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Hesperornithiformes (Aves: Ornithurae) from the Upper Cretaceous Pierre Shale, Southern Manitoba, Canada

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ABSTRACT

A historical collection of hesperornithiform fossils from the Gammon Ferruginous, Pembina, and Millwood members of the Pierre Shale (Campanian, Upper Cretaceous) in southern Manitoba, Canada, was examined to revise their taxonomy. Only two species of *Hesperornis* have been recognized in previous studies on the Pierre Shale in Manitoba, but our study recognizes six species of two genera, including *H. lumgairi* sp. nov. *H. regalis* is the most common species but absent in the uppermost unit within the studied sequence. The result of this study supports the paleobiogeographic subdivision of the Campanian vertebrate fauna within the Western Interior Seaway, but not the faunal boundary that distinguishes the avian fauna of Manitoba from that of South Dakota and Kansas.

1. Introduction

Hesperornithiformes are a group of Cretaceous diving birds (e.g. Marsh, 1880; Martin and Lim, 2002; Bell and Chiappe, 2016). Their remains exclusively occur in the northern hemisphere and they are most commonly reported from the Campanian of North America, but their occurrences in Europe and Asia have also been reported (Rees and Lindgren, 2005). In North America, the geographic range of Hesperornithiformes extends from Ellesmere Island of the Arctic Archipelago to Arkansas where the Western Interior Seaway existed during the Late Cretaceous (Nicholls and Russell, 1990; Davis and Harris, 1997; Tokaryk et al., 1997; Tokaryk, 1998; Hills et al., 1999).

Various marine vertebrate fossils, including those of Hesperornithiformes, have been collected from the Pierre Shale in southern Manitoba (Nicholls, 1989; Nicholls and Russell, 1990; Konishi and Caldwell, 2011; Sato et al., 2011), but publications on the avian fauna from this formation remain few. Bardack (1968) reported the first occurrence of *Hesperornis* from Manitoba, in which five specimens of *H. regalis* from the Vermilion River Formation (Boyne Member of the Carlile Formation in Bamburak and Nicolas, 2009) and those from the Pembina Member of the Pierre Shale were briefly described as well. Nicholls (1989) conducted the first, and currently the most recent, systematic investigation on the marine vertebrates of the Pembina Member in the Morden–Miami area in southern Manitoba. She examined 169 hesperornithiform specimens and assigned all diagnostic specimens to one species, *H. regalis*. Additional specimens have been collected from the Pierre Shale in southern Manitoba since then; however, a systematic study has not been conducted on them.

Since Nicholls' study in the late 1980's, hesperornithiform systematics has amplified the number of recognized species, although their phylogenetic relationships remain poorly resolved (Bell and Chiappe, 2016). In total, two genera and six species of Hesperornithiformes have been recognized in the Pierre Shale. Martin and Lim (2002) described four new species, *H. chowi*, *H. bairdi*, and *H. macdonaldi* from the Sharon Springs Member in South Dakota and *H. mengeli* from the Pembina Member in Manitoba (Sharon Springs Member in Martin and Lim, 2002). Subsequently, *Brodavis varneri* Martin et al., 2012 (formerly *Baptornis varneri*) was reported from the Sharon Springs Member in South Dakota (Martin and Cordes-Person, 2007; Martin et al., 2012).

The current study aims to update the taxonomy of hesperornithiforms of the Pierre Shale in southern Manitoba and discuss their paleobiogeographical significance. During the Late Cretaceous, the current location of southern Manitoba was at the center of the north–south stretch of the Western Interior Seaway. It was one of the five localities analyzed by Nicholls and Russell (1990) to set the faunal

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subdivision of marine vertebrates within the seaway south of Kansas. More recently, Martin and Lim (2002) recognized two faunal regions of hesperornithiforms in the seaway, i.e., one in Kansas to South Dakota and the other in Canada. Southern Manitoba is close to the faunal boundary set by Martin and Lim (2002), and the taxonomic composition of the local avian fauna is crucial in testing the validity of their hypothesis; if the faunal boundary did exist, the hesperornithiform fauna of southern Manitoba would belong to the "northern fauna," and they are expected to differ from the "southern fauna" of South Dakota and Kansas. For this test, we compared the hesperornithiform fauna of the Pembina Member in Manitoba with the contemporaneous fauna of the Sharon Springs Member in South Dakota.

Institutional abbreviations—**CFDC**, Canadian Fossil Discovery Centre, Morden, Manitoba, Canada; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **MM**, Manitoba Museum, Winnipeg, Manitoba, Canada; **PU**, Princeton University, Princeton, New Jersey, USA (now at YPM); **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SDSM**, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **SGU**, Geological Survey of Sweden, Uppsala, Sweden; **UA**, University of Alberta, Edmonton, Alberta, Canada; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

2. Locality and stratigraphy

All of the specimens in this study were collected from the Pembina Mountain region of the Manitoba Escarpment, specifically the Morden–Miami area in southern Manitoba. The CFDC operates excavations at 35 sites, and hesperornithiform fossils have been collected from 20 sites marked in Fig. 1. To prevent vandalism, only the site numbers (indicated as "CFDC site #") are given in this paper and plotted on a regional-scale map; more detailed locality information is available at the CFDC.

All of the specimens in this study originate from the Pierre Shale (Campanian–Maastrichtian; Bamburak and Nicolas, 2009). The formation is approximately 340 m thick and is subdivided into five members: Gammon Ferruginous, Pembina, Millwood, Odanah, and Coulter members (Bamburak and Nicolas, 2010). The vertebrate fossils, including the hesperornithiforms in this study, came from the first three members and most of them are from the Pembina Member. Bamburak and Nicolas (2009) summarized the long history of stratigraphical research in this region and revised the Cretaceous stratigraphic nomenclature; their scheme is adopted in this paper (Fig. 1).

The Gammon Ferruginous Member consists of uniform dark gray mudstone and silty shale containing numerous ferruginous or sideritic concretions (McNeil and Caldwell, 1981). Although the maximum thickness of this member reaches up to 56 m west of Melita, Manitoba, the thickness ranges from 0 to 3 m along the eastern flank of the Pembina Mountain region (Bamburak and Nicolas, 2010). The fossil bones from this member are light brown in color. The age of this member is inferred to be early Campanian by McNeil and Caldwell (1981). No vertebrate fossils had been reported from this member within Manitoba prior to 2010; however, specimens of mosasaurs, plesiosaurs, fishes, and birds (including *Hesperornis*), were recovered in a recent excavation by the CFDC (Hatcher, 2011).

The Pembina Member unconformably overlies the Gammon Ferruginous Member, or the Carlile Formation below where the Gammon Ferruginous Member is absent (Nicolas, 2009). This member comprises alternating layers of buff bentonite seams and grayish-black non-calcareous marine shale beds (Bamburak and Nicolas, 2009). It is approximately 25 m thick and consists of two distinct lithologic units in the Pembina River valley near the studied area where the lectostratotype of the member was designated (McNeil and Caldwell, 1981). The lower unit is a 15 m thick, grayish-black, organic-rich shale unit including approximately 20–30 bentonite seams, whereas the upper unit is 9 m thick, comprising dusky yellowish-brown shale (McNeil and Caldwell, 1981). Many vertebrate fossils have been collected from the lower unit but not from the upper unit (Nicholls and Russell, 1990; this study). The fossil remains from

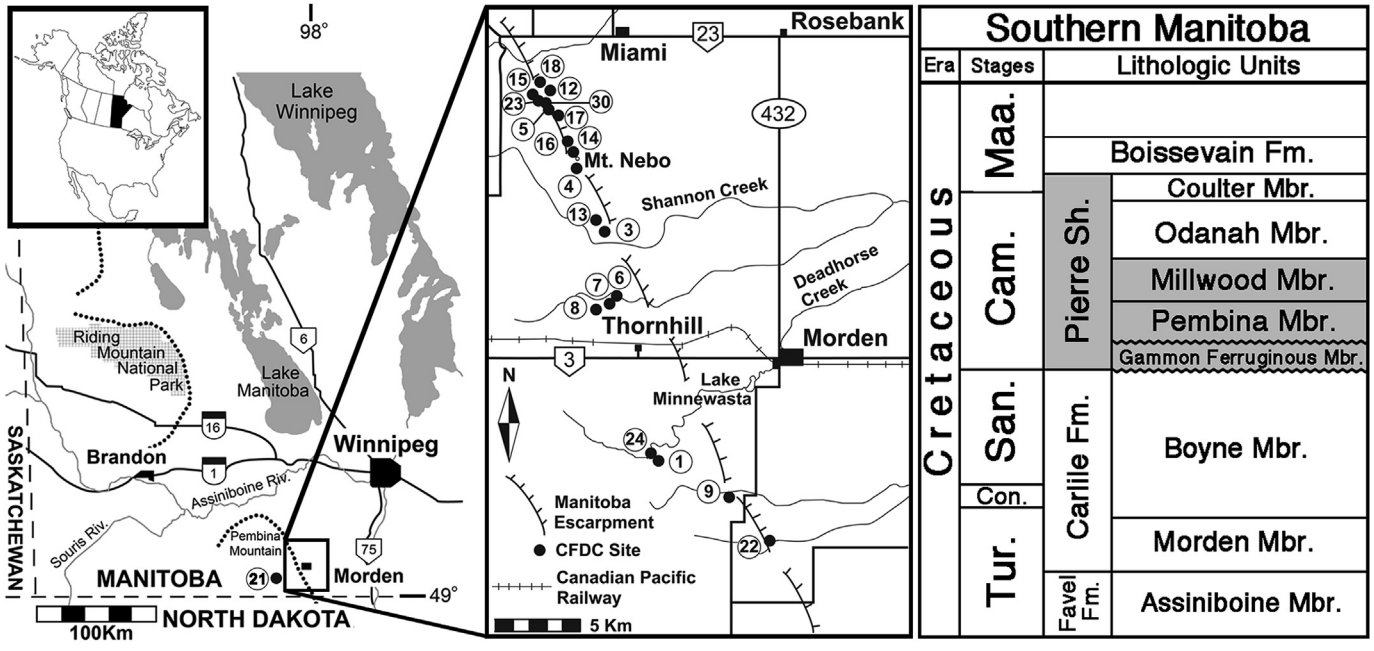

Fig. 1. Localities of hesperornithiform fossils and the local stratigraphy in the Manitoba Escarpment. Our study area is indicated by a square, and circles indicate CFDC sites yielding hesperornithiforms described in this study (CFDC site map information compiled from Bamburak and Nicolas, 2010). Stratigraphy based on Bamburak and Nicolas (2009).