloid process is much more prominent in *Pasquiaornis* than in *Baptornis*.

Radius

The shafts of the *Pasquiaornis* radii are much more slender compared to other known hesperornithiform radii. The proximal end of the radii of *P. tankei* and *P. hardiei* are about 45% and 12% smaller than those of *Baptornis advensus*. The humeral cotyla is larger in *Baptornis* than in *Pasquiaornis*, however, they are both oval in shape. The radial bicipital tuberosity is situated along the rim in the radius of *Baptornis* (Martin and Tate, 1976), while that of *Pasquiaornis* is located slightly more distal to the rim. Both *Baptornis* and *Pasquiaornis* have a faint intermuscular line on the shaft of the radius. About midway along the shaft of the *Baptornis* radius, the bone expands with a nutrient foramen on the palmar side (Martin and Tate, 1976). This feature is not seen in *Pasquiaornis*, although this may be due to that the complete radius of *Pasquiaornis* is not known. The lunar depression is shallower in *Baptornis* than in *Pasquiaornis*.

Carpometacarpus

There are no known carpometacarpus bones from any described taxa within Hesperornithiformes. Since the humeri of *Ichthyornis* were identified from the Bainbridge River locality, *Ichthyornis* will be used as a comparison, to rule out these carpometacarpi being those of *Ichthyornis*. The carpometacarpus of *Ichthyornis* shows many differences from *Pasquiaornis*. Overall, the carpometacarpus of *Pasquiaornis* is more robust than that of *Ichthyornis*. The first obvious difference is that the carpal trochlea is flat in *Ichthyornis*, while in *Pasquiaornis* there is a more distinct groove. This trochlea is also relatively wider in *Pasquiaornis* than it is in *Ichthyornis*. There is no evidence of a large proximo-distally elongate scar in *Pasquiaornis* as there is in *Ichthyornis* at the same position as the intermetacarpal tuberosity. The first metacarpal of *Ichthyornis* has a triangular shape with a 90 degree angle on the most proximal portion close to the second

metacarpal. The first metacarpal of *Pasquiaornis* has a semi-circular shape. An apomorphy of *Ichthyornis* is a large tubercle close to the articular surface of the second metacarpal (Clarke, 2004). This tubercle is not present in *Pasquiaornis*. Similar to *Ichthyornis*, the pisiform is situated relatively proximal to metacarpal one, which is usually found around the midpoint of metacarpal one in Aves (Clarke, 2004). The extensor groove seen in *Ichthyornis* is not visible in *Pasquiaornis*; however this may be due to preservation. The distal articulation in *Ichthyornis* is more distinct than it is in *Pasquiaornis*.

Since there is also a possible enantiornithine bone, Enantiornithes will also be used for comparison here. Like that of *Pasquiaornis*, the metacarpals are coosified. The dorsal portion of the trochlea on metacarpal II extends further proximally than the ventral portion while in *Pasquiaornis* they are even. The distal ends of metacarpal II and III are not typically fused to each other in Enantiornithines (Chiappe and Walker, 2002) while in *Pasquiaornis* they are. The shaft of metacarpal III is also longer than the shaft of metacarpal II in Enantiornithes (Sereno et al., 2002) while in *Pasquiaornis* they are equal in length.

Pelvis

The pelves of *Pasquiaornis* were found separated from the synsacrum while those of other Hesperornithiformes are usually found fused to the synsacrum. The pelves of *P. tankei* and *P. hardiei* are, respectively, about two thirds the size and one third the size of that of *Parahesperornis*, and are, respectively, about a third the size and a quarter the size of that of *Hesperornis*. The pelvis of *P. tankei* is slightly smaller than that of *Baptornis advensus*, while that of *P. hardiei* is about three quarters the size of the pelvis of

Baptornis advensus. The pelvis of *P. tankei* and *Enaliornis* are of similar size while *P. hardiei* is about three quarters the size of *Enaliornis*.

Hesperornithiformes as a group have separate posterior extremities of the ilium, ischium, and pubis (Marsh, 1877). This is also true for *Pasquiaornis*. The ischium and pubis of *Baptornis varneri* are long, thin, rod-like processes. The pubis and ischium are narrow in *Enaliornis* and *Pasquiaornis*. The acetabulum of *Hesperornis* (Figure 20E) and other most known Hesperornithiformes are enclosed by bone except for a foramen that perforates the inner wall (Marsh, 1877). *Pasquiaornis* acetabula are greatly opened compared to other Hesperornithiformes, except that of *B. varneri* whose acetabulum is also open (Martin and Cordes-Person, 2007). Baptornithid pelvises have a preacetabular portion of the ilium relatively longer than in hesperornithids. In *Pasquiaornis*, the preacetabular portion is not preserved in its entirety. *Hesperornis* has a slight prepubis bone that is not present in *Pasquiaornis*, although this lack could be an artefact of preservation.

In general, in hesperornithiforms the antitrochanter does not protrude out significantly laterally and have a wide angle into the acetabulum. In *Pasquiaornis*, the antitrochanter protrudes relatively more laterally and is steeply inclined to the acetabulum compared to other Hesperornithiformes. The antitrochanter of *B. varneri* is even more poorly developed compared to *Baptornis advensus*, *Hesperornis*, and *Pasquiaornis*. The antitrochanter of *Paraheperornis* is very prominent and proportionally wider than that of *Pasquiaornis*. The antitrochanter is smaller in *Enaliornis* compared to that of *Pasquiaornis*. Like *Baptornis* and *Hesperornis*, the anterior end of the ischium in *Pasquiaornis* merges with the antitrochanter, with no distinct margin between them. In *Enaliornis*, the antitrochanter is found on the ilium and protrudes laterally very little.

Figure 20. Bones of *Hesperornis regalis*, the first known hesperornithiform. A, right femur (YPM 1200); B, left tarsometatarsus (YPM 1200); C, left tibiotarsus (YPM 1200); D, left fibula (YPM 1200); E, right pelvis (YPM 1476). Scale bar equals 5 cm.

Femur

The two groups of Bainbridge River specimens are of similar size to the two species of Carrot River *Pasquiaornis* (Figure 19.5 and Figure 19.6). One of the diagnostic characters of *Pasquiaornis* is that the trochanteric ridge of the femur is closer to the shaft than in *Baptornis* (Tokaryk et al., 1997). This characteristic is present in the Bainbridge River femora. In the original description, the two species of *Pasquiaornis*, *P. hardiei* and *P. tankei* are differentiated by *P. hardiei* having the distal rim of the head perpendicular to the shaft and being smaller and *P. tankei* having the distal rim of the head directed toward the shaft and is larger (Tokaryk et al., 1997). In the Bainbridge River femora there are also two main size categories; however, the distal rim direction is not consistently different between the two groups. Both, the Carrot River *Pasquiaornis* and the Bainbridge River locality femora have faint to no observable intermuscular lines. Because the femora from the Bainbridge River are almost identical to those from Carrot River, they are identified as *Pasquiaornis*.

The distal width of the femora of *P. hardiei* are about 22% smaller than *Enaliornis barretti*, 12% smaller than *E. seeleyi* and approximately the same size as *E. sedwicki*. The distal width of the femora of *P. tankei* are about 4% larger than *Enaliornis barretti*, 15% larger than *E. seeleyi* and approximately 27% larger than those of *E. sedwicki*. In size and shape, the *Pasquiaornis* femur resembles that of *Enaliornis* more closely than any other hesperornithiform. In *Enaliornis* the greater trochanter and head are at the same level; while in *Pasquiaornis*, the head is slightly lower than the greater trochanter. The head and greater trochanter of *Enaliornis* are connected by a continuous articular surface. This differs from *Pasquiaornis*, which has more of a notch between the greater trochanter and head. The head of *Enaliornis* and *Pasquiaornis* are rounded with a

slight incline proximally. The neck of the femoral head is shorter and less constricted in *Pasquiaornis* and *Enaliornis* than it is in other Hesperornithiformes. The cross-section of the mid-shaft of *Pasquiaornis* is similar to that of *Enaliornis* and *Baptornis* in that it is sub-circular compared to that of *Hesperornis* (Figure 20A), which is transversely wide and cranio-caudally narrow (Galton and Martin, 2002). The medial condyle is small in relationship to the lateral condyle in *Enaliornis*, *Pasquiaornis* and *Baptornis*. In other hesperornithiforms the medial condyle is not as small. Like *Enaliornis* and *Baptornis*, the *Pasquiaornis* lateral condyle extends further distally, while in other hesperornithids the medial and lateral condyle are more even.

The femora of other hesperornithiforms are far more robust than those of *Pasquiaornis* and *Enaliornis*. The notch between the greater trochanter and head seen in *Pasquiaornis* is not as deep as it is in *Paraheperornis* and *Hesperornis*, but it is deeper than that of *Baptornis* and *Enaliornis*. *Enaliornis* has the smallest notch. The head of the *Paraheperornis* femur extends farther proximally than the greater trochanter, while in *Pasquiaornis* the greater trochanter extends further proximally. The intercondylar sulcus in *Pasquiaornis* femora is broad and rounded as in other hesperornithiforms.

The greatest length of *P. tankei* femora is about 12% smaller than in *Baptornis advensus* (KUV 2290). The greatest length of *P. hardiei* femora is about 33% smaller than in *Baptornis advensus* (KUV 2290). The greater trochanter of *Baptornis* overhangs on the anterior side much more than in *Pasquiaornis*. The outer margin of the greater trochanter in both *Baptornis* and *Pasquiaornis* is almost parallel with the long axis of the shaft. In both *Baptornis* and *Pasquiaornis*, the greater trochanter extends slightly further proximally than the head. Both *Baptornis* and *Pasquiaornis* have a similar rim on the head of the femur. *Baptornis* and *Pasquiaornis* have a sweeping muscle scar from the

greater trochanter to the antero-lateral portion of the shaft extending to the lateral condyle. This muscle scar is far more prominent in *Hesperornis* and *Parahesperornis*. The femora of *Baptornis* have no visible nutrient foramina, while there are at least two on the lateral surface of the shaft in *Pasquiaornis*. The popliteal fossa in both *Baptornis* and *Pasquiaornis* is broad and shallow. *B. varneri* femur possesses a broad, smooth popliteal fossa (Martin and Cordes-Person, 2007), while that of *Pasquiaornis* contain many foramina. *B. varneri* has a deeper intercondylar fossa than that of *Pasquiaornis*. The medial condyle of the femur extends slightly further distally in *B. varneri* than in *Pasquiaornis* (Martin and Cordes-Person, 2007). In both *Baptornis* and *Pasquiaornis*, the lateral condyle extends further distally than the medial condyle.

The greatest length of the *P. tankei* femora is about 37% smaller than that of *Hesperornis regalis* (Figure 20A) and 32% larger than that of *Hesperornis macdonaldi* (LACM 9728). The greatest length *P. hardiei* femora is about 52% smaller than that of *Hesperornis regalis* and 11% larger than that of *Hesperornis macdonaldi* (LACM 9728). The femur of *H. regalis* is much larger and more robust than *Pasquiaornis*. The antero-posterior length of the greater trochanter is less than that of the femoral head in *H. regalis*, while it is much more even in *Pasquiaornis* femora. The head of *H. regalis* extends proximally farther than the greater trochanter with a broad, shallow notch between them, while in *Pasquiaornis* the greater trochanter extends farther proximally than the head and has a relatively less broad notch. The area between the greater trochanter and the head has a relatively more constricted antero-posterior width when compared to the head and greater trochanter of *Pasquiaornis*. The head of the femur of *H. regalis* and *Parahesperornis* has more of an incline on the medial surface than *Pasquiaornis*. The greater trochanter of *H. regalis* extends out laterally over the shaft,

while in *Pasquiaornis* the greater trochanter of the femur is more evenly aligned with the shaft. This causes the medial side of *Hesperornis* to be more curved compared to *Pasquiaornis*. The neck of the femur in *Pasquiaornis* is shorter than in *Hesperornis*. On the ventral surface of the head of the femur of *Hesperornis*, there is an upside down “U” shape along the rim of the head that is not seen in *Pasquiaornis*. The *Fovea lig. Capitis* on the head of the femur is relatively larger and deeper in *Hesperornis* than in *Pasquiaornis*. The shaft of *H. regalis* has strong prominences for the attachment of muscles not seen in *Pasquiaornis*. In *H. regalis* the lateral condyle is much more expanded, making the patellar groove much smaller than in *Pasquiaornis*. The lateral condyle of *H. regalis* is so enlarged that the patellar groove is almost nonexistent. The lateral condyle of *Hesperornis* is also directed more laterally than in *Pasquiaornis*. The lateral and medial condyles are at about the same level in *Hesperornis*, while in *Pasquiaornis* the lateral condyle extends farther distally.

The femora of *P. tankei* are about 7% smaller than that of *Parahesperornis* (KUV 2287); the femora of *P. hardiei* are about 29%. In *Parahesperornis*, there are prominent intramuscular lines on the anterior and posterior surfaces of the shaft that are not visible in *Pasquiaornis*. The neck of the femur in *Pasquiaornis* is shorter than that of *Parahesperornis*. On the ventral surface of the head of the femur of *Parahesperornis*, there is an upside down “U” shape along the rim of the head that is not seen in *Pasquiaornis*. The *Fovea lig. Capitis* is relatively larger and deeper in *Parahesperornis* than in *Pasquiaornis*.

Tibiotarsus

The tibiotarsi of Hesperornithiformes are elongate and nonpneumatic, with a large medullary cavity (Martin and Tate, 1976), which is also true for *Pasquiaornis*. One of the synapomorphies of all Hesperornithiformes is the lack of the supratendinal bridge in the tibiotarsus (Martin and Tate, 1976). *Pasquiaornis* is also lacking the supratendinal bridge. The cnemial crest on the tibiotarsus of Hesperornithiformes is large and shaped much like an isosceles triangle (Galton and Martin, 2002). This is also true for *Pasquiaornis*. Since there are no complete *Pasquiaornis* tibiotarsi known, proximal width was used in size comparisons.

The tibiotarsus of *P. tankei* is about the same size as that of *Baptornis advensus* (KUV 2290) and 24% smaller than that of *B. varneri* (SDSM 68430). The tibiotarsus of *P. hardiei* is about 43% smaller than that of *Baptornis advensus* (KUV 2290) and 57% smaller than that of *B. varneri* (SDSM 68430). The proximal end of the tibiotarsus of *B. advensus* flares out due to the lateral expansion of the outer cnemial crest (Martin and Tate, 1976). The outer cnemial crest of *Pasquiaornis* flares out even more laterally than that of *B. advensus*. The inner cnemial crest of *B. advensus* is low, so the groove between the two crests is broad and shallow (Martin and Tate, 1976). The inner cnemial crest is not low compared to the outer cnemial crest in *Pasquiaornis*. However the groove between the inner and outer cnemial crests in *Pasquiaornis* is shallow and broad as in *B. advensus*. The articular face on the proximal end of *B. advensus* is inclined (Martin and Tate, 1976) while that of *Pasquiaornis* is relatively perpendicular to the shaft. The medial articular facet of *Pasquiaornis* is flat and oval like *B. advensus*, except *B. advensus*' medial articular facet is directed postero-medially (Martin and Tate, 1976), while that of *Pasquiaornis* is directed slightly more postero-distally. The fibular crest extends about half way down the shaft in *B. advensus* and is deeply grooved along the posterior margin

(Martin and Tate, 1976). It is not clear how far the fibular crest extends on *Pasquiaornis* since there is no complete tibiotarsus. However, the fibular crest extends at least a quarter to a third the way down the shaft and does not seem to be as deeply grooved as that of *B. advensus*. The distal end of the tibiotarsus of *Pasquiaornis* is inflected slightly less medially than in *B. advensus*. The tendinal groove of *B. advensus* is broad and ends in a deep lateral pocket (Martin and Tate, 1976). The tendinal groove of *Pasquiaornis* is also broad; however the pocket at the end is more shallow, and broader. The anterior medial ridge connected to the medial condyle is broader in *B. advensus* than in *Pasquiaornis*. Similar to *B. advensus*, the anterior intercondylar sulcus of *Pasquiaornis* is shallow (Martin and Tate, 1976).

The tibiotarsus of *B. varneri* has an expanded proximal articulation with a long and straight fibular crest extending at least half way down the shaft (Martin and Cordes-Person, 2007). Again it is not positive how far the fibular crest of *Pasquiaornis* extended. The tibiotarsus of *B. varneri* has a wide facet for articulation with the fibula (Martin and Cordes-Person, 2007) that is not as large in *Pasquiaornis*.

The tibiotarsi of *P. tankei* and *P. hardiei* are, respectively, about 47% and 70% smaller than that of *Hesperornis regalis* (YPM 1200) (Figure 20C). The proximal end of the tibiotarsus of *Hesperornis* flares out due to the lateral expansion of the outer cnemial crest (Martin and Tate, 1976). The outer cnemial crest of *Pasquiaornis* flares out even more laterally than that of *Hesperornis*. The inner cnemial crest of *Hesperornis* is low, so the groove between the two crests is broad and shallow (Martin and Tate, 1976). The inner cnemial crest is not low compared to the outer cnemial crest in *Pasquiaornis*. However the groove between the inner and outer cnemial crests in *Pasquiaornis* is also shallow and broad, but not as shallow as in *Hesperornis*. The articular face on the

proximal end of the tibiotarsus of *Hesperornis* is inclined (Martin and Tate, 1976), while that of *Pasquiaornis* is relatively perpendicular to the shaft. The external articular face on the proximal end in *Hesperornis* is set apart anteriorly and posteriorly from the medial articular facet by grooves (Martin and Tate, 1976). There are no grooves separating the lateral and medial facies in *Pasquiaornis*. The distal end of the tibiotarsus of *Pasquiaornis* is inflected slightly less medially than in *Hesperornis*.

The tibiotarsi of *P. tankei* and *P. hardiei* are, respectively, about 15% and 52% smaller than that of *Paraesperornis* (KUV 2287). The tibiotarsus of *Paraesperornis* is very long and slender compared to that of *Pasquiaornis*. The cnemial crest is very triangular and straight edged in *Paraesperornis*, while that of *Pasquiaornis* is slightly more rounded. The outer cnemial crest of *Pasquiaornis* flares out much more laterally than that of *Paraesperornis*. The groove between the inner and outer cnemial crests on the anterior end of the tibiotarsus is shallower in *Paraesperornis* than in *Pasquiaornis*. The articular face of the proximal end is slanted laterally in *Paraesperornis*, while that of *Pasquiaornis* is relatively horizontal. Distally, the pocket at the end of the tendinal groove is deeper in *Paraesperornis* than in *Pasquiaornis*. The medial condyle in *Paraesperornis* is flared out slightly more than that of *Pasquiaornis*. On the posterior distal surface, the ridges outlining the sulcus are much more prominent in *Paraesperornis* than in *Pasquiaornis*.

The tibiotarsi of *P. tankei* and *P. hardiei* are, respectively, about 2% and 32% smaller than those of *Enaliornis* (SMC B55316). The proximal tibiotarsus of *Enaliornis barreti* and *Pasquiaornis* has a large lateral flared cnemial crest (Galton and Martin, 2002). The groove between the inner and outer cnemial crests is shallower in *Enaliornis* than in *Pasquiaornis*. The proximal articular surface of the tibiotarsus of *Enaliornis* slants

slightly down on the lateral side, while that of *Pasquiaornis* is almost horizontal. The distal tibiotarsus of *Enaliornis sedgwicki* and *Pasquiaornis* both have small lateral and medial condyles that are nearly equal in size (Galton and Martin, 2002). The *Trochlea cartilaginis tibialis* (intercondylar angle) is directed laterally in *Enaliornis* (Galton and Martin, 2002), while in *Pasquiaornis*, it does not seem to be directed either laterally or medially. Both *E. sedgwicki* and *Pasquiaornis* have a broad shallow cranial intercondylar fossa on the distal tibiotarsus (Galton and Martin, 2002). The distal tibiotarsus of *E. barreti* has larger lateral and medial condyles than *Pasquiaornis*. The medial condyle of *E. barreti* is directed laterally on its distal edge. This differs from that of *Pasquiaornis* whose condyles are directed outward away from the sulcus. The medial condyle of *E. sedgwicki* is also directed slightly laterally on its distal edge, but not as much as *E. barreti*. In *Enaliornis seeleyi*, the lateral ridge along the sulcus on the posterior surface of the distal end is more prominent than it is in *Pasquiaornis*.

Fibula

The fibula of *Baptornis*, *Hesperornis* and *Pasquiaornis* are very similar. Based on the proximal end, the fibula of *P. tankei* and *P. hardiei* are, respectively, about 55% and 67% smaller than that of *H. regalis* (YPM 1200) (Figure 20D). The fibula of *P. tankei* and *P. hardiei* are, respectively, about 10% and 34% smaller than that of *B. advensus* (KUVP 2290), and are about 26% and 46% smaller, respectively, than that of *B. varneri* (SDSM 68430). The caput fibulae in *Baptornis*, *Hesperornis* and *Pasquiaornis* are rectangular (Martin and Tate, 1976). In *B. advensus* there is no tubercle for *m. flexor perforatus digiti III* (Martin and Tate, 1976). It is unknown if the tubercle for *m. flexor perforatus digiti III* is present in *Pasquiaornis* since this portion of the fibula is not

preserved. There is a large triangular roughened area on the proximal-medial surface in both *Baptornis* and *Hesperornis*, similar to that in *Pasquiaornis*. The shaft of the fibula of *B. varneri* is more robust compared to that of *B. advensus* and *Pasquiaornis*. In *Hesperornis*, there is a deep depression on the ventral surface of the posterior overhanging proximal end that is not found in *Pasquiaornis*.

Tarsometatarsus

The three groups of Bainbridge River tarsometatarsi specimens are of a similar size distribution as the Carrot River *Pasquiaornis* specimens (Figure 19.1 and 19.2). Part of the diagnosis for *Pasquiaornis* is that the intercotylar prominence is anterior and overhanging the shaft and the trochlea of metatarsal II is posterior and close to the base of the trochlea of metatarsal III (Tokaryk et al., 1997). These characters are also seen in all three groups of Bainbridge River tarsometatarsi as well as having a prominent ridge along the anterior lateral edge of the bone that dissipates about half way along its length, which seems unique to *Pasquiaornis*. Because of this, the three groups of Bainbridge River tarsometatarsi are referred to as *Pasquiaornis*. The diagnosis for the two described *Pasquiaornis* species from the Carrot River is that *P. hardiei* has the internal cotyla deflected toward the shaft, and the neck of the trochlea of metatarsal III is further anterior than the neck of the metatarsal IV trochlea. *P. tankei* has the internal cotyla nearly anterior-posterior with the neck of the metatarsal IV trochlea further anterior than that of the metatarsal III trochlea, as well as *P. tankei* being larger than *P. hardiei* (Tokaryk et al., 1997). The diagnostic character of the internal cotyla being slanted toward the shaft in *P. hardiei* may be due to erosion and crushing. The internal cotyla in all Bainbridge River specimens is slightly slanted toward the shaft, but no more so than in *P. tankei*. In some

of the Bainbridge River specimens, the neck of the metatarsal III trochlea is further anterior than the neck of the metatarsal IV trochlea, as in *P. hardiei*, while other Bainbridge River specimens have the neck of the metatarsal IV trochlea further anterior than the metatarsal III trochlea, as in *P. tankei*. Overall, the two main groups of Bainbridge River specimens match well with the two species of *Pasquiaornis* from the Carrot River locality.

The third group of Bainbridge River tarsometatarsi is similar to the Carrot River *Pasquiaornis*, but exhibits a few differences. This group is less compressed transversely than the tarsometatarsi of *P. tankei* and *P. hardiei*. *P. tankei* is 30% larger than the third group of Bainbridge River tarsometatarsi, while *P. hardiei* is 6% larger. In this third group of Bainbridge River tarsometatarsi, there are two foramina on the caudal surface of the tarsometatarsus towards the proximal end, one of which is medial and the other lateral, both at the same height. These foramina are not visible in the tarsometatarsi of *P. tankei*. The metatarsal II trochlea of the third group of Bainbridge River tarsometatarsi is slightly larger and more flared than that of *P. hardiei*. The trochlea of metatarsal II in *P. hardiei* is located further behind the trochlea of metatarsal III than in the third group of Bainbridge River tarsometatarsi. However, they do have an intercotylar prominence that is anterior and overhanging the shaft and the metatarsal II trochlea is posterior and close to the base of the metatarsal III trochlea which are the diagnostic characteristics of *Pasquiaornis*. Therefore the third group of Bainbridge River tarsometatarsi are considered to represent a probable a new species of *Pasquiaornis*, previously referred to as *Pasquiaornis* species A.

As in other Hesperornithiformes, *Pasquiaornis* tarsometatarsi are transversely compressed, are missing hypotarsal grooves, and have a craniolateral ridge extending

distally to the metatarsal IV trochlea. However, this ridge in all specimens considered to be *Pasquiaornis* diminishes about halfway down the shaft, while in other Hesperornithiformes the ridge is prominent all the way along the shaft. The trochlea of metatarsal IV, as in all other Hesperornithiformes, is at least as large as the metatarsal III trochlea. Like other baptornithids the trochlea of metatarsals III and IV are about the same length. This is different from hesperornithids, in which the metatarsal IV trochlea is extends further distally than the metatarsal III trochlea. The distal foramen of the *Pasquiaornis* specimens, like other baptornithids, appears to be an open groove.

The tarsometatarsus of *P. tankei* is 22% larger than that of *Enaliornis* (SMC B55331), while *P. hardiei* and *Pasquiaornis* species A are, respectively, about 27% and 37% smaller than *Enaliornis* (SMC B55331), using the proximal transverse diameter since there are no complete *Enaliornis* tarsometatarsi. In the diagnosis of *Enaliornis*, the proximal end of the tarsometatarsus is described as having a small medial cotyla, and the distal end is arched in distal view with the dorsal edge of the metatarsal IV trochlea planar to the prominent dorsal edge of the subequal metatarsal III trochlea (Galton and Martin, 2002). The medial cotyla in *Pasquiaornis* is slightly smaller than the lateral cotyla. The distal end in distal view of the tarsometatarsus of *Pasquiaornis* is also slightly arched like that of *Enaliornis*. In *Pasquiaornis*, as in *Enaliornis*, the metatarsal III trochlea is at least as large and distally extending as the metatarsal IV trochlea. The intercotylar eminence in *Enaliornis*, *Baptornis* and *Pasquiaornis* is low and gently rounded. There are no caudal proximal foramina in *Enaliornis* as in *P. tankei*, but unlike *P. hardiei* and *Pasquiaornis* species A. As in *Baptornis* and *Enaliornis*, the dorsolateral ridge of *Pasquiaornis* merges with the shaft about half way along the length of the tarsometatarsus, although it is slightly more prominent in *Baptornis*. In *E. barretti*, the

trochlea of metatarsal II is flared, similar to that of *Pasquiaornis* species A. In *Enaliornis*, the metatarsal III is the most anterior trochlea, while in *Pasquiaornis*, the metatarsal IV trochlea extends the farthest anteriorly. The metatarsal III trochlea of *Enaliornis* extends relatively farther anterior to the rest of the trochleae, more so than that of *Pasquiaornis*. In *Enaliornis* the metatarsal II trochlea is expanded similar to that of *Pasquiaornis* species A.

Comparison with *Enaliornis* shows that the metatarsal II trochlea of *Pasquiaornis* is situated further posterior and behind the third metatarsal trochlea than in *Enaliornis*. In *Enaliornis*, the metatarsal IV trochlea is extended slightly farther distally than the metatarsal III trochlea. In *Pasquiaornis*, trochlea of metatarsal III and IV are closer to even in length. *H. regalis* has a greatly enlarged medial-lateral metatarsal IV trochlea compared to that of *Pasquiaornis* and other Hesperornithiformes. Compared to *Baptornis* and *Hesperornis*, *Pasquiaornis* has a less pronounced, or less proximally extending intercotylar prominence.

The greatest length of the tarsometatarsus in *P. hardiei* is about 27% smaller than that of *B. advensus* (KUVP 2290) and 37% smaller than that of *B. varneri* (SDSM 68430). The greatest length of the *P. tankei* tarsometatarsus is about 3% smaller than that of *B. advensus* (KUVP 2290) and 15% smaller than that of *B. varneri* (SDSM 68430). The greatest length of the *Pasquiaornis* species A tarsometatarsus is about 32% smaller than that of *B. advensus* (KUVP 2290) and 41% smaller than that of *B. varneri* (SDSM 68430). In *Pasquiaornis* the trochleae of metatarsal III and IV are of similar size, as in *Baptornis*. The intercotylar prominence in *Baptornis* and *Pasquiaornis* is low and blunt compared to *Hesperornis* (Figure 20B). The medial cotyla is slightly smaller than the lateral and both are directed slightly distally in both *Baptornis* and *Pasquiaornis*. In *B.*

advensus there are no caudal proximal foramina as in *P. tankei*, however *Pasquiaornis* species A and *P. hardiei* in the Bainbridge River specimens do have two proximal posterior foramina. Like *Pasquiaornis* species A and *P. hardiei*, *B. varneri* has proximal foramina (Martin and Cordes-Person, 2007). The trochlea of metatarsal II in *P. hardiei* is located farther behind the trochlea of metatarsal III than in *Baptornis*. In *Baptornis*, the intertrochlear notch between the trochlea of metatarsal III and IV narrows and then widens. This widening is not seen in *Pasquiaornis*. The intertrochlear notches of *B. varneri* extend proximally to near the midpoint of the shaft, while those of *Pasquiaornis* do not extend as far (Martin and Cordes-Person, 2007). The metatarsal II trochlea of *Baptornis* is expanded similarly compared to that of *Pasquiaornis* species A, but expands more than in *P. tankei* and *P. hardiei*.

The greatest length of the tarsometatarsus of *P. hardiei* is about 58% smaller than that of *Hesperornis regalis* (UA 9716), 56% smaller than *H. chowi* (PU 17208), 40% smaller than *H. bairdi* (PU 17208A), 29% smaller than *H. mengeli* (BO 780106) and 62% smaller than that of *H. rossicus* (ZIN PO 5464). The greatest length of the *P. tankei* tarsometatarsus specimens is about 45% smaller than that of *H. regalis*, 41% smaller than *H. chowi*, 21% smaller than *H. bairdi*, 5% smaller than *H. mengeli* and 49% smaller than that of *H. rossicus*. The greatest length of the tarsometatarsus of *Pasquiaornis* species A is about 61% smaller than that of *Hesperornis regalis* (UA 9716), 59% smaller than *H. chowi* (PU 17208), 44% smaller than *H. bairdi* (PU 17208A), 34% smaller than *H. mengeli* (BO 780106) and 64% smaller than that of *H. rossicus* (ZIN PO 5464). The *Hesperornis* tarsometatarsus is much more robust than the more slender tarsometatarsus of *Pasquiaornis*. There are prominent grooves running lengthwise along the tarsometatarsus distinguishing the three fused metatarsals, which are not seen in

Pasquiaornis. The intercotylar prominence is inflected up much more in *Hesperornis* than in *Pasquiaornis*. On the medial side toward the posterior, the bone is directed higher in *H. gracilis* than it is in *Pasquiaornis*. There are no caudal proximal foramina in *Hesperornis* as in *P. tankei* of the Bainbridge River specimens, but unlike the Bainbridge River *P. hardiei* and *Pasquiaornis* species A specimens. The depressions on the lateral and medial surfaces of the trochlea are larger in *Hesperornis* than in *Pasquiaornis*. In *Hesperornis* the metatarsal IV trochlea is greatly enlarged compared to metatarsals two and three. In *Pasquiaornis*, the metatarsal IV trochlea is not so enlarged and is much closer in size to the other metatarsal. In *Hesperornis*, the metatarsal IV trochlea extends further distally and is expanded more than the III, while in *Pasquiaornis* the trochlea of metatarsal III and IV extend about the same distance distally. In *Hesperornis* the metatarsal II trochlea is almost behind the metatarsal III trochlea. In *Pasquiaornis*, the metatarsal II trochlea is slightly medial to the metatarsal III trochlea in its posterior position.

The tarsometatarsus of *P. tankei* is about 19% smaller than that of *Parahesperornis* (KUV 2287); *P. hardiei* is 39% smaller than *Parahesperornis* (KUV 2287); and *Pasquiaornis* species A is 43% smaller than *Parahesperornis* (KUV 2287). There are no caudal proximal foramina in *Parahesperornis* as in the Bainbridge River *P. tankei* specimens, but unlike the Bainbridge River *P. hardiei* and *Pasquiaornis* species A specimens, in which the foramina are present. *Parahesperornis* has a larger metatarsal IV trochlea than metatarsal III trochlea. In *Pasquiaornis* they are more similar in size. The trochlea of metatarsal IV is more distally situated in *Parahesperornis* than in *Pasquiaornis*. The metatarsal II trochlea is expanded more in *Parahesperornis* than in *Pasquiaornis*, but is closest to that of *Pasquiaornis* species A.

Phalanges

P. hardiei and *P. tankei* phalanges from similar positions are much smaller than those of *Baptornis advensus* (FMNH 395). In *Baptornis* on the 1st phalanx of the 4th digit, the medial condyle on the distal end is still a bit larger than the lateral condyle, but not as enlarged or extend over the lateral condyle as in *Hesperornis* or extant grebes (Martin and Tate, 1976). This is similar to *Pasquiaornis*; however, *Baptornis* medial condyle is still slightly more enlarged than that of *Pasquiaornis*.

P. hardiei and *P. tankei* phalanges from similar positions are both significantly smaller than those of *Hesperornis regalis* (YPM 1200). In *Hesperornis*, the medial condyle on the distal end of the 1st phalanx of the 4th digit, is much more greatly enlarged than the rounded lateral condyle and extends over it (Martin and Tate, 1976). In *Pasquiaornis* the lateral condyle is not as rounded as in *Hesperornis*, and the medial condyles are not as enlarged and do not extend over the lateral condyle as far. There is a large prominent ridge on the ventral surface along the medial edge of the phalanx of *Hesperornis*. This ridge is much less prominent in *Pasquiaornis*. On the proximal articular surface there are two cotyla. These are much more concave in *Hesperornis* than they are in *Pasquiaornis*.

The terminal phalanges known from the Bainbridge River and tentatively referred to here as *Pasquiaornis* are not typical terminal phalanges for a diving bird. Most extant diving bird terminal phalanges are flattened to create a larger surface area for the power stroke like in Grebes (Martin and Tate, 1976). The terminal phalanx of *Pasquiaornis* looks like that of a less specialized bird, transversely flattened and slightly curved. The terminal phalanx of *Baptornis* is somewhat flattened, but not like in Grebes, and slightly

curved and pointed (Martin and Tate, 1976). Marsh (1880) described the terminal phalanx of *Hesperornis* as “wedge” shaped, short, depressed, and pointed. In *Pasquiaornis*, the phalanx is not flattened or wedge shaped and has a larger flexor tuberculum.

The terminal phalanx of *Pasquiaornis* is somewhat similar to that of Enantiornithes, which also have a midline groove and a rounded flexor tuberculum (Lamanna et al., 2006), although this is not uncommon among birds. The Bainbridge River terminal phalanges, like those of *Archaeopteryx*, look similar to those of ground-dwelling birds, featuring slight curvature, robust construction, and shallow, poorly defined flexor tubercles (Ostrom, 1984). This may hint to *Pasquiaornis* being evolutionarily closer to ground-dwelling birds, that it was not an obligate swimmer/diver, or conversely, that these terminal phalanges do not belong to *Pasquiaornis*. The terminal phalanx is also similar to that of *Gansus yumenensis*, a Cretaceous bird from China (You et al., 2006). The flexor tuberculum is slightly larger in relative terms in *Gansus yumenensis*. You et al. (2006) state that the terminal phalanx of *Gansus* is similar to that of extant shorebirds (Charadriiformes), herons (Ardeidae), and diving ducks (Anatidae) (Shufeldt, 1909). The fact that similar terminal phalanges are seen in diving ducks and other extant birds that spend time in water give some confidence to the view that these may belong to *Pasquiaornis*. More work will be needed in this area.

DISCUSSION

The Bainbridge River and Carrot River locality Hesperornithiformes are the oldest known in North America and the second oldest known globally after *Enaliornis* from England. Consequently, this avian fossil material significantly enhances our knowledge of the early evolution and diversity of this group. As described here, there are at least four species of Hesperornithiformes known from the Bainbridge River locality. Three of the species are from the genus *Pasquiaornis* and a fourth is an undescribed hesperornithiform taxon. The amount of avian material and presence of these four species show that Hesperornithiformes were abundant and diverse in this area of the Western Interior Seaway during the Cenomanian.

Taxonomic Identification

A significant difficulty in the identification and taxonomic assignment of the bird bones from the Bainbridge River locality is that they are disarticulated and none are associated. The nature of the bonebed involves transport and thus each individual bone could belong to a different individual. For example, it is easy to see that one femur differs from another, but how to decide which tarsometatarsus goes with that femur? How is the decision made on which bones belong to which species? Seeley (1876), who studied the bones of *Enaliornis* from England, faced a similar problem. He split the bones into two species based on size. Galton and Martin (2002) later split the two species into three, but did so again using size to group the different elements together.

Tokaryk et al. (1997) applied the same method to the bones of *Pasquiaornis* from the Carrot River locality in Saskatchewan. This method was also used in this study for the separation of the Bainbridge River specimens, along with other characteristics in the

bones that would differentiate them into different species. Alternate explanations such as sexual dimorphism, individual variation or ontogenetic stages will be discussed separately.

Evidence that supports the grouping of the great majority of the Bainbridge River fossil avian bones is the presence of diving characteristics found in the bones in order to distinguish diving from non-diving taxa. All the fossil bones seem to be relatively robust with thickened compact bone compared to non-diving birds showing the following characters: the pelves and synsacra are compressed transversely; a large cnemial crest on the tibiotarsus; and the tarsometatarsi are compressed transversely, all of which are characteristic of diving birds (Cracraft, 1982; Martin and Tate, 1976).

Four species are identified from the Bainbridge River site as belonging to the order Hesperornithiformes. Three of the four species are identified within the genus *Pasquiaornis*. In the Tokaryk et al. (1997) paper which described *Pasquiaornis*, two species were named from a locality on the Carrot River, Saskatchewan, namely *P. hardiei* and *P. tankei*. The bones from the Carrot River site were also from a marine bonebed, and were not found in articulation or in association with each other, similar to the bones in the Bainbridge River locality. Tokaryk et al. (1997) separated the species into a large and a small species, since two distinct size differences were found in the humeri, tarsometatarsi, and femora, as well as morphological differences which, when coupled with size differences, ruled out sexual dimorphism.

The bonebed investigated here, 100 km away from the Carrot River and of the same stratigraphic interval, allows for a similar distinction of bones. The great majority of fossil bird bones from the locality were very similar, and divided easily into two size classes among the frontals, jaw bones, vertebrae, coracoids, scapulae, humeri, ulnae,

pelves, femora, tibiotarsi, fibulae, tarsometatarsi, and phalanges. Since the humeri, femora, and tarsometatarsi were identical or very similar to those from the Carrot River locality, they were identified as the two distinct species previously described by Tokaryk et al. (1997). The rest of the bones were identified as *P. tankei* and *P. hardiei*, because they also fell into the two size ranges and generally had characteristics of diving birds with greatest similarity to hesperornithiforms. The pectoral and wing bones are not very hesperornithiform-like; however, they are slightly reduced and robust, characteristics of diving birds. Since these bones also appeared in two distinct size categories they were also identified as probable *P. tankei* and *P. hardiei* bones.

Two additional species awaiting formal description are separated from *P. hardiei* and *P. tankei* by distinct characteristics seen in individual bones. The third species, which is considered another species of *Pasquiaornis* (*Pasquiaornis* sp. A), is only known from a tarsometatarsus. This is easily distinguished from the tarsometatarsi of *P. hardiei* and *P. tankei*, by having a more flared 2nd trochlea, and being less transversely compressed and more robust. This tarsometatarsus is placed in the genus *Pasquiaornis* because the intercotylar prominence of the tarsometatarsus is anterior, overhanging the shaft, the trochlea for digit 2 is posterior and close to the base of the trochlea for digit 3; and the anterior ridge along metatarsal III dissipates half way down the shaft.

The fourth species is known from a humerus that is much more reduced than the humeri of *Pasquiaornis* and is a more typical looking hesperornithiform humerus. This humerus probably represents a new species and maybe a new genus of hesperornithiform, because the humerus differs greatly from other reduced hesperornithiform humeri. There is a possible fifth species of hesperornithiform identified from a synsacrum. Alternatively, this synsacrum may, however, belong to the third *Pasquiaornis* species or to the unknown

hesperornithiform species. This synsacrum differs from the synsacra of *P. hardiei* and *P. tankei* in that it is slightly smaller and more curved dorso-ventrally. This synsacrum does belong to a diving bird because, like synsacra of other diving birds, it is greatly compressed transversely. Neither of these likely new taxa are formally described or named here.

Ontogenetic Stages, Sexual Dimorphism or Intraspecific Variability

There are other possible explanations for the differences in size between elements of *P. hardiei* and *P. tankei* without regarding them as two species. These possibilities include the larger group being adults and smaller being juveniles; individual variation within the species; or sexual dimorphism between males and females.

Is it possible that these bones are one species, with the smaller group being juveniles? This is very unlikely since the smaller group of bones do not show the usual signs of juvenile bone. The distal and proximal ends of the bones are fully fused as in adult birds, showing no natural pitting or incompletely formed epiphyses which would be expected of juvenile bones (King and McLelland, 1984; Bellairs and Osmond, 1998; Chiappe et al., 2007).

There is one possible exception among the tibiotarsi. One distal tibiotarsus (RSM P2997.39) seems to have some pitting along the anterior portion of the condyles. However, no epiphyseal line of fusion is evident. This tibiotarsus is the smallest of all the other distal tibiotarsi. There is some erosion on the very distal portion and along the posterior of the condyles, so the pitting on the anterior end may also be erosion. RSM P2997.39 is the best possibility for a bone with juvenile characteristics, but even if it is, it

does not explain the overall significant size difference between all elements of *P. tankei* and *P. hardiei*.

Within each of the species *P. hardiei* and *P. tankei* is a difference in size within some elements. This is probably due to individual variation, but the large size difference between *P. tankei* and *P. hardiei* is most likely not due to individual variation within one species. There is no described species of hesperornithiform with such a range in the size of individual elements.

Could the variability be a case of sexual dimorphism within one species? There are characteristics in many of the bones that differ in ways other than just size that could be explained with sexual dimorphism. Sexual dimorphism has not previously been known among other Hesperornithiformes, with the possible exception of *Enaliornis*. Galton and Martin (2002) suggest a possibility of sexual dimorphism for the three species of *Enaliornis* because of pocketing that occurs proximally in the femurs of the larger individuals of each of the three species of *Enaliornis*. In extant diving birds some sexual dimorphism is present (Johnsgard, 1987). This is seen in cormorants, where males on average are larger than the female (Koffijberg and Van Eerden, 1995). Sexual dimorphism as a possibility is not completely ruled out here. However, the size differences and morphological distinctions between these two sets of bones appear greater than has yet been reported in single species of Hesperornithiformes.

Relationship within Hesperornithiformes

In the Tokaryk et al. (1997) paper introducing *Pasquiaornis*, the genus is placed in the order Hesperornithiformes and family Baptornithidae. However, the paper does not

specifically list the characters of *Pasquiaornis* that would place it in these groups. The next paragraphs will discuss *Pasquiaornis*' placement within Hesperornithiformes.

A trait common among Hesperornithiformes, although not unique to the order, is the presence of robust bones, which is seen in *Pasquiaornis*. However, having robust bones is a common character among all diving birds. *Pasquiaornis* bones are robust, but less so than other Hesperornithiformes, with the exception of *Enaliornis*.

Hesperornithiformes also have non-pneumatic bones (Martin and Tate, 1976), which is a character also present in *Pasquiaornis*. Hesperornithiformes have short and broad femora (Martin and Tate, 1976), like those of *Pasquiaornis*. In Hesperornithiformes, the cnemial crest on the tibiotarsus is large and triangular with the distal end of the tibiotarsus also lacking the supratendinal bridge (Martin and Tate, 1976). Both these traits are present in *Pasquiaornis*. The tarsometatarsi of Hesperornithiformes are transversely compressed with a distinct craniolateral ridge leading distally to lateral trochlea (metatarsal IV). The distal lateral trochlea is at least as large and extends distally as far as the middle trochlea (metatarsal III). The tarsometatarsus also lacks a hypotarsal groove (Martin and Tate, 1976). All of these characters are present in the tarsometatarsus of *Pasquiaornis*.

However, *Pasquiaornis* also lacks many characters seen in Hesperornithiformes. A common trait among known Hesperornithiformes is the extremely reduced wing (Figure 12) (Martin and Tate, 1976). *Pasquiaornis* is primitive in Hesperornithiformes in having a much less reduced humerus. Hesperornithiformes are known to have all heterocoelous vertebrae (Galton and Martin, 2002). *Pasquiaornis* has the primitive character of the dorsal vertebrae being not truly heterocoelous, but almost amphicoelous. The acetabulum of *Pasquiaornis* is also completely open, while those of most other Hesperornithiformes are partly closed, with the exception of *Baptornis varneri* (Galton

and Martin, 2002; Martin and Cordes-Person, 2007; Martin and Tate, 1976). The coracoid of all known Hesperornithiformes has the glenoid facet on the tip of the scapular end (Martin and Tate, 1976), while in *Pasquiaornis* it is distal to this point. In the tarsometatarsus, the distinct craniolateral ridge leading distally to the lateral trochlea in *Pasquiaornis* is only distinct about halfway along the tarsometatarsus while in other Hesperornithiformes it is distinct all the way along (Martin and Tate, 1976). Overall *Pasquiaornis* is much less specialized than other Hesperornithiformes. The lack of many of these characters can be explained by *Pasquiaornis* being a basal form of hesperornithiform. *Pasquiaornis* is closer to Hesperornithiformes than any other known order.

There are three main families of Hesperornithiformes: Hesperornithidae, Baptornithidae, and Enaliornithidae. Tokaryk et al. (1997) placed *Pasquiaornis* in Baptornithidae. The reason for this is that Baptornithidae are less robust than Hesperornithidae (Martin and Tate, 1976), and *Pasquiaornis* is much less robust compared to species in Hesperornithidae. In Baptornithidae the metatarsal IV trochlea is about equal in size with the metatarsal III trochlea (Martin and Tate, 1976), as in *Pasquiaornis*, while in Hesperornithidae the metatarsal IV trochlea is greatly enlarged.

Pasquiaornis appears to be more closely related to the family Enaliornithidae than to Hesperornithidae. *Enaliornis*, the only genus in Enaliornithidae, is, like *Pasquiaornis*, much less robust than other Hesperornithiformes (Galton and Martin, 2002). *Enaliornis* and *Pasquiaornis* are also the oldest known Hesperornithiformes, with *Enaliornis* known from the early Cenomanian (Galton and Martin, 2002) and *Pasquiaornis* from the mid to late Cenomanian (Tokaryk et al., 1997). The distinguishing character of Enaliornithidae that is missing from *Pasquiaornis* is an antitrochanter on the ilium that is not strongly

produced laterally and the absence of a distinct neck on the proximal femur (Galton and Martin, 2002). *Enaliornis*, like *Pasquiaornis*, is known only from disarticulated specimens. However, with the material reported here, the skeletal record of *Pasquiaornis* is much more complete than that of *Enaliornis*. On the basis of available fossil evidence, *Pasquiaornis* seems reasonably placed within the Baptornithidae.

Importance of the Bainbridge River Assemblage and the Early Evolution of Hesperornithiformes

Pasquiaornis is the oldest known genus of Hesperornithiformes known in North America, and offer important insights into the early evolution of the order. *Pasquiaornis* shows many primitive characters for Hesperornithiformes. First, *Pasquiaornis* is much less robust compared to other Hesperornithiformes, with the exception of *Enaliornis*. The later species of Hesperornithiformes have an extremely reduced humerus. In *Pasquiaornis*, the humerus is much less reduced, showing characters related to flight such as well developed distal condyles and proximal pectorodeltoid and bicipital crests, which are not seen in other Hesperornithiformes. The wing is still slightly reduced and robust, meaning it may still have been flightless or had minimal ability to fly. The ulna, only known before from *Baptornis*, is present in *Pasquiaornis* and is much less reduced, as is the radius. The carpometacarpus is also present in *Pasquiaornis*, which is not known from any other hesperornithiform species. The bones of the pectoral girdle are also much less reduced in *Pasquiaornis* compared to later Hesperornithiformes.

A character that makes *Pasquiaornis* less specialized for diving than other hesperornithiforms is the position of their legs. The legs of later hesperornithiforms are

positioned directly lateral to their body, so that they could not be put underneath.

Pasquiaornis may have been able to place its legs much further underneath the body than other Hesperornithiformes. The antitrochanter on the pelvis is developed much more laterally than in other Hesperornithiformes, not allowing the femur to rest completely perpendicular to the pelvis. The femur and tibiotarsus of later Hesperornithiformes was articulated such that the tibiotarsus was directed dorsally. The proximal end of the tibiotarsus of *Pasquiaornis* is flat compared to the greatly slanted *Hesperornis* tibiotarsus, meaning that the tibiotarsus would not have been directed dorsally as in *Hesperornis*.

Another primitive character known for *Pasquiaornis* is the much less specialized toes. Later species of hesperornithiform, like *Hesperornis* species, have a well developed capacity for toe rotation. The toes of *Pasquiaornis* lack the overlapping condyles that allow toe rotation in *Hesperornis* and *Parahesperornis*. Earlier groups of Hesperornithiformes like *Pasquiaornis*, *Baptornis* and *Enaliornis* lack the specialized phalanges for toe rotation.

A characteristic common to all Hesperornithiformes is fully heterocoelous vertebra. *Pasquiaornis* dorsal vertebrae are not fully heterocoelous. This may mean that *Pasquiaornis* lacked the extensive lateral and vertical flexion motion that later Hesperornithiformes had. All these primitive characters point to *Pasquiaornis* being much less specialized for diving than later Hesperornithiformes.

Even though *Pasquiaornis* shows a less reduced humerus than later Hesperornithiformes, the presence of an extremely reduced humerus from an undescribed hesperornithiform at the Bainbridge River locality suggests that Hesperornithiformes by the mid-late Cenomanian had already evolved to be so specialized at diving that they had

lost the ability to fly. *Pasquiaornis* shows us though that other groups of Hesperornithiformes had not yet become so specialized.

Functional morphology

Flight

Was *Pasquiaornis* able to fly? The lack of a sternum from the Bainbridge River assemblage makes it very difficult to tell. Usually a large keeled sternum would suggest ability for flight, since there would be a large attachment area for flight muscles. Conversely, the lack of a keeled sternum would suggest a reduced or inability to fly. The question is easier with other known Hesperornithiformes because the presence of a non-keeled sternum and extremely reduced humeri indicate that flight would be impossible. Later hesperornithiform species evolved such a reduced humerus that the lower wing bones, like ulna, radius and carpometacarpus are lost. However, with *Pasquiaornis*, the humerus is far less reduced, and the ulna, radius and carpometacarpus are all present.

In a study of bone microstructure in a femur, Chinsamy et al. (1998) suggested because of the thickness of the compact bone in a Cretaceous loon, which was about 37% of the diameter of the bone, that the bird may have been flightless or had minimal flight capabilities. Due to the thickness of its compact bone this logic would also suggest that *Pasquiaornis* was flightless or had minimal flight. The compact bone thickness of *Pasquiaornis* femora ranged from approximately 40 to 50% of the diameter of the bone. Habib and Ruff (2008) looked at cortical thickness and concluded that percentages of cortical area (cortical area/total periosteal area) over 50% of the bone categorizes the bird as aquatic. In *Pasquiaornis*, the compact bone area is about 75 to 64% of the femur, which would put it easily in the range of aquatic birds. The humerus of *Pasquiaornis* is

also very robust and has thick compact bone when compared to species of birds that are efficient flyers. Overall the humerus, ulna, radius and carpometacarpus of *Pasquiaornis* are still robust and slightly reduced. *Pasquiaornis* may have been able to fly, but probably not very well, or for very long distances.

The wing in *Pasquiaornis* could have played a role for movement under water. The wings of other Hesperornithiformes like *Hesperornis* are so small that they probably did very little in movement under water except perhaps to act as a stabilizer or as a rudder to help steer the animal (Martin and Tate, 1976). However, the larger wing of *Pasquiaornis* may have had a lot more involvement. Some birds, like eiders and scoters move under water by using both their wings and feet in alternating strokes (Heath et al., 2006). *Pasquiaornis* was not a true wing propelled diver, as it has many characteristics of a foot propelled diver, but probably used its wing in some assistive way, even if just for steering purposes, as in some ducks that use their wings to increase manoeuvrability, but still use only their feet for propulsion (Townsend, 1909). Further study needs to be done in this area.

Movement

As mentioned earlier, Hesperornithiformes are foot propelled diving birds. The genus *Pasquiaornis* too possesses several characters that would suggest a foot propelled diver. The presence of a narrowly compressed pelvis; short and robust femur; a large cnemial crest on the tibiotarsus for increased attachment for leg muscles; and a transversely compressed tarsometatarsus. In modern diving birds and most likely in fossil birds the origin of the gastrocnemius muscle, the principal muscle involved in the power stroke, is switched from the femur to the cnemial crest (Fjeldsa, 2004).

Most Hesperornithiformes have very reduced wing bones suggesting they were unable to fly. The humerus of the unknown hesperornithiform species from the Bainbridge River locality is extremely reduced as well suggesting this bird could not fly. The wing bones of *Pasquiaornis* are not as reduced and may have had some ability for flight. In all other Hesperornithiformes as well as *Pasquiaornis*, the leg bones are robust and lower leg bones elongated, suggesting specialization for propelling themselves through the water. Hesperornithiformes were so specialized for hind limb propulsion through the water that it was probably very difficult for them to move on land (Bühler et al., 1988; Martin and Tate, 1976). *Pasquiaornis* would have most likely also had some difficulty moving on land, but less so than *Hesperornis*, which could not tuck its legs under the body (center of gravity) and must have waddled awkwardly at best.

Martin and Tate (1976) suggest that the proportions of the femur of *Baptornis* show that the legs were not bound to the pelvis as closely as they were in *Hesperornis* and as a result would have slightly greater freedom of movement. *Baptornis* may have been able to rotate the legs ventrally for paddling and then abduct them for diving as do some diving ducks (Martin and Tate, 1976; Raikow, 1970). The greater mobility in movement of the legs may also suggest that *Pasquiaornis* was able to rotate the legs ventrally for paddling and then abduct them for diving as do some diving ducks (Raikow, 1970).

The tibiotarsus of *Baptornis* and *Hesperornis* was bound to the pelvis, meaning that when they moved their legs, it was only the tarsometatarsi moving as the femur and tibiotarsus were held in place by muscle attachments. The tibiotarsus was probably more closely compressed to the acetabular region in *Hesperornis* as compared to *Baptornis* (Martin and Tate, 1976). In *Baptornis* the tibiotarsus extended beyond the posterior

margin of the pelvis, while in *Hesperornis* it was about even (Martin and Tate, 1976). This would also suggest that *Baptornis* had some capacity to rotate the feet under the body, possibly for swimming on the surface (Martin and Tate, 1976). In *Pasquiaornis*, the complete tibiotarsus and pelvis are not known so it is not positive if this would be the case, however, since *Pasquiaornis* is more similar and closely related to *Baptornis* than *Hesperornis*, some capacity to rotate the feet under the body for swimming may have been possible.

In *Hesperornis*, the femur may have been so bound to the pelvis that it was permanently held in an extended position, lateral to the body (Martin and Tate, 1976). This would suggest that *Hesperornis* could not walk on land but only push itself along (Martin and Tate, 1976). Galton and Martin (2002) suggest that *Enaliornis* may have been capable of some type of waddling walk. They make this suggestion based on the fact that the head of the femur is well rounded and slightly inclined proximally and the attachment for the round ligament (*fovea ligamentous capitis*) is situated more medially than in other hesperornithiforms, as well as the antitrochanter being proportionally smaller than in *Baptornis* (Galton and Martin, 2002). In *Pasquiaornis*, a well rounded head on the femur is also present and slightly inclined proximally, with the attachment for the round ligament situated more medially, which may also suggest that *Pasquiaornis* was capable of some sort of waddling walk. The antitrochanter of *Pasquiaornis* was also produced further laterally, meaning the femur could not sit in the laterally extended position like that of later Hesperornithiformes, and that the femur could be brought further underneath the body. The medial condyle of the femur of *Pasquiaornis*, like that of *Enaliornis*, is small compared to the lateral condyle, which means that the leg would

have been held more vertically than in other Hesperornithiformes (Galton and Martin, 2002). This would also suggest a better ability for some type of walking on land.

Toe-Rotation

For diving birds and other birds that spend significant time in water, it is important to develop an expanded surface area of the feet for efficient propulsion through water. This is the advantage of webbed feet, in which skin has grown between the toes, connecting them together. This condition is found in many groups including ducks (family Anatidae) and loons (genus *Gavia*) (Johansson and Norberg, 2001).

An alternative to webbed feet is lobate feet that are characterized by toes that are flattened and edged with flexible ridges that collapse on the forward stroke of the foot through water (Johansson and Norberg, 2001). Lobate feet are found in grebes (order Podicipedidae) and coots (family Rallidae). Lobate feet increase thrust during the power stroke and reduce drag during the recovery stroke (Johansson and Norberg, 2001). The toes may also act like multiple slots during swimming to increase their efficiency during the power stroke by increasing hydrodynamic/energetic efficiency, maximum lift and lift-to drag ratio and decreasing drag production (Johansson and Norberg, 2001).

When swimming with lobate or webbed feet, the bird's toes are spread for the power stroke. During the recovery stroke, birds like loons with webbed feet, fold their toes posteriorly, while birds with lobate feet, like grebes, rotate their toes 90 degrees so that the edges of the lobed toes cut through the water more easily (Storer, 1958). Both of these actions are reflected in the morphology of phalanges on digit 4. In loons, and most birds, the distal articulations of the phalanges are parallel and about the same size. This restricts the movement of the toes in an up and down direction. In grebes, the medial

ridge in the distal articular surface of the phalanx is enlarged compared to the lateral ridge.

In Hesperornithiformes, the later forms like *Hesperornis* show even more specialized phalanges of the 4th digit (Figure 21) (Martin and Tate, 1976) than even grebes. The medial articulation on the distal end is greatly enlarged and extends over the smaller rounded lateral articulation (Martin and Tate, 1976). This suggests a highly specialized form of toe rotation and the presence of lobed feet (Martin and Tate, 1976). However, *Baptornis* is not as specialized as *Hesperornis* or grebes (Figure 21). The medial ridge is still a bit larger, but not as enlarged as compared to *Hesperornis* or to grebes and it does not extend over the lateral articulation (Martin and Tate, 1976). The articular surfaces are also inclined, suggesting *Baptornis* had some ability for toe rotation (Martin and Tate, 1976).

In *Pasquiaornis* the 4th digit shows even less specialization (Figure 21), so that toe rotation was probably not possible. The lateral and medial articulations are about the same size and parallel to each other, much as in the common loon. This may mean that earlier forms like *Baptornis* and *Pasquiaornis* probably had webbed feet, with their toes being more similar to those of loons. This might suggest that the evolution of toe rotation and lobate feet in Hesperornithiformes did not evolve until later forms like *Hesperornis*.

Functional morphology in the limbs of Pasquiaornis

A Regularized Discriminant Analysis (RDA) was applied to the limb bones of *Pasquiaornis*, as per methods used in Hinić-Frlog and Motani (*in press*), in an attempt to learn more about the functional anatomy of these late-Cretaceous birds by comparing them to extant birds. The results from the RDA have added possible clues to how

Figure 21. Distal end of phalanx 1 of digit 4 showing increasing modification for toe rotation from left to right: A, loon, *Gavia immer*; B, *Pasquiaornis tankei*; C, *Baptornis advenus*; D, grebe, *Aechmophorus occidentalis*; E, *Hesperornis regalis*. (Not to scale.). Modified from Martin and Tate, 1976.

Pasquiaornis swam. When using measurements from the wing elements, pectoral elements and leg elements of *P. tankei* (*P. hardiei* was left out because of lack of complete elements) the RDA predicted with a 98.5% confidence interval that *P. tankei* was a foot-propelled diver. This agrees with the observations of the osteology of the bird. The morphospace of *P. tankei* (Figure 22) indicates overlap with extant surface swimmers, wing propelled divers and foot propelled divers.

When the RDA is restricted to leg elements for both *P. tankei* and *P. hardiei*, *P. tankei* is predicted to be a surface swimmer with 98.1% confidence and *P. hardiei* is predicted to be a plunger with 100% confidence. When these same elements were applied to RDA's with extant species, 18 out of 245 species were placed in the wrong locomotor categories, which mean this selective RDA is less reliable than the previous more inclusive (wing and hind limb) analysis in which a wrong locomotor category was assigned in only 6 out of 245 extant species. When comparing the above posterior probabilities with the morphospace of the fossil birds (Figure 23), *P. tankei* is grouped in the middle of the extant surface swimmers, just outside the edges of wing propelled divers and foot propelled divers. *P. hardiei* is placed near the edge of the surface swimmers and plunger morphospace, which overlaps with non-swimmers. The discrepancy between the posterior probabilities and morphospace may be explained by the fact that the number of extant species of surface swimmers and non-swimmers were much higher than those of foot-propelled and wing-propelled divers. This may create a bias as to how unknown specimens are categorized.

What might this analysis tell us about *Pasquiaornis*? *Pasquiaornis* appears to be basal among Hesperornithiformes, and by looking at the osteology it has already been shown to be much less specialized as a diver. So it is not a surprise that it may plot closer

Figure 22. RDA diagram showing how *P. tankei* plots against other birds categorized by swimming style. *P. tankei* seems to fall in between all the groups. Comparative data from Hinić-Frlog and Motani (*in press*). ♦, foot-propelled swimmers; ■, foot and wing propelled divers; ▲, non swimmers; X, plungers; +, surface swimmers; ●, wing-propelled divers; ◆, *P. tankei*.

Figure 23. RDA diagram showing how *P. tankei* and *P. hardiei* plot against other birds categorized by swimming style. *P. tankei* falls in closest among the surface swimmers, while *P. hardiei* is on the edge of plungers. Comparative data from Hinić-Frlog and Motani (*in press*). ♦, foot-propelled swimmers; ■, foot and wing propelled divers; ▲, non-swimmers; X, plungers; +, surface swimmers; ●, wing-propelled divers; ◆, *P. tankei*; ◆, *P. hardiei*.

to surface swimmers, or in the first chart (Figure 22) somewhere in between surface swimmers, foot-propelled divers and wing propelled divers. It is interesting to see that *P. tankei* and *P. hardiei* plotted differently, although their bones look very similar. Their different positions may be explained by the greater size of *P. tankei* and increased robustness.

It must be realized that the *Pasquiaornis* individuals inserted into the RDA are composites, while the measurements of the comparative extant material from Hinić-Frlog and Motani (*in press*), were taken from single individuals from each species. As well, many measurements were not able to be put into the analysis because they were not available from the sometimes incomplete *Pasquiaornis* material. Both of these points will most likely affect the accuracy of the RDA. The measurements of all bones of comparative species were done by Hinić-Frlog and Motani (*in press*) and so may have differed slightly in how this author took the measurements of the *Pasquiaornis* material. It must also be considered that the categories are based on extant species. Extinct species of birds, like *Pasquiaornis*, may have had different swimming modes that are not directly comparable to those of extant species. Additional comparative research in the skeletal morphology of extant surface swimmers may shed more light on the mechanics of locomotion in *Pasquiaornis*.

Paleoecology

The eastern shore of the Western Interior Seaway was full of life during the Cenomanian. The avian diversity is greater than was previously known. This study documents evidence for at least four species of Hesperornithiformes living along the shores as well as species of *Ichthyornis* and Enantiornithes (Figure 24). The avian fauna

Figure 24. Bones of other known Aves orders from the Bainbridge locality. 1, possible *Enantiornithes* right scapula (RSM P2989.26); 1a, medial view; 1b, proximal view; 1c, lateral view; 2, right humerus of *Ichthyornis* (RSM P2988.8); 2a, posterior view; 2b, anterior view. Scale bar equals 1 cm.

known from Saskatchewan shows a great size disparity. Some of the birds were as small as hummingbirds (from unknown Aves not described in this study) and others as large as a loon. The species of *Ichthyornis* and Enantiornithes would have been able to fly, venturing from the shore to the sea looking for food while the Hesperornithiformes, flightless diving birds, were probably spending almost all their time in shallow coastal waters or out at sea. There are several other Aves bones (Figure 25) found in the Bainbridge River locality that do not seem to be hesperornithiform, enantiornithine or ichthyornithiform, suggesting that avian diversity in this area was even greater than documented in this study.

Martin and Lim (2002) proposed a correlation between size of the hesperornithiform and marine environments. Larger individuals are found in paleoenvironments more distant from shore, while the smaller individuals are found in nearshore environments. The Bainbridge River Hesperornithiformes are small relative to other known Hesperornithiformes, which in turn may suggest that the Bainbridge River deposits reflect a nearshore environment. As mentioned earlier, other paleoenvironmental parameters observed in the Bainbridge River deposits also are consistent with a nearshore paleoenvironment, which in turn supports the Martin and Lim (2002) hypothesis that smaller hesperornithiform species are found nearshore.

It is also interesting to note the quantity of bird bones found in the Bainbridge River locality. This study has identified over 300 elements, theoretically all from different individuals in addition to many more in blocks that have not been prepared yet, and many broken and unidentifiable elements that are clearly bird but not included in the count. One has to ask what caused such a high accumulation of bird bones knowing that bird bonebeds are extremely rare (Cumbaa et al., 2006). The high accumulation of vertebrate

Figure 25. Dentaries of unknown Aves from the Bainbridge River. 1, right dentary showing sockets and a single tooth (RSM P2526.1); 1a, medial view; 1b, lateral view; 1c, close up of the lingual side of the tooth; 2, dentary showing tooth sockets (RSM P2831.19); 2a, medial view; 2b, lateral view. Scale bar equals 1 mm.

debris was interpreted by Schröder-Adams et al. (2001) as being the result of reworking during a transgression of the WIS on the clastic sediment-starved eastern margin. In diving birds, the bones are denser, and therefore more likely to preserve. They are also found in a marine environment making them more likely to preserve. But this is the same with other hesperornithiform sites, yet we do not get such a high accumulation at any other site. The more famous Kansas hesperornithiforms are often found intact, probably from complete carcasses that drifted down from deep waters offshore to settle in quite, soft, sometimes anoxic mud, making them likely to preserve. The Kansas specimens are almost always single occurrences, but are better preserved showcasing a fossilization process clearly different from that of the Bainbridge River locality. A possible scenario that would explain the accumulation in the Bainbridge River locality is a mass death assemblage. From the Pliocene of Florida, a mass cormorant death assemblage has been explained as the result of a toxic dinoflagellate bloom or “red tide” (Emslie et al., 1996). Further study would be needed to check such a scenario in the Bainbridge River deposits. This area may also have been an area of major hesperornithiform activity such as a rookery, and therefore would make a high accumulation of bones more likely. However, no evidence of breeding birds or of immature or juvenile birds (with the exception of one possible bone) was found. There are, of course, other explanations for mass die-offs, including volcanic activity. The Bainbridge River bonebed has numerous bentonite inclusions, indicating that a blanket of potentially deadly volcanic ash had settled on the seabed, and become incorporated into the bioclastic layer as mud balls during the transgressive cycle. Further work needs to be done in this area.

CONCLUSION

Two mid-Cenomanian (95 Ma) marine bonebed localities in the Pasquia Hills of east-central Saskatchewan have produced between them more than 300 identified fossil bird bones representing the earliest diverse avifauna known from North America. The bones from just the Bainbridge River locality examined here represent roughly 50 times the number of Cenomanian age bird bones known from the rest of North America combined. This study focused on loon-sized toothed birds of the order Hesperornithiformes. These birds shared their environment with a host of invertebrates including giant inoceramid mollusks and ammonites, as well as vertebrates such as sharks, rays, bony fishes, turtles, long and short-necked plesiosaurs, and other birds including the tern-like *Ichthyornis* and one or more primitive enantiornithine birds.

Comparisons with previously described species indicate that three of the four hesperornithiform species identified belong to the genus *Pasquiaornis* (Figure 26). *Pasquiaornis* is known from strata of similar age from RSM locality DH1 on the Carrot River, which is approximately 100 km southwest of the Bainbridge River. Two species of *Pasquiaornis*, *P. hardiei* and *P. tankei*, were briefly described by Tokaryk et al. (1997) on the basis of the quadrate, distal humerus, femur, and tarsometatarsus. These two species of *Pasquiaornis* are also found in the Bainbridge River locality and have been further described using cranial and jaw elements, scapula, coracoid, the complete humerus, ulna, radius, carpometacarpus, pelvis, femur, tibiotarsus, tarsometatarsus, and phalanges. A possible new species of *Pasquiaornis* is also described from a tarsometatarsus and an unknown species of hesperornithiform from a humerus.

Pasquiaornis is the oldest known hesperornithiform in North America and shows many clues to the early evolution of the order. This genus shows many primitive

A

B

Figure 26. Comparison of *Baptornis* (A) with the reconstruction of *Pasquiaornis tankei* (B). The less reduced wing of *Pasquiaornis* is highlighted in red; note *Baptornis* wing for comparison. Modified from image of *Baptornis* by Martin and Tate (1976). Scale bar equals 5 cm in A and 10 cm in B.

characters that are not yet as specialized for foot-propelled diving as in later Hesperornithiformes. *Pasquiaornis* is much less robust than later hesperornithiform species and has a much less reduced humerus, ulna and pectoral elements. *Pasquiaornis* is the only known hesperornithiform with a carpometacarpus. Later hesperornithiform species are highly specialized for foot-propelled diving and have lost the ability to fly as the wing has been so reduced as to be truly vestigial. *Pasquiaornis* however may have had some ability to fly as seen from the less reduced pectoral and wing elements.

Another characteristic that makes *Pasquiaornis* less specialized for diving is the position of the legs. In later, more derived hesperornithiform taxa, the legs are positioned laterally to the body so that the birds were not able to put their legs underneath the body. *Pasquiaornis* may have been able to place its legs much further underneath the body than other Hesperornithiformes. The antitrochanter on the pelvis is developed much more laterally than in other Hesperornithiformes, not allowing the femur to rest completely perpendicular to the pelvis. This may mean that *Pasquiaornis* was capable of some sort of waddle on land while later Hesperornithiformes were most likely not able to walk on land. Egg-laying would have required all hesperornithiforms to have at least limited mobility on land. Additionally, the distal end of phalanx 1 of digit 4 of *Pasquiaornis* lacks the overlapping condyles that allow toe rotation in *Hesperornis* and *Paraesperornis*. All these primitive characters point to *Pasquiaornis* being much less specialized for diving than later Hesperornithiformes.

The presence of an extremely reduced humerus from an unidentified hesperornithiform at the Bainbridge River site shows that at least one taxon in the order had already evolved to be so specialized at diving that it had lost the ability to fly by the mid to late Cenomanian. *Pasquiaornis*, with its more developed humerus, shows us that

other groups of Hesperornithiformes had not yet become so specialized at the time. The fossils found at the Bainbridge River locality also show that Hesperornithiformes seemed to be thriving in the area with a possible four or more different species. The cooler northern waters of the Western Interior Seaway may have been an important locus for the evolution and diversification of the order.

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PLATES

PLATE I

Figure 1: *Pasquiaornis tankei* right maxilla (RSM P2995.5); 1a, lateral view; 1b, medial view; 1c, dorsal view.

Scale bar is equal to 0.5 cm.

1a

1b

1c

PLATE II

Figure 1: *Pasquiaornis tankei* right frontal (RSM P2995.4); 1a, ventral view; 1b, dorsal view.

Figure 2: *Pasquiaornis hardiei* left frontal (RSM P2957.12); 2a, dorsal view; 2b, ventral view.

Figure 3: unidentified Aves right frontal (RSM P2997.36); 3a, dorsal view; 3b, ventral view.

Scale bars equal 1 cm

1a

1b

2a

2b

3a

3b

PLATE III

Figure 1: *Pasquiaornis tankei* right quadrate (RSM P2988.25); 1a, caudal view; 1b, cranial view; 1c, medial view.

Figure 2: *Pasquiaornis tankei* left quadrate (RSM P2831.52); 2a, caudal view; 2b, cranial view; 2c, ventral view.

Scale bar equals 1 cm.

1a

1b

1c

2a

2b

2c

PLATE IV

Figure 1: rostral end of *Pasquiaornis tankei* left dentary (RSM P2985.10); 1a, lateral view; 1b, medial view.

Figure 2: rostral end of *Pasquiaornis tankei* right dentary (RSM P2988.11); 2a, lateral view; 2b, medial view.

Figure 3: rostral end of *Pasquiaornis hardiei* left dentary (RSM P2831.6); 3a, lateral view; 3b, medial view.

Scale bar equals 1 cm.

1a

1b

2a

2b

3a

3b

PLATE V

Figure 1: *Pasquiaornis* possible tooth (Type A) (RSM P2831.22); 1a, labial view; 1b, lingual view.

Figure 2: *Pasquiaornis* possible tooth (Type B) (RSM P2831.23); 2a, labial view; 2b, lingual view.

Figure 3: *Pasquiaornis* possible tooth (Type A) (RSM P2831.31); 3a, labial view; 3b, lingual view.

Figure 4: *Pasquiaornis* possible tooth (Type A) (RSM P2831.32); 4a, labial view; 4b, lingual view.

Figure 5: *Pasquiaornis* possible tooth (Type A) (RSM P2831.33); 5a, labial view; 5b, lingual view.

Figure 6: *Pasquiaornis* possible tooth (Type A) (RSM P2831.34); 6a, labial view; 6b, lingual view; 6c, close up of the crown in labial view.

Scale equals 1 mm.

PLATE VI

Figure 1: *Pasquiaornis* possible tooth (Type A) (RSM P2831.24); 1a, labial view; 1b, lingual view.

Figure 2: *Pasquiaornis* possible tooth (Type A) (RSM P2831.25); 2a, labial view; 2b, lingual view.

Figure 3: *Pasquiaornis* possible tooth (Type A) (RSM P2831.27); 3a, labial view; 3b, lingual view.

Figure 4: *Pasquiaornis* possible tooth (Type A) (RSM P2831.30); 4a, labial view; 4b, lingual view.

Figure 5: *Pasquiaornis* possible tooth (Type A) (RSM P2831.26); 5a, labial view; 5b, lingual view.

Figure 6: *Pasquiaornis* possible tooth (Type A) (RSM P2831.28) in lingual view.

Scale equals 1 mm.

PLATE VII

Figure 1: *Pasquiaornis* possible tooth (Type A) (RSM P2831.35) in lingual view.

Figure 2: *Pasquiaornis* possible tooth (Type A) (RSM P2831.36) in lingual view.

Figure 3: *Pasquiaornis* possible tooth (Type A) (RSM P2831.37) in lingual view.

Figure 4: *Pasquiaornis* possible tooth (Type A) (RSM P2831.38) in lingual view.

Figure 5: *Pasquiaornis* possible tooth (Type A) (RSM P2831.39) in lingual view.

Figure 6: *Pasquiaornis* possible tooth (Type A) (RSM P2831.40) in lingual view.

Figure 7: *Pasquiaornis* possible tooth (Type A) (RSM P2831.41) in lingual view.

Figure 8: *Pasquiaornis* possible tooth (Type A) (RSM P2831.42) in lingual view.

Figure 9: *Pasquiaornis* possible tooth (Type A) (RSM P2831.43) in lingual view.

Figure 10: *Pasquiaornis* possible tooth (Type A) (RSM P2831.44) in lingual view.

Figure 11: *Pasquiaornis* possible tooth (Type A) (RSM P2831.46) lingual view.

Figure 12: *Pasquiaornis* possible tooth (Type A) (RSM P2831.47) in lingual view.

Scale equals 1 mm.

PLATE VIII

Figure 1: *Pasquiaornis hardiei* right angular (RSM P2831.18); 1a, medial view; 1b, lateral view.

Figure 2: *Pasquiaornis tankei* left angular (RSM P2986.2); 2a, lateral view; 2b, medial view.

Figure 3: *Pasquiaornis hardiei* right splenial (RSM P2985.9); 3a, lateral view; 3b, medial view.

Scale bar equals 1 cm.

1a

1b

2a

2b

3a

3b

PLATE IX

Figure 1: *Pasquiaornis tankei* left articular, prearticular and surangular (RSM P2989.21); 1a, lateral view; 1b, medial view.

Figure 2: *Pasquiaornis hardiei* left articular, prearticular and surangular (RSM P2989.19); 2a, lateral view; 2b, medial view.

Scale equals 1 cm.

1a

1b

2a

2b

PLATE X

Figure 1: *Pasquiaornis tankei* 4th to 6th cervical vertebra (RSM P2626.15); 1a, ventral view; 1b, dorsal view; 1c, lateral view; 1d, cranial view.

Figure 2: *Pasquiaornis tankei* 4th to 6th cervical vertebra (RSM P2626.16) in caudal view.

Scale equals 1 cm.

PLATE XI

Figure 1: *Pasquiaornis hardiei* cervical vertebra (RSM P2831.8); 1a, caudal view; 1b, cranial view; 1c, dorsal view; 1d, ventral view; 1e, lateral view.

Scale equals 1 cm.

1a

1b

1c

1d

1e

PLATE XII

Figure 1: *Pasquiaornis tankei* 14th or 15th cervical vertebra (RSM P2988.13); 1a, dorsal view; 1b, lateral view.

Figure 2: *Pasquiaornis tankei* 14th or 15th cervical vertebra (RSM P2987.14); 2a, dorsal view; 2b, cranial view; 2c, ventral view.

Figure 3: *Pasquiaornis tankei* last cervical or 1st dorsal vertebra (RSM P2988.12); 3a, dorsal view; 3b, lateral view; 3c, cranial view; 3d, caudal view.

Scale equals 1 cm.

PLATE XIII

Figure 1: *Pasquiaornis tankei* dorsal vertebra (RSM P2957.15); 1a, lateral view; 1b, cranial view; 1c, dorsal view; 1d, ventral view.

Figure 2: *Pasquiaornis hardiei* dorsal vertebra (RSM P2957.15); 2a, lateral view; 2b, dorsal view; 2c, ventral view; 2d, cranial view; 2e, caudal view.

Scale equals 1 cm.

1a

1b

1c

1d

2a

2b

2c

2d

2e

PLATE XIV

Figure 1: *Pasquiaornis tankei* synsacrum (RSM P2997.56); 1a, dorsal view; 1b, lateral view; 1c, ventral view.

Figure 2: Unidentified hesperornithiform synsacrum (RSM P2987.19); 2a, dorsal view; 2b, lateral view; 2c, ventral view.

Scale equals 1 cm.

PLATE XV

Figure 1: *Pasquiaornis hardiei* synsacrum (RSM P2985.25). 1a, cranial view; 1b, dorsal view; 1c, right lateral view; 1d, left lateral view; 1e, ventral view.

Scale equals 1 cm.

1a

1b

1c

1d

1e

PLATE XVI

Figure 1: *Pasquiaornis tankei* left coracoid (RSM P2988.9); 1a, dorsal view; 1b, ventral view; 1c, medial view.

Figure 2: *Pasquiaornis hardiei* left coracoid (RSM P2831.54); 2a, dorsal view; 2b, ventral view.

Figure 3: *Parahesperornis* right coracoid (KUVP24090) in dorsal view.

Scale equals 1 cm.

PLATE XVII

Figure 1: *Pasquiaornis tankei* right scapula (RSM P2997.58); 1a, dorsal view; 1b, ventral view.

Figure 2: *Pasquiaornis tankei* proximal right scapula (RSM P2997.59) showing coracoidal articulation; 2a, dorsal view; 2b, ventral view.

Figure 3: *Pasquiaornis hardiei* left scapula (RSM P2985.8); 3a, dorsal view; 3b, ventral view.

Scale equals 1 cm.

1a

1b

2a

3a

2b

3b

PLATE XVIII

Figure 1: *Pasquiaornis tankei* left humerus (RSM P2995.1); 1a, medial view; 1b, lateral view; 1c, close up of the distal condyles.

Figure 2: *Pasquiaornis tankei* left humerus (RSM P2989.11) showing a close up of the proximal end.

Figure 3: *Pasquiaornis hardiei* distal right humerus (RSM P2989.15); 3a, anterior view; 3b, posterior view.

Scale equals 1 cm.

PLATE XIX

Figure 1: *Pasquiaornis tankei* proximal right ulna (RSM P2989.17); 1a, anterior view; 1b, dorsal view; 1c, posterior view; 1d, close up of proximal right ulna in anterior view.

Figure 2: *Pasquiaornis tankei* distal left ulna and shaft (RSM P2997.30); 2a, anterior view; 2b, posterior view.

Scale equals 1 cm.

1a

1b

1c

1d

2a

2b

PLATE XX

Figure 1: *Pasquiaornis* proximal right radius (RSM P2831.20); 1a, lateral view; 1b, ventral view; 1c, medial view; 1d, dorsal view.

Figure 2: *Pasquiaornis* proximal right radius (RSM P2989.30) in proximal view.

Figure 3: *Pasquiaornis* proximal left radius and shaft (RSM P2831.57); 3a, ventral view; 3b, dorsal view.

Scale equals 1 cm.

PLATE XXI

Figure 1: *Pasquiaornis tankei* proximal end of left carpometacarpus (RSM P2831.4); 1a, ventral view; 1b, medial view; 1c, dorsal view; 1d, proximal view carpal trochlea; 1e, cross sectional view of shafts of metacarpal two and three.

Figure 2: *Pasquiaornis tankei* distal end of left carpometacarpus (RSM P2989.34); 2a, anterior view; 2b, ventral view; 2c, dorsal view; 2d, distal view.

Scale equals 1 cm.

PLATE XXII

Figure 1: *Pasquiaornis tankei* right pelvis (RSM P2626.27); 1a, lateral view; 1b, medial view; 1c, cranial view.

Figure 2: *Pasquiaornis hardiei* right pelvis (RSM P2997.62) in lateral view.

Scale equals 1 cm.

PLATE XXIII

Figure 1: *Pasquiaornis tankei* right femur (RSM P2997.2); 1a, anterior view; 1b, posterior view; 1c, medial view; 1d, left femur lateral view (RSM P2997.3).

Figure 2: *Pasquiaornis hardiei* right femur (RSM P2997.4); 2a, anterior view; 2b, posterior view; 2c, medial view; 2d, lateral view.

Figure 3: Cross section of right *Pasquiaornis* femur (RSM P2997.2).

Scale equals 1 cm.

PLATE XXIV

Figure 1: *Pasquiaornis tankei* proximal right tibiotarsus (RSM P2997.44); 1a, anterior view; 1b, lateral view; 1c, posterior view; 1d, posterior view close up.

Figure 2: *Pasquiaornis tankei* proximal left tibiotarsus (RSM P2957.22) showing a more complete cnemial crest; 2a, anterior view; 2b, posterior view.

Figure 3: *Pasquiaornis tankei* distal left tibiotarsus (RSM P2957.21); 3a, anterior view; 3b, posterior view.

Figure 4: *Pasquiaornis hardiei* distal right tibiotarsus (RSM P2997.42); 4a, posterior view; 4b, anterior view.

Scale equals 1 cm.

PLATE XXV

Figure 1: *Pasquiaornis tankei* proximal right fibula (RSM P2997.80); 1a, medial view; 1b, lateral view; 1c, dorsal view.

Figure 2: *Pasquiaornis hardiei* proximal left fibula (RSM P2988.21); 2a, lateral view; 2b, dorsal view; 2c, medial view.

Scale equals 1 cm.

PLATE XXVI

Figure 1: *Pasquiaornis tankei* left tarsometatarsus (RSM P2957.27); 1a, anterior view; 1b, medial view; 1c, posterior view.

Figure 2: *Pasquiaornis tankei* right tarsometatarsus (RSM P2997.21) in proximal view.

Figure 3: *Pasquiaornis hardiei* left tarsometatarsus (RSM P2997.18); 3a, posterior view; 3b, lateral view; 3c, anterior medial view; 3d, anterior view.

Figure 4: proximal end of *Pasquiaornis hardiei* left tarsometatarsus (RSM P2997.81); 4a, posterior view; 4b, anterior view.

Scale equals 1 cm.

PLATE XXVII

Figure 1: *Pasquiaornis tankei* possible 1st digit of 3rd toe (RSM P3015.9); 1a, dorsal view; 1b, lateral view; 1c, ventral view; 1d, proximal view; 1e, distal view.

Figure 2: *Pasquiaornis tankei* possible 1st digit of 4th toe (RSM P2997.68); 2a, dorsal view; 2b, lateral view; 2c, ventral view; 2d, proximal view; 2e, distal view.

Scale equals 1 cm.

PLATE XXVIII

Figure 1. *P. tankei* distal phalanx (RSM P2989.27); 1a, dorsal view; 1b, distal view.

Figure 2. *P. tankei* distal phalanx (RSM P2989.41); 2a, dorsal view; 2b, ventral view.

Figure 3. Possible *Pasquiaornis* terminal phalanx (RSM P2831.14) in lateral view.

Scale bar equals 1 cm.

1a

1b

2a

2b

3

APPENDIX C—SPECTROSCOPY

APPENDICES

APPENDIX I – SPECIMEN INVENTORY

Specimen #	Element	Identification	Notes
RSM P2526.1	Jaw bone with tooth - right side	Aves	sockets
RSM P2526.2	Radius - proximal right	hesperornithiform	
RSM P2526.3	Radius - proximal right	hesperornithiform	
RSM P2526.4	Dentary	hesperornithiform	
RSM P2626.1	Coracoid - distal left	hesperornithiform	has shaft and a bit of proximal end, highly eroded
RSM P2626.11	Coracoid - distal right	hesperornithiform	just the tip of one side
RSM P2626.12	Frontal - right	hesperornithiform	
RSM P2626.15	Vertebrae - 6-9 cervical	hesperornithiform	6-9 cervical
RSM P2626.16	Vertebrae - 6-9 cervical	hesperornithiform	6-9 cervical
RSM P2626.17	Vertebrae	hesperornithiform	
RSM P2626.18	Synsacrum - ventral half of cranial end	hesperornithiform	
RSM P2626.19	Phalanx - left foot	hesperornithiform	Phalanx 2 on digit 3
RSM P2626.2	Tibiotarsus - distal left		
RSM P2626.27	Pelvis - right	hesperornithiform	
RSM P2626.28	Carpometacarpus - left	hesperornithiform	
RSM P2626.29	Pelvis - left	hesperornithiform	
RSM P2626.30	Coracoid - left	hesperornithiform	
RSM P2626.31	Phalanx	hesperornithiform	
RSM P2626.32	Tarsometatarsus - distal left	hesperornithiform	
RSM P2626.33	Tarsometatarsus - distal left	hesperornithiform	
RSM P2626.34	Femur distal left and shaft	hesperornithiform	
RSM P2626.35	Femur distal right and shaft	hesperornithiform	
RSM P2626.36	Femur proximal left	hesperornithiform	
RSM P2626.37	Femur distal left	hesperornithiform	
RSM P2626.38	Tarsometatarsus - distal right	hesperornithiform	
RSM P2626.39	vertebra - dorsal	hesperornithiform	
RSM P2626.40	tibiotarsus - distal left	hesperornithiform	
RSM P2626.41	fibula - proximal right	hesperornithiform	
RSM P2626.42	surangular/prearticular - right	hesperornithiform	
RSM P2626.43	humerus - right shaft	hesperornithiform	
RSM P2626.9	Humerus - right	ichthyornithiform	
RSM P2830.1	Tarsometatarsus - proximal left	hesperornithiform	small-good condition
RSM P2830.2	Tarsometatarsus - distal left	hesperornithiform	trochlea 3 and 4 ends eroded
RSM P2830.3	Scapula - proximal right	hesperornithiform	Glenoid facet flat
RSM P2830.4	Tibiotarsus - proximal right	hesperornithiform	Proximal end eroded
RSM P2831.1	Femur - proximal left	hesperornithiform	small-hollow shaft visible,
RSM P2831.10	Vertebrae	hesperornithiform	
RSM P2831.11	Vertebrae	hesperornithiform	
RSM P2831.12	Synsacrum	hesperornithiform	Block B
RSM P2831.13	Phalanx	Aves	very small
RSM P2831.14	Phalanx - terminal	hesperornithiform	
RSM P2831.15	Phalanx - left foot	hesperornithiform	Block A
RSM P2831.16	Phalanx - left foot	hesperornithiform	Block A
RSM P2831.17	Radius - proximal unidentified side	hesperornithiform	
RSM P2831.18	Angular - left	hesperornithiform	

Specimen #	Element	Identification	Notes
RSM P2831.19	Dentary	Aves	
RSM P2831.2	Humerus - proximal left	hesperornithiform	Block B, all edges eroded except caput humeri
RSM P2831.20	Radius - proximal unidentified side	hesperornithiform	
RSM P2831.21	Splénial - right	hesperornithiform	
RSM P2831.22	tooth	hesperornithiform?	
RSM P2831.23	tooth	hesperornithiform?	
RSM P2831.24	tooth	hesperornithiform?	
RSM P2831.25	tooth	hesperornithiform?	
RSM P2831.26	tooth	hesperornithiform?	
RSM P2831.27	tooth	hesperornithiform?	
RSM P2831.28	tooth	hesperornithiform?	
RSM P2831.29	tooth	hesperornithiform?	
RSM P2831.3	Humerus - proximal left	ichthyornithiform	
RSM P2831.30	tooth	hesperornithiform?	
RSM P2831.31	tooth	hesperornithiform?	
RSM P2831.32	tooth	hesperornithiform?	
RSM P2831.33	tooth	hesperornithiform?	
RSM P2831.34	tooth	hesperornithiform?	
RSM P2831.35	tooth	hesperornithiform?	
RSM P2831.36	tooth	hesperornithiform?	
RSM P2831.37	tooth	hesperornithiform?	
RSM P2831.38	tooth	hesperornithiform?	
RSM P2831.39	tooth	hesperornithiform?	
RSM P2831.4	Carpometacarpus - proximal left	hesperornithiform	Block B, yellowish substance on it
RSM P2831.40	tooth	hesperornithiform?	
RSM P2831.41	tooth	hesperornithiform?	
RSM P2831.42	tooth	hesperornithiform?	
RSM P2831.43	tooth	hesperornithiform?	
RSM P2831.44	tooth	hesperornithiform?	
RSM P2831.45	tooth	hesperornithiform?	
RSM P2831.46	tooth	hesperornithiform?	
RSM P2831.47	tooth	hesperornithiform?	
RSM P2831.48	tooth	hesperornithiform?	
RSM P2831.49	tooth	hesperornithiform?	
RSM P2831.5	Dentary - left	hesperornithiform	open groove
RSM P2831.50	tooth	hesperornithiform?	
RSM P2831.51	tooth	hesperornithiform?	
RSM P2831.52	Quadrate - left	hesperornithiform	
RSM P2831.53	Pelvis - right	hesperornithiform	
RSM P2831.54	Coracoid - left	hesperornithiform	Posterior and anterior ends not preserved
RSM P2831.55	Frontal - left	hesperornithiform	Cranial and caudal ends not preserved
RSM P2831.56	Scapula- proximal left	hesperornithiform	
RSM P2831.57	Radius - left	hesperornithiform	distal end not preserved. Proximal end slightly eroded
RSM P2831.6	Dentary - right	hesperornithiform	tip of dentary before predentary bone
RSM P2831.7	Vertebrae - dorsal	hesperornithiform	Block B
RSM P2831.8	Vertebrae - 12th to 13th cervical	hesperornithiform	Block B/12-13 cervical
RSM P2831.9	Vertebrae - 5th to 8th cervical	hesperornithiform	Block B

Specimen #	Element	Identification	Notes
RSM P2957.1	Coracoid - proximal right	hesperornithiform	white, edges all eroded
RSM P2957.11	Skull bone		Unknown
RSM P2957.12	Frontal - left	hesperornithiform	not a positive identification
RSM P2957.13	Tibiotarsus - distal left	hesperornithiform	broken up, condyles eroded
RSM P2957.14	Tibiotarsus - distal right	hesperornithiform	long shaft, condyles eroded
RSM P2957.15	Vertebrae - 3rd to 6th dorsal	hesperornithiform	3-6 dorsal
RSM P2957.16	Vertebrae - 4th to 6th cervical	hesperornithiform	4-6 cervical
RSM P2957.17	Vertebrae - 13th to 14th cervical	hesperornithiform	13-14 cervical
RSM P2957.18	Synsacrum	hesperornithiform	
RSM P2957.19	Scapula - proximal left	hesperornithiform	flat glenoid facet
RSM P2957.2	Coracoid - right unidentified side	hesperornithiform	From East end
RSM P2957.20	Radius - proximal unidentified side	hesperornithiform	not sure
RSM P2957.21	Tibiotarsus - distal left		From East end
RSM P2957.22	Tibiotarsus - proximal left		From East end
RSM P2957.23	Surangular/articular - left	hesperornithiform	From East end
RSM P2957.24	Humerus - distal right	hesperornithiform	From East end
RSM P2957.25	Humerus - distal left	hesperornithiform	From East end
RSM P2957.26	Humerus - distal right	hesperornithiform	From East end
RSM P2957.27	Tarsometatarsus - left	hesperornithiform	From East end
RSM P2957.28	Rib - shaft	hesperornithiform	
RSM P2957.29	Pelvis - right	hesperornithiform	From East end
RSM P2957.5	Femur - proximal left	hesperornithiform	large-no shaft, trochanter eroded
RSM P2957.6	Tarsometatarsus - distal right	hesperornithiform	has some shaft- missing tops of trochlea
RSM P2957.7	Humerus - proximal unidentified side	hesperornithiform	could not tell right or left, very eroded, still sediment
RSM P2957.9	Coracoid - proximal right	hesperornithiform	has triosseal canal - most of shaft
RSM P2985.1	Vertebrae - dorsal	hesperornithiform	
RSM P2985.10	Dentary - right	hesperornithiform	
RSM P2985.2	Vertebrae - dorsal	hesperornithiform	Block B, presacral/1-6 dorsal (presacral)
RSM P2985.3	Vertebrae - dorsal	hesperornithiform	Block B/1-6 dorsal (presacral)
RSM P2985.4	Vertebrae	hesperornithiform	
RSM P2985.5	Phalanx - left foot	hesperornithiform	1st phalanx of 2nd toe
RSM P2985.6	Tarsometatarsus - distal left	hesperornithiform	trochlea 4 eroded
RSM P2985.7	Coracoid - proximal right	hesperornithiform	
RSM P2985.8	Scapula - proximal left	hesperornithiform	
RSM P2985.9	Splénial - right	hesperornithiform	
RSM P2986.1	Humerus - right	hesperornithiform	reduced wing
RSM P2986.2	Angular - left	hesperornithiform	
RSM P2987.1	Tarsometatarsus - left	hesperornithiform	missing 2nd and 3rd trochlea
RSM P2987.10	Tibiotarsus - proximal right	hesperornithiform	large, no cnemial crest
RSM P2987.11	Tibiotarsus - distal left	hesperornithiform	broken up, medial condyle projects, has shaft
RSM P2987.13	Vertebrae - 9th to 10th cervical	hesperornithiform	9-10 cervical
RSM P2987.14	Vertebrae - 14th to 15th cervical	hesperornithiform	14-15 cervical
RSM P2987.15	Vertebrae - 6th to 9th cervical	hesperornithiform	6-9 cervical
RSM P2987.16	Vertebrae - 4th to 13th cervical	hesperornithiform	4-13 cervical

Specimen #	Element	Identification	Notes
RSM P2987.17	Vertebrae - 4th to 13th cervical	hesperornithiform	4-13 cervical
RSM P2987.18	Vertebrae	hesperornithiform	
RSM P2987.19	Synsacrum - cranial end	hesperornithiform	may be complete
RSM P2987.2	Humerus - distal right	hesperornithiform	condyles visible, has much of shaft
RSM P2987.20	Synsacrum - ventral half cranial end	hesperornithiform	
RSM P2987.21	Scapula - proximal right	hesperornithiform	flat glenoid facet
RSM P2987.23	Phalanx	Aves	really small
RSM P2987.24	Phalanx - left foot	hesperornithiform	
RSM P2987.25	Radius - proximal unidentified side	hesperornithiform	
RSM P2987.26	Radius - proximal left	hesperornithiform	
RSM P2987.3	Humerus - distal right	hesperornithiform	much of shaft, part of external condyle eroded
RSM P2987.4	Humerus - proximal left	hesperornithiform	missing all edges of end
RSM P2987.5	Coracoid - right	hesperornithiform	small proximal end, missing right side of distal end
RSM P2987.6	Coracoid - distal left	hesperornithiform	foremost at top of proximal end
RSM P2987.7	Coracoid - proximal left	hesperornithiform	very large, white and brown
RSM P2987.8	Carpometacarpus - proximal left	hesperornithiform	transverse crack in shaft
RSM P2987.9	Tibiotarsus - distal left	hesperornithiform	highly cracked, medial condyle projects
RSM P2988.1	Femur - proximal right	hesperornithiform	small-very cracked, most of shaft
RSM P2988.10	Surangular - left	hesperornithiform	
RSM P2988.11	Dentary - left	hesperornithiform	possible sockets, end before prementary bone
RSM P2988.12	Vertebrae - last cervical or 1st dorsal	hesperornithiform	last cervical to first dorsal
RSM P2988.13	Vertebrae - 14th to 15th cervical	hesperornithiform	14-15 cervical
RSM P2988.14	Vertebrae - 5th to 6th cervical	hesperornithiform	5 or 6 cervical
RSM P2988.15	Vertebrae	ichthyornithiform?	
RSM P2988.16	Synsacrum	hesperornithiform	
RSM P2988.17	Pelvis - right	hesperornithiform	partial acetabulum and pubis
RSM P2988.18	Radius - proximal of unidentified side	hesperornithiform	
RSM P2988.19	Angular - left	hesperornithiform	
RSM P2988.2	Femur - distal left	hesperornithiform	large- posterior side eroded
RSM P2988.20	Femur - distal left	hesperornithiform	
RSM P2988.21	Fibula - proximal left	hesperornithiform	
RSM P2988.22	Maxilla - left	hesperornithiform	
RSM P2988.23	Phalanx - left foot	hesperornithiform	
RSM P2988.24	Phalanx - right foot	hesperornithiform	
RSM P2988.25	Quadrate - right	hesperornithiform	
RSM P2988.26	Radius - proximal left	hesperornithiform	
RSM P2988.27	Splenial - right	hesperornithiform	
RSM P2988.3	Tarsometatarsus - distal left	hesperornithiform	missing ends of trochlea, very eroded, compressed
RSM P2988.4	Tarsometatarsus - proximal left	Aves?	very skinny, has shaft
RSM P2988.5	Humerus - proximal right	hesperornithiform	a lot of shaft, medial edge eroded
RSM P2988.6	Humerus - proximal left	hesperornithiform	still on matrix, very eroded and glued
RSM P2988.7	Humerus - proximal right	hesperornithiform	missing deltoid crest side, no shaft
RSM P2988.8	Humerus - right	ichthyornithiform	
RSM P2988.9	Coracoid - left	hesperornithiform	good condition
RSM P2989.1	Femur - left	hesperornithiform	largest-missing head

Specimen #	Element	Identification	Notes
RSM P2989.10	Humerus - distal left	hesperornithiform	put in acid, condyles eroded away
RSM P2989.11	Humerus - proximal left	hesperornithiform	has much of shaft deltoid crest visible
RSM P2989.12	Humerus - proximal left	hesperornithiform	no shaft, jagged edges
RSM P2989.13	Humerus - proximal left	hesperornithiform	no shaft, deltoid crest edge gone
RSM P2989.14	Humerus - proximal right	hesperornithiform	white and brown, complete, bit of deltoid crest visible
RSM P2989.15	Humerus - distal right	hesperornithiform	
RSM P2989.16	Ulna - distal left	hesperornithiform	good condition, end very visible
RSM P2989.17	Ulna - proximal right	hesperornithiform	largest, has much of shaft
RSM P2989.18	Carpometacarpus - proximal right	hesperornithiform	missing metacarpal 3, very fragmented
RSM P2989.189	tooth	hesperornithiform?	
RSM P2989.19	Surangular/articular - left	hesperornithiform	Small, may be Ichthyornis
RSM P2989.190	tooth	hesperornithiform?	
RSM P2989.191	tooth	hesperornithiform?	
RSM P2989.192	tooth	hesperornithiform?	
RSM P2989.193	Splenial - right	hesperornithiform	
RSM P2989.194	Splenial - right	hesperornithiform	
RSM P2989.2	Tarsometatarsus - proximal right	hesperornithiform	small-a lot of glue, crack transversely
RSM P2989.20	Frontal - right	hesperornithiform	
RSM P2989.21	Surangular/articular - left	hesperornithiform	
RSM P2989.22	Vertebrae - dorsal	hesperornithiform	presacral/1-6 dorsal (presacral)
RSM P2989.23	Vertebrae - dorsal	hesperornithiform	1-6 dorsal (presacral)
RSM P2989.24	Vertebrae - 3rd to 4th cervical	hesperornithiform	3-4 cervical
RSM P2989.25	Synsacrum - cranial end	hesperornithiform	
RSM P2989.26	Scapula - proximal unidentified side	Enantiornithes?	
RSM P2989.27	Phalanx - left foot	hesperornithiform	
RSM P2989.28	Phalanx - left foot	hesperornithiform	
RSM P2989.29	Phalanx - proximal right foot	hesperornithiform	
RSM P2989.3	Tarsometatarsus - distal right	hesperornithiform	all trochlea eroded, has shaft
RSM P2989.30	Radius - proximal right	hesperornithiform	
RSM P2989.34	Carpometacarpus - distal left	hesperornithiform	
RSM P2989.35	Fibula - proximal right	hesperornithiform	
RSM P2989.36	Angular - right	hesperornithiform	CBB (large)
RSM P2989.37	Angular - right	hesperornithiform	CBB (small)
RSM P2989.38	Frontal - right	hesperornithiform	CBB
RSM P2989.39	Pelvis - left	hesperornithiform	CBB
RSM P2989.4	Tarsometatarsus - distal right	hesperornithiform	has shaft, trochlea 4 missing
RSM P2989.40	Phalanx	hesperornithiform	distal condyles eroded
RSM P2989.41	Phalanx	hesperornithiform	distal end not preserved. Proximal end slightly eroded
RSM P2989.5	Tarsometatarsus - distal right	hesperornithiform	has 2nd trochlea
RSM P2989.6	Tarsometatarsus - distal left	hesperornithiform	missing all trochlea
RSM P2989.7	Tarsometatarsus - right	hesperornithiform	proximal end nice, missing tips of 3 and 4 trochlea
RSM P2989.8	Tarsometatarsus - proximal right	hesperornithiform	still sediment on end, some shaft
RSM P2989.9	Tarsometatarsus - proximal left	hesperornithiform	end eroded, transverse crack
RSM P2995.3	Ulna - proximal left	hesperornithiform	smallest proximal, middle is missing bone
RSM P2995.4	Frontal - right	hesperornithiform	

Specimen #	Element	Identification	Notes
RSM P2995.5	Maxilla	hesperornithiform	Block A, has sockets
RSM P2995.6	Beak	Aves	Block A
RSM P2995.7	Tibiotarsus - proximal right	hesperornithiform	small, has cnemial crest
RSM P2995.8	Phalanx - proximal right foot	hesperornithiform	may be juvenile
RSM P2995.9	Fibula - proximal left	hesperornithiform	
RSM P2997.10	Femur - right	hesperornithiform	small-medial condyle eroded, very cracked
RSM P2997.11	Femur - distal right	hesperornithiform	large-a lot of shaft, heavily cracked
RSM P2997.12	Femur - right	hesperornithiform	small-sediment on head, heavily glued
RSM P2997.13	Femur - right shaft	hesperornithiform	large, extremes of ends missing
RSM P2997.14	Femur - left shaft	hesperornithiform	mall-condyles missing on distal end
RSM P2997.15	Tarsometatarsus - right	hesperornithiform	missing 2nd trochlea, compressed
RSM P2997.16	Tarsometatarsus - proximal right	hesperornithiform	end eroded, has shaft
RSM P2997.17	Tarsometatarsus - proximal left	hesperornithiform	very eroded
RSM P2997.18	Tarsometatarsus - left	hesperornithiform	proximal end mostly eroded, compressed
RSM P2997.19	Tarsometatarsus - proximal left	hesperornithiform	small-has shaft, end eroded
RSM P2997.2	Femur - right	hesperornithiform	large-cement on bone
RSM P2997.20	Tarsometatarsus - distal left	hesperornithiform	missing tips of trochlea, eroded posterior
RSM P2997.21	Tarsometatarsus - proximal right	hesperornithiform	large-some shaft
RSM P2997.22	Tarsometatarsus - proximal right	hesperornithiform	small-good condition
RSM P2997.23	Tarsometatarsus - distal right	hesperornithiform	large, has 4th trochlea
RSM P2997.24	Humerus - distal right	hesperornithiform	Condyles visible, no shaft, small
RSM P2997.25	Humerus - distal left	hesperornithiform	has bit of shaft, condyles not visible
RSM P2997.26	Humerus - left shaft	hesperornithiform	reduced wing or rib
RSM P2997.27	Ulna - proximal left	hesperornithiform	some external surface bone missing
RSM P2997.28	Ulna - proximal right	hesperornithiform	missing end
RSM P2997.29	Ulna - distal left	hesperornithiform	small, only the very end
RSM P2997.3	Femur - left	hesperornithiform	large-missing head
RSM P2997.30	Ulna -distal left	hesperornithiform	good, crack in bone common
RSM P2997.31	Coracoid - proximal left	hesperornithiform	very broken up, facets good
RSM P2997.32	Carpometacarpus - proximal right	hesperornithiform	metacarpal 3 missing
RSM P2997.33	Carpometacarpus - proximal left	hesperornithiform	metacarpal 1 missing
RSM P2997.34	Carpometacarpus - proximal right	hesperornithiform	hollow shaft visible
RSM P2997.35	Surangular/articular - right	hesperornithiform	
RSM P2997.36	Frontal - right	hesperornithiform	
RSM P2997.37	Skull bone	hesperornithiform	Unknown skull piece, may be part of pelvis
RSM P2997.38	Frontal - left	hesperornithiform	
RSM P2997.39	Tibiotarsus - distal left	hesperornithiform	very small, vascular, medial condyle projects out
RSM P2997.4	Femur - right	hesperornithiform	small-cement on bone
RSM P2997.40	Tibiotarsus - distal left	hesperornithiform	small, jagged end, condyles complete
RSM P2997.41	Tibiotarsus - distal left	hesperornithiform	small, condyles eroded, white posterior
RSM P2997.42	Tibiotarsus - distal right	hesperornithiform	larger, medial condyle eroded
RSM P2997.43	Tibiotarsus - proximal left	hesperornithiform	no shaft, not much of cnemial crest, large
RSM P2997.44	Tibiotarsus - proximal right	hesperornithiform	large, has more shaft and cnemial crest
RSM P2997.45	Tibiotarsus - right shaft	hesperornithiform	

Specimen #	Element	Identification	Notes
RSM P2997.46	Tibiotarsus - proximal right	hesperornithiform	not sure on right or left, small fragile
RSM P2997.47	Tibiotarsus - distal right	hesperornithiform	small, highly eroded, condyles good
RSM P2997.48	Tibiotarsus - distal right	hesperornithiform	larger, lateral condyle eroded
RSM P2997.49	Tibiotarsus - distal right	hesperornithiform	long shaft, medial condyle projects out
RSM P2997.5	Femur - distal right	hesperornithiform	large-medial condyle eroded
RSM P2997.50	Vertebrae - 3rd to 6th dorsal	hesperornithiform	3-6 dorsal
RSM P2997.51	Vertebrae - dorsal	hesperornithiform	1-6 dorsal (presacral)
RSM P2997.52	Vertebrae - cervical	hesperornithiform	
RSM P2997.53	Vertebrae - cervical	hesperornithiform	
RSM P2997.54	Vertebrae - 10th to 13th cervical	hesperornithiform	10-13 cervical
RSM P2997.55	Vertebrae - 4th to 6th cervical	hesperornithiform	4-6 cervical
RSM P2997.56	Synsacrum - cranial end	hesperornithiform	
RSM P2997.57	Synsacrum	hesperornithiform	
RSM P2997.58	Scapula - proximal right	hesperornithiform	flat glenoid facet
RSM P2997.59	Scapula - proximal right	hesperornithiform	bulbous glenoid facet
RSM P2997.6	Femur - right	hesperornithiform	large-lateral condyle eroded, cement on bone
RSM P2997.60	Scapula - proximal left	hesperornithiform	flat glenoid facet
RSM P2997.61	Rib - proximal	hesperornithiform	
RSM P2997.62	Pelvis - right	hesperornithiform	open acetabulum, inclined antitrochanter
RSM P2997.63	Pelvis - left	hesperornithiform	antitrochanter
RSM P2997.64	Pelvis - right	hesperornithiform	antitrochanter
RSM P2997.65	Phalanx - left foot	hesperornithiform	2nd phalanx on 3rd digit
RSM P2997.66	Phalanx - right foot	hesperornithiform	2nd phalanx of 3rd toe, 2nd biggest in group
RSM P2997.67	Phalanx - right foot	hesperornithiform	1st phalanx of 2nd toe, large toe of group
RSM P2997.68	Phalanx - left foot	hesperornithiform	1st phalanx of 2nd toe
RSM P2997.69	Phalanx - right foot	hesperornithiform	
RSM P2997.7	Femur - left	hesperornithiform	large-head missing, medial condyle eroded
RSM P2997.70	Phalanx - proximal right foot	hesperornithiform	
RSM P2997.71	Phalanx - proximal right foot	hesperornithiform	
RSM P2997.72	Phalanx - proximal right foot	hesperornithiform	1st phalanx of 2nd toe, maybe a juvenile
RSM P2997.73	Phalanx - proximal left foot	hesperornithiform	1st phalanx of 2nd toe
RSM P2997.74	Radius - shaft of unidentified side	hesperornithiform	
RSM P2997.75	Radius - shaft of unidentified side	hesperornithiform	smaller
RSM P2997.76	Angular - right	hesperornithiform	
RSM P2997.77	Femur - proximal right	hesperornithiform	just the head
RSM P2997.78	Carpometacarpus - distal right	hesperornithiform	
RSM P2997.79	Femur - proximal right	hesperornithiform	
RSM P2997.8	Femur - right shaft	hesperornithiform	large-edges of proximal end missing
RSM P2997.80	Fibula - proximal right	hesperornithiform	
RSM P2997.81	Tarsometatarsus - proximal left	hesperornithiform	
RSM P2997.82	Scapula - proximal right	hesperornithiform	glenoid facet partially eroded
RSM P2997.83	Tarsometatarsus - proximal right	hesperornithiform	
RSM P2997.84	Vertebra - caudal	hesperornithiform	
RSM P2997.85	Frontal - left	hesperornithiform	Cranial and caudal ends not preserved
RSM P2997.9	Femur - distal left	hesperornithiform	small-white and brown-lateral condyle eroded
RSM P3015.1	Femur - proximal right	hesperornithiform	small-bit of shaft, end eroded
RSM P3015.10	Radius - proximal right	hesperornithiform	float

Specimen #	Element	Identification	Notes
RSM P3015.11	Carpometacarpus - proximal left	hesperornithiform	
RSM P3015.12	Femur - left shaft	hesperornithiform	large species
RSM P3015.13	Humerus - distal left	hesperornithiform	reduced
RSM P3015.14	Phalanx - right foot	hesperornithiform	
RSM P3015.15	Phalanx - right foot	hesperornithiform	
RSM P3015.16	Scapula - proximal left	hesperornithiform	small
RSM P3015.17	Scapula - proximal right	hesperornithiform	large
RSM P3015.18	Tarsometatarsus - distal right	hesperornithiform	small species
RSM P3015.19	Tarsometatarsus - left shaft	hesperornithiform	large species
RSM P3015.2	Femur - proximal right	hesperornithiform	small-no shaft
RSM P3015.20	Vertebra - cervical	hesperornithiform	Cranial end not preserved
RSM P3015.3	Femur - proximal right	hesperornithiform	small-has some shaft, white and brown
RSM P3015.4	Tarsometatarsus - proximal right	hesperornithiform	large-some shaft, good condition
RSM P3015.5	Ulna - distal right	hesperornithiform	sediment still on bone, parts of surface bone missing
RSM P3015.6	Vertebrae - 4th to 6th cervical	hesperornithiform	float/4-6 cervical
RSM P3015.7	Vertebrae - 3rd to 4th cervical	hesperornithiform	float/3-4 cervical
RSM P3015.8	Scapula - proximal left	hesperornithiform	float, flat glenoid facet
RSM P3015.9	Phalanx - right foot	hesperornithiform	float, 1st phalanx of 4th digit

APPENDIX II – COMPARATIVE MEASUREMENTS

The following measurements are in millimeters.

Dentition:

Catalogue Number	Greatest length	Crown length	Crown Width	Root length	Root Width	Waist Width
RSM P2831.22	2.3		0.629	1.4	0.954	0.632
RSM P2831.23	2.86	1.12	0.614	1.72	0.961	0.607
RSM P2831.24		1.66	0.948			
RSM P2831.25		3.05	1.91			
RSM P2831.26		3.4	1.52			
RSM P2831.27		2.75	1.62			
RSM P2831.28	4.36	2.3	1.34		1.62	1.2
RSM P2831.29		1.42	0.685			
RSM P2831.30		1.22	0.599			
RSM P2831.31	3.35	1.89	1.33			1.15
RSM P2831.32	3.08	1.63	1.06		1.02	0.918
RSM P2831.33	3.8	1.73	1.12	2.07	1.42	1.02
RSM P2831.34	3.84	1.78	1.12	2.08	1.33	1.03
RSM P2831.35	4.24		1.62	3.09	2.2	1.48
RSM P2831.36		1.96	1.02			0.901
RSM P2831.37		1.7	1.06			
RSM P2831.38		1.92	1.38			
RSM P2831.39		2.45	1.15			
RSM P2831.40		1.55	0.88			
RSM P2831.41		2.25	1.8			
RSM P2831.42		1.56	0.948			
RSM P2831.43		1.9	1.03			
RSM P2831.44		1.52	1.05			
RSM P2831.45		2.56	1.54			
RSM P2831.46		2.4	1.65			
RSM P2831.47	2.51	1.48	0.786		1.13	0.738
RSM P2831.48		1.64	0.907			
RSM P2831.49		2.33	1.57			
RSM P2831.50		2.07	1.28			
RSM P2831.51		3.2	1.66			
RSM P2989.189		2.52	1.34			
RSM P2989.190	3.05		0.875	1.85	1.18	0.811
RSM P2989.191	3.63		0.938	1.96	1.4	0.926
RSM P2989.192	3.19	1.34	0.799	1.85	0.98	0.814

Vertebrae:

Catalogue Number	Centrum length (mm)	Cranial width of centrum	Caudal width of centrum	Width between cranial articulations	Width between caudal articulations	Distance between transverse processes	Length of sinous process
RSM P2626.15	25.7	8.4	7.1	15.4			
RSM P2626.16	23.9	7.3	6.4	15.4	16.4		
RSM P2626.17							
RSM P2626.39	17.8	10.2	7.6				
RSM P2831.10	14.7	10.3	6.8				
RSM P2831.11	16.7	13.5	9.9				
RSM P2831.7	10.0		4.8				
RSM P2831.8	14.8	5.3	3.8	10.8	10.9		
RSM P2831.9	18.9	7.2	7.0				
RSM P2957.15	17.4	13.4	11.2	10.8	9.8	20.7	13.1
RSM P2957.16			5.3		16.2		
RSM P2957.17	11.4	6.7	5.1		14.1		
RSM P2985.1		11.0		9.0			
RSM P2985.2	12.0	5.9	4.8	4.8	3.6		
RSM P2985.3	16.0	9.5	6.6		7.3		
RSM P2985.4							
RSM P2987.13	19.5	7.8	6.4	14.5			
RSM P2987.14	17.8	11.5	7.0				
RSM P2987.15	21.6	8.3	6.1		13.1		
RSM P2987.16	20.0		6.4	15.4			
RSM P2987.17	18.5	7.6	6.2				
RSM P2987.18	16.9	10.9	8.4				
RSM P2988.12	15.0	11.4	8.0	13.3			
RSM P2988.13							
RSM P2988.14	17.8	8.0	6.9				
RSM P2988.15					7.8		
RSM P2989.22	15.9	10.4	6.9	8.6	6.2	10.9	
RSM P2989.23	15.5	9.8	7.4		6.7		
RSM P2989.24	16.2		5.2	15.4	14.9		
RSM P2997.50	17.0	13.7	8.7				
RSM P2997.51	17.4	9.5	6.6	8.9	6.0		
RSM P2997.52					14.2		
RSM P2997.53							
RSM P2997.54	17.3	9.0	5.8				
RSM P2997.55		9.2		16.1			
RSM P3015.6			5.4		11.3		
RSM P3015.7	14.3	7.8	5.5		12.3		

Scapulae:

Catalogue Numbers	Greatest Length	Cranial diagonal length	Length of glenoid facet
RSM P2830.3			6.5
RSM P2957.19		11.0	6.6
RSM P2985.8		9.0	6.3
RSM P2987.21		9.6	6.2
RSM P2997.58	47.0	11.0	6.4
RSM P2997.59		10.5	6.5
RSM P2997.60		10.1	6.5
RSM P3015.16			6.9
RSM P3015.17			7.3
RSM P3015.8		11.0	8.0
KUVP 2290 ¹		10.5	9.4
YPM 1476 ²	135		8.0

Coracoids:

Catalogue numbers	Greatest Length	Medial Length	Breadth of facies <i>articularis basalis</i>	Length of glenoid facet	Width of scapular facet	Length of scapular facet
RSM P2626.10						
RSM P2626.11						
RSM P2626.30	42.8			5.7		
RSM P2957.10						
RSM P2957.2	46.6			6.0	2.9	2.9
RSM P2957.9				7.9	3.0	3.3
RSM P2985.7				5.6	3.3	3.2
RSM P2987.5		39.1		4.2	2.7	2.7
RSM P2987.6						
RSM P2987.7				7.1	3.2	3.3
RSM P2988.9	45.4	42.4	17.5	6.1	2.8	3.0
RSM P2997.31				6.9	3.2	3.6
KUVP 2290 ¹	53			8.0		7.5
UNSM 20030 ³				7.6		7.0
YPM 1206 ²	54					
YPM 1207 ²	55					

Humeri:

Catalogue Numbers	Greatest Length	Breadth of proximal end	Dorsal ventral diameter of mid-shaft	Transverse diameter of mid-shaft	Breadth of distal end
RSM P2626.43					
RSM P2831.2		12.8			
RSM P2957.24			6.9	5.2	13.1
RSM P2957.25			6.2	4.4	12.2
RSM P2957.26			6.4	4.5	12.1
RSM P2957.7					
RSM P2986.1	74.0	6.9	4.3	4.0	5.5
RSM P2987.2			5.6	4.7	10.3
RSM P2987.3			5.4	4.7	12.5
RSM P2987.4		14.2			
RSM P2988.5			6.6	5.4	
RSM P2988.6		19.8			
RSM P2988.7		17.1			
RSM P2989.10			5.7	4.8	12.0
RSM P2989.11		15.7		5.7	
RSM P2989.12		17.9			
RSM P2989.13		18.6			
RSM P2989.14		17.8			
RSM P2989.15					7.8
RSM P2995.1	102.8	12.8	3.0	7.4	11.1
RSM P2997.24					11.2
RSM P2997.25					13.7
RSM P2997.26			4.3	3.9	
RSM P3015.13					6.6
KUVP 2290 ¹	118	8.9	6.5		6.8
YPM 1206 ²	152	11.5	2.2	7	6.0

Ulnae:

Catalogue Numbers	Greatest Length	Diagonal length from olecranon to lateral articulation	Transverse diameter of proximal end	Transverse diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of distal end
RSM P2989.16					8.6	5.2
RSM P2989.17		9.6	8.0	4.2		
RSM P2995.3		7.4	6.3			
RSM P2997.27		6.9	6.9	3.7		
RSM P2997.28						
RSM P2997.29					7.4	4.4
RSM P2997.30					7.3	4.9
RSM P3015.5					7.5	4.6
KUVP 2290 ¹	21.6		4.2		2.9	3.5

Radii:

Catalogue Numbers	Greatest Length	Transverse diameter of mid-shaft	Transverse diameter of proximal end
RSM P2526.2			4.1
RSM P2526.3			4.2
RSM P2831.17			5.2
RSM P2831.20			3.9
RSM P2957.20			5.5
RSM P2987.25			4.2
RSM P2988.18			4
RSM P2988.26			3.8
RSM P2989.30			4.2
RSM P2997.74	58.3	2.7	3.4
RSM P2997.75			
RSM P3015.10			3.1
KUVP 2290 ¹	20.5		3

Carpometacarpi:

Catalogue Numbers	Greatest Length	Length of metacarpal 2	Breadth of proximal end	Breadth of distal articulation	Length of metacarpus 1
RSM P2626.28	50.6				
RSM P2831.4			11.1		9.2
RSM P2987.8			11.9		9.8
RSM P2989.18		47.1	8.6		7.6
RSM P2989.34				5.0	
RSM P2997.32			11.7		10.1
RSM P2997.33			7.3		
RSM P2997.34			10.7		8.7
RSM P2997.78				4.7	
RSM P3015.11			7.9		8.9

Pelves:

Catalogue Numbers	Greatest diameter of acetabulum
RSM P2626.6	11.3
RSM P2626.27	12.3
RSM P2626.29	9.2
RSM P2957.8	9.0
RSM P2988.17	
RSM P2997.62	7.2
RSM P2997.63	
RSM P2997.64	

Femora:

Catalogue Numbers	Greatest Length	Transverse diameter of proximal end	Anterior-posterior diameter of proximal end	Transverse diameter of mid-shaft	Anterior-posterior diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of distal end	Anterior-posterior diameter of head
RSM P2626.34				7.6	8.6	17.2	11.1	
RSM P2626.35				6.3	7.4	13.7	9.8	
RSM P2626.36		18.8	9.1					9.0
RSM P2626.37								
RSM P2831.1		11.6	5.9	5.3	6.3			5.9
RSM P2957.5		20.2	10.0					10.0
RSM P2988.1		12.2	7.2	5.7	6.5			7.2
RSM P2988.2						20.0	12.3	
RSM P2988.20						17.6	11.7	
RSM P2989.1	68.4		10.2	9.7	11.1	22.2	14.7	
RSM P2997.10	49.9	13.4	6.8	6.0	7.0	13.1	8.9	6.7
RSM P2997.11				8.2	9.9	18.7	12.6	
RSM P2997.12	48.2	16.4	7.3	6.5	8.2	15.5	9.9	6.3
RSM P2997.13				9.1	10.9			
RSM P2997.14				5.3	6.3			
RSM P2997.2	65.1	18.9	9.4	8.4	10.0	20.0	13.0	9.3
RSM P2997.3	66.0		7.8	7.2	9.8	17.5	10.3	
RSM P2997.4	50.7	14.9	7.2	6.5	7.4	16.5	10.1	7.1
RSM P2997.5						18.3	12.8	
RSM P2997.6	60.2	17.8	9.5	8.5	10.1	15.8	11.6	6.6
RSM P2997.7	57.6		8.8	7.1	8.2	17.8	11.5	
RSM P2997.77								8.2
RSM P2997.79		12.8	6.1					
RSM P2997.8						15.2	9.7	
RSM P2997.9			8.1	7.5	8.7			
RSM P3015.1		10.4	6.2	5.0	6.0			6.4
RSM P3015.12				8.0	9.6			

Femora (continued):

Catalogue Numbers	Greatest Length	Transverse diameter of proximal end	Anterior-posterior diameter of proximal end	Transverse diameter of mid-shaft	Anterior-posterior diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of distal end	Anterior-posterior diameter of head
RSM P3015.2		12.0	5.9					5.8
RSM P3015.3		12.9	6.5	5.6	6.8			6.5
KUVP 2290 ¹	75	28.0		11.0	12.5	26		11.5
SDSM 68430 ³				15.0	15.8	31.6		
LACM 9728 ⁴	44.7	23.2				21.7		
RSM P2077.60 ⁵	46.8	15	7.3	6.8	8	16.3	10.4	7.3
RSM P2077.108 ⁵	64.5	20.8	9.8	10.2	12	21.8	14.8	10
BMNH A5803 ⁶		17.5						
BMNH A163 ⁶						21.3		
YPM 1200 ²	99					53		18.5
YPM 1206 ²	96	51	19.1	22	18.1	49	28.5	18
YPM 1207 ²	98.5	52				52		19
YPM 1476 ²	105	54.4	19	22.4	18	51.7	27	19
YPM 1477 ²	97				20	52		19

Catalogue Numbers	Greatest length	Transverse diameter of proximal end	Transverse diameter of mid-shaft	Anterior-posterior diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of distal end	Elevation of cnemial process
RSM P2626.20					9.8	5.8	
RSM P2626.40					10.4	7.5	
RSM P2957.13			5.2	3.4	10.3	6.6	
RSM P2957.14			5.4	4.2	9.5	7.5	
RSM P2957.21					14.9	9.4	
RSM P2957.22		13.3					10.9
RSM P2987.10		18.5					
RSM P2987.11			5.3	4.2	9.7	7.7	
RSM P2987.9			5.5	4.1	9.1	7.9	
RSM P2995.7		10.5					1.5
RSM P2997.39					10.3	6.8	
RSM P2997.40					7.9	6.4	
RSM P2997.41					9.2	5.8	
RSM P2997.42			6.6	4.1	11.5	8.0	
RSM P2997.43		14.4					
RSM P2997.44		17.9					5.7
RSM P2997.45			9.1	6.1			
RSM P2997.46		8.9	5.5	3.8			5.9
RSM P2997.47			5.6	3.7	9.3	6.1	
RSM P2997.48			6.6	4.2	11.7	8.1	
RSM P2997.49			5.1	4.0	9.3	7.7	
USNM 20030 ¹	195	18	12	9	19		14
SDSM 68430 ³	206.5	24.5	15.5	11.9	24.9		15.5
SMC B55316 ⁶					15.2		
YPM 1200 ²	320	35	23	16	26	32	22
YPM 1476 ²	335	36	22	16.5	32.5	30.5	23

Fibulae:

Catalogue Numbers	Greatest length	Anterior-posterior diameter of proximal end	Transverse diameter of proximal end
RSM P2626.41		6.7	3.8
RSM P2988.21		7.7	3.5
RSM P2989.35		9.9	5.4
RSM P2995.9		7.2	4.8
RSM P2997.80		8.4	4.9
KUVP 2290 ¹		11	8.5
SDSM 68430 ³		13.4	8.1
YPM 1200 ²	240	15	22
YPM 1476 ²		12	23

Tarsometatarsi:

Catalogue Number	Greatest Length	Transverse diameter of proximal end	Anterior-posterior diameter of proximal end	Transverse diameter of mid-shaft	Anterior-posterior diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of 2nd Trochlea	Anterior-posterior diameter of 3rd Trochlea	Anterior-posterior diameter of 4th Trochlea	Distance from distal end of 2nd trochlea to 3rd trochlea
RSM P2626.32						10				
RSM P2626.33						8.2				
RSM P2626.38										
RSM P2830.1		9.1	6.7							
RSM P2830.2						8.3	4.4		5.0	
RSM P2957.27	81.3	16.0	7.8	6.4	8.4	13.5		9.6	9.9	
RSM P2957.6				3.6						
RSM P2985.6						9.1	5.1	6.5		7.2
RSM P2987.1	56.5	7.9	6.1	3.7	5.3				6.5	
RSM P2988.3				2.9		6.5	4.3		4.4	5.1
RSM P2988.4		9.5	5.2							
RSM P2989.2		9.4	7.0	3.4	5.2					
RSM P2989.3						7.5	3.4	5.3	4.7	7.5
RSM P2989.4				3.5		7.9	5.2	6.4		6.7
RSM P2989.5							5.7			
RSM P2989.6										
RSM P2989.7	56.9	11.8	8.3	4.7	6.4	10.0	7.0			
RSM P2989.8										
RSM P2989.9		9.2	7.5							
RSM P2997.15	51.9	9.0	6.5	3.8	5.1	7.5		6.1	6.0	
RSM P2997.16		11.5	7.2							
RSM P2997.17		13.5	8.0							
RSM P2997.18	60.8	9.1	6.0	3.8	5.1	8.0	5.2	6.0	5.8	7.0
RSM P2997.19		8.7	7.4							
RSM P2997.20										
RSM P2997.21		15.8	11.7							
RSM P2997.22		9.4	7.0							

Tarsometatarsi (continued):

Catalogue Number	Greatest Length	Transverse diameter of proximal end	Anterior-posterior diameter of proximal end	Transverse diameter of mid-shaft	Anterior-posterior diameter of mid-shaft	Transverse diameter of distal end	Anterior-posterior diameter of 2nd Trochlea	Anterior-posterior diameter of 3rd Trochlea	Anterior-posterior diameter of 4th Trochlea	Distance from distal end of 2nd trochlea to 3rd trochlea
RSM P2997.23									10.4	
RSM P2997.81		8.6	5.7							
RSM P3015.18						6.9	4.3			
RSM P3015.19				5.5	7.2					
RSM P3015.4		15.1	9.6							
SMC B55331 ⁶		12.5	8.6							
KUVP 2290 ¹	84	18.0	13.5			16				12
SDSM 68430 ³	96.1	23.9	10.9			27.3				11.3
PU 17208 ⁴	137.5	31.5	26.5			20.3				
PU 17208A ⁴	102.4	22.6	15.7			18.4				
BO 780106 ⁴	85.6	15.9	10.0			11.25				
ZIN PO 5464 ⁷	158.8	40.8	23.8			24.5				
RSM P2077.117 ⁵	52.4	8.9	6.1							6.4
RSM P2077.63 ⁵	85.6	16.0	13.0							
YPM 1200 ²	136	34.0	21.0	14						
YPM 1206 ²	132	32	21	13.5						
YPM 1207 ²	136	33		13						
YPM 1476 ²	136	31	21	12.5						

Phalanges:

Catalogue Number	Greatest Length	Medial lateral proximal width	Dorsal ventral proximal width	Medial lateral distal width	Dorsal ventral distal width
RSM P2626.19	24.4	4.8	8.1	5	5.4
RSM P2626.31	22.5	5.3	5.4	5	3.7
RSM P2831.15	17	4	4.3	3.4	2.6
RSM P2831.16	14.4	2.9	2.9	2.7	1.8
RSM P2985.5	18.8	4.4	4.9	4.1	3.2
RSM P2987.24	25.1	6.2	7.7	5.7	5.6
RSM P2988.23		6.1	7.3		
RSM P2988.24				4.7	5.3
RSM P2989.27	18.7	4.5	4.5	4.9	3
RSM P2989.28	21.4	4.7	5.3	5.4	3.7
RSM P2989.29		6.3	7.7		
RSM P2995.8		5.9	7.1		
RSM P2997.65	24.1	5	7.6	5	5.5
RSM P2997.66	24.4	5.8	5.2	5.3	3.1
RSM P2997.67	22.8	5.1	6.8	4.7	5.3
RSM P2997.68	24.8	5.9	7.7	4.9	5.3
RSM P2997.69	20.1			3.5	2
RSM P2997.70		5.2	6.7		
RSM P2997.71	36	6.4	7	5.1	4.4
RSM P2997.72		5.6	7.9		
RSM P2997.73		5.7	7.7		
RSM P3015.9	31.8	5.9	8.2	4.6	4.9
RSM P3015.14				2.9	2.9
RSM P3015.15				4.6	3.4

¹Measurements from Martin and Tate (1976).²Measurements from Marsh (1880).³Measurements from Martin and Cordes-Person (2007).⁴Measurements from Martin and Lim (2002).⁵Measurements from Tokaryk et al. (1997).⁶Measurements from Galton and Martin (2002).⁷Measurements from Penteleyev et al. (2004).

APPENDIX III – COMPARISONS WITH *ICHTHYORNIS*

Ichthyornis, a member of Ornithurae along with Hesperornithiformes, is a late Cretaceous (Cenomanian to Campanian) bird known from North America and is often found in similar areas as Hesperornithiformes. *Ichthyornis* is a tern-like bird that spent much time out at sea, but was not adapted for diving like Hesperornithiformes.

Ichthyornis humeri were found in the Bainbridge River locality and because of this will be an important comparison with *Pasquiaornis* as to make sure bones identified as *Pasquiaornis* are not those of *Ichthyornis*.

Maxilla

The maxillae of *Pasquiaornis* are about twice the depth of those of *Ichthyornis*. In *Ichthyornis*, the medial edge of the maxilla is slightly rounded edge similar to that of *Pasquiaornis*, which does not bear any indication of articular surfaces (Clarke, 2004). On the medial surface of the *Ichthyornis* maxilla posterior to the alveoli there are small foramina (Clarke, 2004) similar to that of *Pasquiaornis*. The teeth of *Ichthyornis* are set in sockets similar to those of *Pasquiaornis*.

Frontals

The frontals of *P. hardiei* and *P. tankei* are both larger than those of *Ichthyornis*. In *Ichthyornis* the frontals are fused (Clarke, 2004), unlike those of *Pasquiaornis* whose frontals are separate. The frontal of *Ichthyornis* shows paired shallow glandular depressions on the dorsal supraorbital margins which do not reach the midline; the antero-ventral midline of the frontal is fused with mesethmoid (Clarke, 2004). These glandular depressions are not seen in *Pasquiaornis*.

Dentary

The dentaries of *P. hardiei* and *P. tankei* are about 20% and 60% larger than those of *Ichthyornis*, respectively. In *Ichthyornis*, Martin and Stewart (1977) describe seven mental foramina on the lateral surface of the dentary. Only two foramina are preserved in the known dentary of *Pasquiaornis* on the lateral side; however the whole dentary is not preserved, so it cannot be determined how many foramina the specimen would have had. Clarke (2004) notes that there are no terminal facets on *Ichthyornis* that would suggest articulation with a prementary. This is unlike *Pasquiaornis* which does have distinguishable terminal facets. The dentary of *Ichthyornis* has sockets for where the teeth are set. The dentary of *Pasquiaornis* has slight indications of sockets.

Splénial

The splénials of *P. hardiei* are approximately 20% larger than those of *Ichthyornis*. The splénial of *Ichthyornis* makes up the ventral margin of part of the lower jaw (Clarke, 2004). The splénial was not found in articulation with the rest of the lower jaw in *Pasquiaornis* although this is the most likely scenario, as this condition is seen in all other Hesperornithiformes.

Angular

The angular of *P. tankei* and *P. hardiei* are about 60% and 20% larger than those of *Ichthyornis*, respectively. Noted by Gingerich (1972), the angular of *Ichthyornis* forms the ventral edge of the mandible posterior to the contact between the angular and splénial. Since the mandibles of the *Pasquiaornis* specimens were not found articulated, it is not known if this was the case although it is likely. At the contact between the angular and the splénial, the angular of *Ichthyornis* has an articular facet for the splénial (Gingerich, 1972), also seen in *Pasquiaornis*.

Articular/Prearticular/Surangular

The surangular, articular and prearticular of *P. tankei* and *P. hardiei* are about 60% and 25% larger than those of *Ichthyornis*, respectively. In *Ichthyornis*, Clarke (2004) describes a large foramen visible in medial view near the ventral edge of the preserved surangular and close to the midpoint of the mandibular fossa. This foramen is not seen in *Pasquiaornis*. Much as in *Pasquiaornis*, sutures between the prearticular and articular are not visible in *Ichthyornis* (Clarke, 2004). Directly posterior to the medial cotyla, the entrance and exit of the *n. Corda tympani* are visible in what would be part of the prearticular in *Ichthyornis* (Clarke, 2004). This is not noticeable in *Pasquiaornis*.

Cervical Vertebrae

The cervical vertebrae of *Pasquiaornis* are much larger than those of *Ichthyornis* and are heterocoelous, while those of *Ichthyornis* are only heterocoelous cranially (Galton and Martin, 2002).

Dorsal Vertebrae

The dorsal vertebrae of *P. tankei* and *P. hardiei* are, respectively, about 71% and 60% larger than those of *Ichthyornis* (YPM 1732). The dorsal vertebrae of *Ichthyornis* are amphicoelous (Clarke, 2004). The dorsal vertebrae assigned to *Pasquiaornis* are also slightly amphicoelous, but less so than *Ichthyornis*. Both *Ichthyornis* and *Pasquiaornis* dorsal vertebrae have large lateral excavations. *Ichthyornis* also has several pneumatic foramina and fossa that are not seen in *Pasquiaornis*.

Coracoid

The coracoids of *P. tankei* are 25% larger than those of *Ichthyornis* (YPM1743). Overall the *Pasquiaornis* coracoids are much more robust than those of *Ichthyornis*. *Ichthyornis* and the *Pasquiaornis* coracoids do look similar, both having a long slender

neck that broadens posteriorly. The neck of the coracoid of *Pasquiaornis* is relatively longer than that of *Ichthyornis*. In both, the scapular end is extended so that the glenoid facet is located further posterior on it and not right at the tip. The scapular facet of *Ichthyornis* has a deeper depression than that of *Pasquiaornis* coracoids. The glenoid facet of *Ichthyornis* is slightly shallower than in those of *Pasquiaornis*. The procoracoid of the *Ichthyornis* extends and wraps around further mesially than in *Pasquiaornis*.

Scapula

The scapulae of *P. tankei* and *P. hardiei* are about 70% and 50% larger than those of *Ichthyornis* (YPM 1734). *Ichthyornis* has an acromion process that does not extend as far as it does in *Pasquiaornis*. *Pasquiaornis* also has a bulbous coracoidal articulation which is not present in *Ichthyornis*. Both *Pasquiaornis* and *Ichthyornis* have elongate recurved scapular blades; however, the blade of *Ichthyornis* remains relatively the same width (Clarke, 2004) while that of *Pasquiaornis* becomes slightly less broad distally. On the ventral surface of the scapula in *Ichthyornis*, just distal to the glenoid facet, is a small foramen that is not present in any of the *Pasquiaornis* specimens. Also present in *Ichthyornis* is a narrow ridge just distal to the foramen, which extends a third of the proximal end of the scapular blade (Clarke, 2004). This ridge is not found in *Pasquiaornis*.

Humerus

The humeri of *Pasquiaornis* are about 30% larger than those of *Ichthyornis* (YPM 1742). The humerus of *Ichthyornis* has a prominent ectepicondylar process situated relatively high on the shaft, with a pit on its proximal surface (Clarke, 2004). The humerus of *Ichthyornis* also has a well-developed entepicondylar process (Clarke, 2004). Neither of these processes is as prominent in *Pasquiaornis*. In cross section, the compact

bone of *Ichthyornis* is much thinner than that in *Pasquiaornis*. The deltopectoral crest of *Ichthyornis* is much thinner than the crest in *Pasquiaornis*, and extends proportionally further from the shaft, but not as far down the shaft as in *Pasquiaornis*. The deltopectoral crest of *Pasquiaornis* is also directed anteriorly, which is not the case in *Ichthyornis*. Overall, the humeri of *Pasquiaornis* are much more robust than those of *Ichthyornis*.

Ulna

No *Pasquiaornis* ulna is complete; however they are much larger and more robust than those of *Ichthyornis*. An apomorphy of *Ichthyornis* is that “the dimensions of the dorsal condyle are such that the length of the trochlear surface along the posterior surface of the distal ulna is approximately equal to the width of the trochlear surface taken across the distal end” (Clarke, 2004). This apomorphy does not hold true for *Pasquiaornis*, since the length of the dorsal condyle is larger than the width. *Ichthyornis* has a very prominent bicipital tubercle compared to that of the *Pasquiaornis* ulnae. In both *Ichthyornis* and *Pasquiaornis*, the bicipital tubercle lies at the distal edge of the triangular radial depression. Distal to the *Impressio brachialis*, *Ichthyornis* and *Pasquiaornis* ulnas have a nutrient foramen. The ventral and dorsal cotyla in *Ichthyornis* are of about the same size, while the dorsal cotyla is largest in the ulna of *Pasquiaornis*. The ulna of *Pasquiaornis* has a more distinct intercotyla than does *Ichthyornis*. In both *Ichthyornis* and *Pasquiaornis*, the dorsal cotyla is slightly convex. The semi-lunar notch is more concave in *Ichthyornis* than it is in *Pasquiaornis*. No scars indicating the insertion of the follicular ligaments of the secondary flight feathers are visible on *Pasquiaornis* ulnae, unlike *Ichthyornis* specimens. In *Ichthyornis*, on the distal end of the ulna, there is a tendinal pit and ridge indicating a tendinal groove that does not appear in *Pasquiaornis*. The styloid process of the *Ichthyornis* ulnae is slightly more prominent than in *Pasquiaornis*.

Radius

The radii of *P. tankei* and *P. hardiei* are much larger and more robust than those of *Ichthyornis*.

Carpometacarpus

The carpometacarpus of *Ichthyornis* shows many differences from that of *Pasquiaornis*. Overall, the carpometacarpus of *Pasquiaornis* is more robust than that of *Ichthyornis*. The first obvious difference is that the carpal trochlea is flat in *Ichthyornis*, while in *Pasquiaornis* there is a more distinct groove. This trochlea is also relatively wider in *Pasquiaornis* than it is in *Ichthyornis*. There is no evidence of a large proximo-distally elongate scar in *Pasquiaornis* as there is in *Ichthyornis* at the same position as the intermetacarpal tuberosity. The first metacarpal of *Ichthyornis* has a triangular shape with a 90 degree angle on the most proximal portion close to the second metacarpal. The first metacarpal of *Pasquiaornis* has a semi-circular shape. An apomorphy of *Ichthyornis* is a large tubercle close to the articular surface of the second metacarpal (Clarke, 2004). This tubercle is not present in *Pasquiaornis*. Similar to *Ichthyornis*, the pisiform is situated relatively proximal to metacarpal one, which is usually found around the midpoint of metacarpal one in Aves (Clarke, 2004). The extensor groove seen in *Ichthyornis* is not visible in *Pasquiaornis*; however this may be due to preservation. The distal articulation in *Ichthyornis* is more distinct than it is in *Pasquiaornis*.

Femurs

The femora of *P. tankei* and *P. hardiei* are approximately 62% and 51% larger than those of *Ichthyornis* (YPM 1450). The femur of *Pasquiaornis* is far more robust compared to that of *Ichthyornis*. *Ichthyornis* has a well developed capital ligament fossa on the head, which is not noticeable on *Pasquiaornis*. The distal end of the femur in

Pasquiaornis has a very large and triangular groove compared to that of *Ichthyornis* and a much more expanded lateral condyle.

Tarsometatarsus

Overall the tarsometatarsi of *Pasquiaornis* are larger and more robust than those of *Ichthyornis*. The medial and lateral cotyla of both *Ichthyornis* and *Pasquiaornis* are of relatively the same size. The medial and lateral cotyla of *Pasquiaornis* are slightly slanted distally, while in *Ichthyornis* they are more perpendicular. On the posterior surface toward the proximal end, there are two large vascular foramina in *Ichthyornis* that are present in *Pasquiaornis*. In *Ichthyornis*, a hypotarsal is present, while it is not present in *Pasquiaornis*. *Pasquiaornis* has a prominent lateral ridge on the anterior surface that is found in all Hesperornithiformes, but is missing in *Ichthyornis*. *Ichthyornis* metatarsal III extends farther distally than metatarsal IV, while in *Pasquiaornis*, metatarsal III and IV are closer in size. Metatarsal IV of *Ichthyornis* also extends out further laterally than it does in *Pasquiaornis*. The trochlea of metatarsal IV is placed further posterior in *Pasquiaornis* than in *Ichthyornis*.

APPENDIX IV – COMPARISONS WITH *GANSUS*

Along with Hesperornithiformes, *Ichthyornis* and Neornithes (modern birds), *Gansus yumenensis* constitutes the Ornithurae (Chiappe, 2002). *Gansus*, a web-toed aquatic bird from the Early Cretaceous (Albian) of China, is the oldest known of the Ornithurae. *Gansus* was about the size of a pigeon, but similar in appearance to loons and diving ducks. This relationship and similarity in lifestyle makes *Gansus* an important comparison to *Pasquiaornis*.

Overall, the bones of *Gansus* are apneumatic like that of *Pasquiaornis*, although *Pasquiaornis* seems more robust. The cervical and thoracic vertebrae of *Gansus* are not heterocoelous (You et al., 2006), while in *Pasquiaornis* the cervical vertebrae are heterocoelous, but the thoracic vertebrae are not. The coracoid of *Gansus* has a well developed procoracoid, similar to that of *Pasquiaornis*. Both *Pasquiaornis* and *Gansus* have well-projected cnemial crests on the tibiotarsus. Both *Pasquiaornis* and *Gansus* have an extensor groove on the tibiotarsus that lacks a supratendinal bridge. *Gansus* has a hypotarsal on the tarsometatarsus while *Pasquiaornis* does not. *Gansus* has a distal foramen on the tarsometatarsus which seems to be present in *P. hardiei* (You et al., 2006). *Gansus* lacks the prominent cranio-lateral crest on the tarsometatarsus seen in *Pasquiaornis*.