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An avian femur from the Late Cretaceous of Vega Island, Antarctic Peninsula: removing the record of cursorial landbirds from the Mesozoic of Antarctica

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In 2006, a partial avian femur (South Dakota School of Mines and Technology [SDSM] 78247) from the Upper Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation of Sandwich Bluff on Vega Island of the northern Antarctic Peninsula was briefly reported as that of a cariamiform – a clade that includes extant and volant South American species and many extinct flightless and cursorial species. Importantly, SDSM 78247 has never been the subject of a detailed description, hindering a definitive assessment of its affinities. Here we provide the first comprehensive description, illustration, and comparative study of this specimen. Comparison of characters that may be assessed in this femur with those of avian taxa scored in published character matrices refutes the purported inclusion of SDSM 78247 within Cariamiformes, instead supporting its assignment to a new, as-yet unnamed large-bodied species within the genus *Vegavis* and therefore its referral to a clade of semiaquatic anseriforms. This clade was previously known only from *V. iaai*, a smaller-bodied taxon from the same locality and stratigraphic unit. Our reassignment of SDSM 78247 to *Vegavis* sp. removes the record of cariamiform landbirds from the Antarctic Cretaceous.

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Abstract

In 2006, a partial avian femur (South Dakota School of Mines and Technology [SDSM] 78247) from the Upper Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation of Sandwich Bluff on Vega Island of the northern Antarctic Peninsula was briefly reported as that of a cariamiform – a clade that includes extant and volant South American species and many extinct flightless and cursorial species. Importantly, SDSM 78247 has never been the subject of a detailed description, hindering a definitive assessment of its affinities. Here we provide the first comprehensive description, illustration, and comparative study of this specimen. Comparison of characters that may be assessed in this femur with those of avian taxa scored in published character matrices refutes the purported inclusion of SDSM 78247 within Cariamiformes, instead supporting its assignment to a new, as-yet unnamed large-bodied species within the genus *Vegavis* and therefore its referral to a clade of semiaquatic anseriforms. This clade was previously known only from *V. iaai*, a smaller-bodied taxon from the same locality and stratigraphic unit. Our reassignment of SDSM 78247 to *Vegavis* sp. removes the record of cariamiform landbirds from the Antarctic Cretaceous.

Introduction

In 2005, an expedition co-directed by one of us (J.A. Case) recovered a partial avian left femur as part of a field investigation of Upper Cretaceous sedimentary units in the James Ross Basin of the northern Antarctic Peninsula (Fig. 1). The femur (South Dakota School of Mines and Technology [SDSM] 78247; Figs. 2, 3) was recovered from the Sandwich Bluff locality on the western half of Vega Island. The stratigraphic position of the specimen places it approximately in the middle of the uppermost Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation, at a level about 1 m below the hadrosaur tooth described by Case et al. (2000) and some 60 m upsection from the concretionary horizon that yielded the holotype and referred skeletons of the anseriform bird *Vegavis iaai* (Clarke et al., 2005, 2016).

A preliminary report of SDSM 78247 provisionally identified this femur as that of a terrestrial, cursorial bird belonging to either the otherwise exclusively Cenozoic Phorusrhacidae ('terror birds') or the extant Cariamidae (seriemas) within Cariamiformes (Case et al., 2006). This taxonomic assignment was based on the large size of the femur and three features of its distal morphology: an enlarged and ventrally prominent tibiofibular crest, a laterally expansive lateral condyle, and a broad fibular trochlea. Nevertheless, in a review of Antarctic phorusrhacid fossils, Cenizo (2012) questioned this referral and instead identified a number of femoral character states that SDSM 78247 shares with various extant and Mesozoic foot-propelled diving birds (e.g., Hesperornithiformes, Gaviidae, Podicipedidae). Subsequently, Agnolín et al. (2017) attributed SDSM 78247 to an indeterminate taxon within Vegaviidae, their newly-proposed clade of Gondwanan neognathous waterbirds that diversified in the Late Cretaceous and allegedly survived into the Paleocene. Agnolín et al. (2017) regarded SDSM 78247 as a member of Vegaviidae based on a suite of features that the specimen shares with the putative vegaviids *Polarornis gregorii* and *Vegavis iaai*. Agnolín et al.'s (2017) referral of several other Cretaceous and Paleogene taxa to Vegaviidae has recently been contested (Mayr et al., 2018). Here we provide the first detailed description and systematic comparison of SDSM 78247.

Systematic Paleontology

Aves Linnaeus, 1758
Galloanserae Sibley, Ahlquist, and Monroe, 1988
Anseriformes Wagler, 1831
Vegavis Clarke, Tambussi, Noriega, Erickson, and Ketcham, 2004
Species indeterminate

Referred Specimen: SDSM 78247, a partial left femur preserved in two pieces.

Locality and Horizon: Locality V2005-3, 'Plesiosaur Papoose,' Sandwich Bluff, Vega Island, Antarctic Peninsula. Base of the 'Reptile Horizon' of Case et al. (2000) (≈ Unit SBM12 of Roberts et al. [2014]; J.A. Case, pers. obs.) of the Upper Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation. See Roberts et al. (2014) for detailed stratigraphic information on the Sandwich Bluff site.

Description

SDSM 78247 is a largely complete left femur (Figs. 2, 3) that is preserved in two pieces; both ends are present but the middle portion of the shaft is missing. The proximal piece is 3.2 cm in length and 1.4 cm wide across the proximalmost portion of the shaft. The distal piece is 4.7 cm in length and 2.2 cm wide across the distal condyles. Though the femoral head and most of the femoral trochanter are not preserved, the latter was probably dorsoventrally narrow as estimated from its broken base. On the ventral surface of the proximal fragment, near the proximal end and immediately lateral to the broken base of the femoral head, there is a well-defined, circular proximoventral fossa (Fig. 3B, D). The insertion of the m. iliotrochantericus takes the form of a prominent quadrangular tubercle on the lateral side of the proximal end of the shaft (Fig. 3B, C). Overall, the proximal fragment of the femur is wider mediolaterally than deep dorsoventrally, though these dimensions become progressively more equal distally such that the broken distal end of the proximal fragment is subcircular in cross section. Although a portion of the shaft is missing, the femur was clearly markedly bowed dorsally.

The distal portion of SDSM 78247 is laterally compressed (i.e., deeper dorsoventrally than wide mediolaterally) and oval in cross section at its broken proximal end. The relative bone wall thickness (RBT, sensu Smith and Clarke, 2014) is approximately 36. There is a subtle distolateral scar located on the lateral face of the shaft at the approximate midlength of the distal piece (i.e., roughly three-fourths the estimated length of the femur from its proximal end; Fig. 3A–C). At approximately the same proximodistal level, the medial supracondylar crest expands into a massive, proximodistally elongate tuberosity that projects ventrally from the remainder of the femoral shaft (Fig. 3B). Distally, there is a broad, shallow patellar sulcus on the dorsal surface of the bone, and the region of the intercondylar sulcus is poorly preserved (Fig. 3A, F). The medial condyle is damaged, inhibiting comparisons with the lateral condyle. On the lateral condyle, the fibular trochlea is broad, laterally expansive, and strongly proximally deflected (Fig. 3B, C, F). Its lateral and medial margins are formed by the prominent but slightly weathered fibular and tibiofibular crests, respectively, with a broad, shallow, proximodorsally-directed groove occupying the space between these crests (Fig. 3B, C, F). There is a low medial epicondyle proximal to the medial condyle (Fig. 3A, B, D).

Comparisons

SDSM 78247 and *Vegavis iaai* share two features that were proposed by Clarke et al. (2016) to differentiate *Vegavis* from *Polarornis*. The first of these is the presence of a deep, round ligament scar on the proximoventral face. The new femur exhibits a condition similar to that of *V. iaai*: in both, this scar forms a round fossa with a distinct lip around at least the proximolateral margin (Fig. 4I, J). By contrast, this scar is shallow and poorly defined in anatids (e.g., *Mergus serrator*, *Anas platyrhynchos*, *Anser anser*) and absent in screamers (e.g., *Chauna torquata*) and galliforms (e.g., *Gallus gallus*, *Meleagris gallopavo*). The scar is present as a raised structure in other foot-propelled diving taxa such as loons (e.g., *Gavia stellata*) and grebes (e.g., *Aechmophorus occidentalis*, *Podilymbus podiceps*).

The new femur and *V. iaai* also share a elongate scar on the distolateral margin, a feature that is not observed in the holotypic specimen of *Polarornis gregorii* (Fig. 4A, B, E, F, I. J). A similar distolateral scar has been reported in a distal femur from the López de Bertodano Formation of Seymour Island that has been tentatively assigned to *Polarornis* (MLP 96-I-6-2; Acosta Hospitaleche and Gelfo, 2015; Agnolín et al., 2017; Mayr et al., 2018); however, this specimen is poorly preserved, and we were unable to assess the presence or form of this scar as it was originally figured. The presence, form, and position of this distolateral scar is highly variable across Neognathae. In *V. iaai* and SDSM 78247, the scar forms a single, low ridge that is positioned near the dorsal margin in lateral view and well proximal to the lateral condyle. Among anatids, this scar abuts the lateral condyle near the ventral margin in *Anas platyrhynchos* and *Anser anser*; in *M. serrator*, by contrast, it occupies a position similar to that seen in *V. iaai* but is bipartite, forming two distinct scars. A scar in this location is not observed in screamers (e.g., *C. torquata*) and galliforms (e.g., *G. gallus*, *M. gallopavo*). In other foot-propelled diving birds, this scar is present as two widely spaced tubercula either near the ventral margin (in crown-group loons) or near the midline (in grebes). However, a conspicuous raised scar in this location is absent in proposed stem loons (e.g., *Colymboides minutus*; Storer, 1956).

SDSM 78247 can easily be differentiated from the holotype and referred specimens of *V. iaai* (Clarke et al., 2005, 2016) by several features, including absolute size; the former is nearly twice the size of the femora of the latter two skeletons. Also, in SDSM 78247, the intersection between the lateral margin of the femoral shaft and the articular surface of the fibular trochlea appears abrupt rather than gradational in ventral view. In the new femur, the proximal part of the trochlea is rotated dorsally, generally a notch-like intersection (Worthy et al., 2017:character 220) (Fig. 4I). By contrast, in *V. iaai*, as well as in *P. gregorii*, the proximal margin of the fibular trochlea grades smoothly into the shaft (Fig. 4J, K). Additionally, the round proximoventral ligament scar of *Vegavis* is positioned near the midline in the new femur (Fig. 4I) but is closer to the lateral margin in *V. iaai* (Fig. 4J). Furthermore, in *V. iaai*, the margin of this fossa is encircled by a prominent lip, though this lip is least conspicuous medially. In the new femur, however, only the proximolateral margin of this fossa is bordered by a lip. The raised distolateral scar characteristic of *Vegavis* is better developed in *V. iaai* than SDSM 78247 (Fig. 4A, B, E, F, I, J), though this may be due to weathering of the latter. Finally, the bone wall of the new femur is proportionally thicker (RBT = 36) than in *V. iaai* (RBT = 21.6; Garcia Marsà et al., 2017).

Of the 290 characters in the phylogenetic data matrix of Worthy et al. (2017), 35 pertain to the femur, and 22 of these (i.e., 7% of the total character set) could be definitively scored in SDSM 78247. SDSM 78247 was scored identically to both *V. iaai* and *P. gregorii* for 21 of the 22 femoral characters in the Worthy et al. (2017) matrix that could be assessed in the new fossil.

These characters include: (188) a concave antitrochanteric articular face; (193) a lack of pneumatic openings on the ventral face adjacent to the antitrochanteric articular face; (194) the conformation of the obturator impression as a single large scar near the antitrochanteric articular face; (195) a weakly-developed scar for insertion of the medial part of the m. puboischiofemoralis; (198) a weakly-marked impression for the m. iliofemoralis internus; (199) an elongate shaft with subparallel medial and lateral margins; (200) a strongly dorsoventrally bowed shaft; (201) a relatively straight medial face in ventral view; (202) the position of the scar for insertion of the m. iliotrochantericus caudalis at mid-dorsoventral depth on the lateral face; (203) a distinct tuberosity at the point of convergence between the medial supracondylar crest and the ventral intermuscular line; (204) the position of the tuberosity of the medial crest at the medial margin of the ventral face; (205) orientation of the lateral condyle in dorsal view parallel with the shaft; (206) widely separated insertions for the m. obturatorius lateralis and the m. ischiofemoralis; (207) the m. gastrocnemialis lateralis tubercle forms a rugose scar on the lateral face proximodorsal to the fibular trochlea; (209) the presence of a distinct depression on the ventral face immediately proximal to the fibular trochlea; (211) the medial condyle comprises approximately half of the total width across the condyles; (213) the patellar sulcus is broad and flat in dorsal view; (214) the presence of a notch for the tendineus m. tibialis on the distal end of the lateral condyle; (215) a shallow popliteal fossa; (218) the medial supracondylar crest is short with a notched medial profile; (219) the fibular trochlea and lateral condyle extend equally distally; and (220) the proximal part of the articular surface of the fibular trochlea is rotated dorsally, forming a prominence that is markedly offset from the lateral face. Additionally, although the trochanteric crest in SDSM 78247 is missing, it was likely dorsoventrally narrow as in *V. iaai* and *P. gregorii*.

Although SDSM 78247 was originally assigned to Cariamiformes (Case et al., 2006), it differs markedly from the femora of all members of this clade; for example, no taxon within Cariamiformes possesses the distinct scars discussed above. The new femur also differs from *Cariama cristata* with respect to 11 of the 22 scorable characters from the Worthy et al. (2017) matrix, including the following states that are present in *C. cristata* but not in the new specimen: (195) the presence of a strongly developed scar for the insertion of the m. puboischiofemoralis pars medialis; (198) the impression for the m. iliofemoralis internus is a well-marked rugosity; (200) a shaft that is straight in lateral view; (203) the absence of a tuberosity in the area of convergence between the medial supracondylar crest and the ventral intermuscular line; (205) the lateral condyle oriented at an oblique angle relative to the shaft; (206) closely spaced areas of insertion for the m. ischiofemoralis; (207) the presence of the tubercle for the m. gastrocnemialis lateralis as a round scar near the fibular trochlea; (209) the absence of a distinct depression immediately proximal to the ventral articular surface of the fibular trochlea; (211) the medial condyle contributing more than half of the maximum mediolateral width across the condyles; (218) the lateral edge of the distal end of the shaft in ventral view is smoothly curving and continuous with the condyle; and (220) the fibular trochlea is ventrally directed, merging smoothly into the shaft. Additionally, the circular proximoventral fossa present in the new femur is absent in both *C. cristata* (which is convex in this area, lacking any depressions) and phorusrhacids (Alvarenga and Hofling, 2003). The distolateral scar present in SDSM 78247 is also absent in both *C. cristata* and phorusrhacids (Alvarenga and Hofling, 2003). Furthermore, in Cariamiformes, the patellar sulcus is deep and is bordered by sharp crests on the dorsal parts of the condyles (Alvarenga and Hofling, 2003). By contrast, in the new femur, the patellar sulcus is shallow and broad.

Discussion

The morphology of SDSM 78247 is consistent with its membership in *Vegavis*. This assertion is based on the identical scores of the new femur and *V. iaai* with respect to 20 of the 22 scorable characters from the phylogenetic data matrix of Worthy et al. (2017). SDSM 78247 also exhibits the circular proximoventral fossa that is synapomorphic of *Vegavis*, as well as the elongate distolateral scar that is diagnostic of *Vegavis* but not *Polarornis*. SDSM 78247 may be differentiated from *V. iaai* based on the one remaining scorable femoral character (the shape of the ventral condyle), as well the overall size of the element and the position and shape of the proximoventral fossa. These distinctions suggest that the new specimen likely represents a new species of *Vegavis*; however, this putative new form is, at present, too incompletely represented to warrant formally erecting a new taxon.

Of the four femoral character states proposed by Agnolín et al. (2017) as diagnostic for Vegaviidae that are scorable in SDSM 78247, the new femur is consistent with three: (1) dorsoventral bowing of the shaft; (2) the presence of a distinct fossa just proximal to the fibular trochlea; and (3) a broad and flat shape of the patellar sulcus. SDSM 78247 is inconsistent with the fourth proposed state, the presence of the obturator impressions as two separate, rugose scars. However, *V. iaai* is also inconsistent with this state (sensu Worthy et al. [2017] but contra Agnolín et al. [2017]). Thus, this conformation of the obturator impressions is likely not diagnostic of *Vegavis* + *Polarornis*.Our reassessment of the partial avian femur SDSM 78247 reveals the presence of a comparatively large-bodied and likely new *Vegavis* species from the latest Cretaceous of Vega Island, Antarctica, and unambiguously removes the only record of a cursorial bird (specifically Cariamiformes; Case et al., 2006) from the Mesozoic of that continent. Morphological comparisons presented herein ally SDSM 78247 more closely with *V. iaai* than with any other sampled taxon, and as such are consistent with the placement of the specimen within *Vegavis*. SDSM 78247 is distinguished from *V. iaai* both by morphology and by overall size; the new femur is closer in size to that of *P. gregorii*, though still considerably larger than that taxon as well.

The osteohistology of all previously described *Vegavis* (MLP 93-I-3-1, MACN-PV 19.748) and *Polarornis* (TTU P 9265) specimens indicates that these birds had reached adulthood, or nearly so, at the time of death (Chinsamy et al., 1998; Clarke et al., 2005, 2016; Garcia Marsà et al., 2017). As such, the much greater size of SDSM 78247 cannot be easily explained by ontogenetic variability, and instead suggests taxonomic distinction. The new femur exhibits *Vegavis*-like states of some characters that have been proposed to differentiate that genus from *Polarornis* (i.e., proximoventral fossa, distolateral scar; Clarke et al., 2016; Agnolín et al., 2017; Mayr et al., 2018). SDSM 78247 also has a much greater relative bone thickness than *V. iaai*, corresponding more closely to *P. gregorii* (RBT = 37; Chinsamy et al., 1998; de Mendoza and Tambussi, 2015) in this regard, but this may be a consequence of allometric considerations and/or functional scaling in aquatic/diving-specialized taxa. Extensive long bone osteosclerosis such as that observed in SDSM 78247 has been proposed as a correlate of diving specialization and it scales with positive allometry (e.g., Chinsamy et al., 1998; de Mendoza and Tambussi, 2015). The identification of SDSM 78247 as belonging to a previously unrecognized species within *Vegavis* substantially increases the known body size range of this taxon.

Conclusions

Our restudy of the isolated avian femur SDSM 78247 from the Upper Cretaceous López de Bertodano Formation of Antarctica—which was previously attributed to Cariamiformes, constituting the lone Cretaceous record of that clade—demonstrates that the specimen instead pertains to a close relative of the waterbird *Vegavis iaai*, known from the same locality. SDSM 78247 bears a strong morphological resemblance to the femur of *V. iaai* but is much larger than both this taxon and *Polarornis gregorii*, which is known from penecontemporaneous deposits on nearby Seymour Island. The refutation of SDSM 78247 as a member of Cariamiformes has important paleobiogeographical implications. The geographical connectivity and the timing of exchange between faunas from South America and other parts of the globe during the Mesozoic and Cenozoic remain contentious (e.g., Mayr, 2009). However, this proposed cariamiform record from the Cretaceous of Antarctica—which was formerly the most ancient, globally—no longer requires an explanation. The earliest records of Cariamiformes instead consist of forms from the Paleogene of Europe and a tentatively referred specimen from South America (Mayr, 2009; Mayr et al., 2011).

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Figure 1(on next page)

Map of Vega Island, Antarctica, modified from Roberts et al. (2014).

Star indicates approximate location of Sandwich Bluff, the si te that yielded the avian femur (SDSM 78247) described herein.

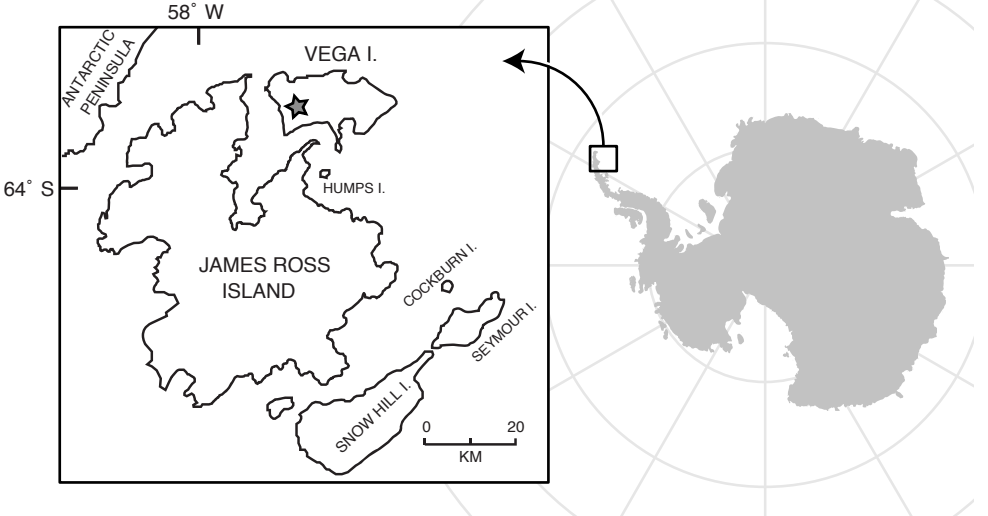
58˚ W
64˚ S
ANTARCTIC PENINSULA
VEGA I.
HUMPS I.
JAMES ROSS ISLAND
COCKBURN I.
SEYMOUR I.
SNOW HILL I.
0
20
KM

Figure 2

Photographs of left femur of *Vegavis* sp. (SDSM 78247).

Proximal fragment in (A) dorsal, (B) ventral, (C) lateral, (D) medial, and (E) proximal views; distal fragment in (F) dorsal, (G) ventral, (H) lateral, (I) medial, and (J) distal views. Arrows in E and J indicate dorsal (top of image) and medial (left side of image) directions.

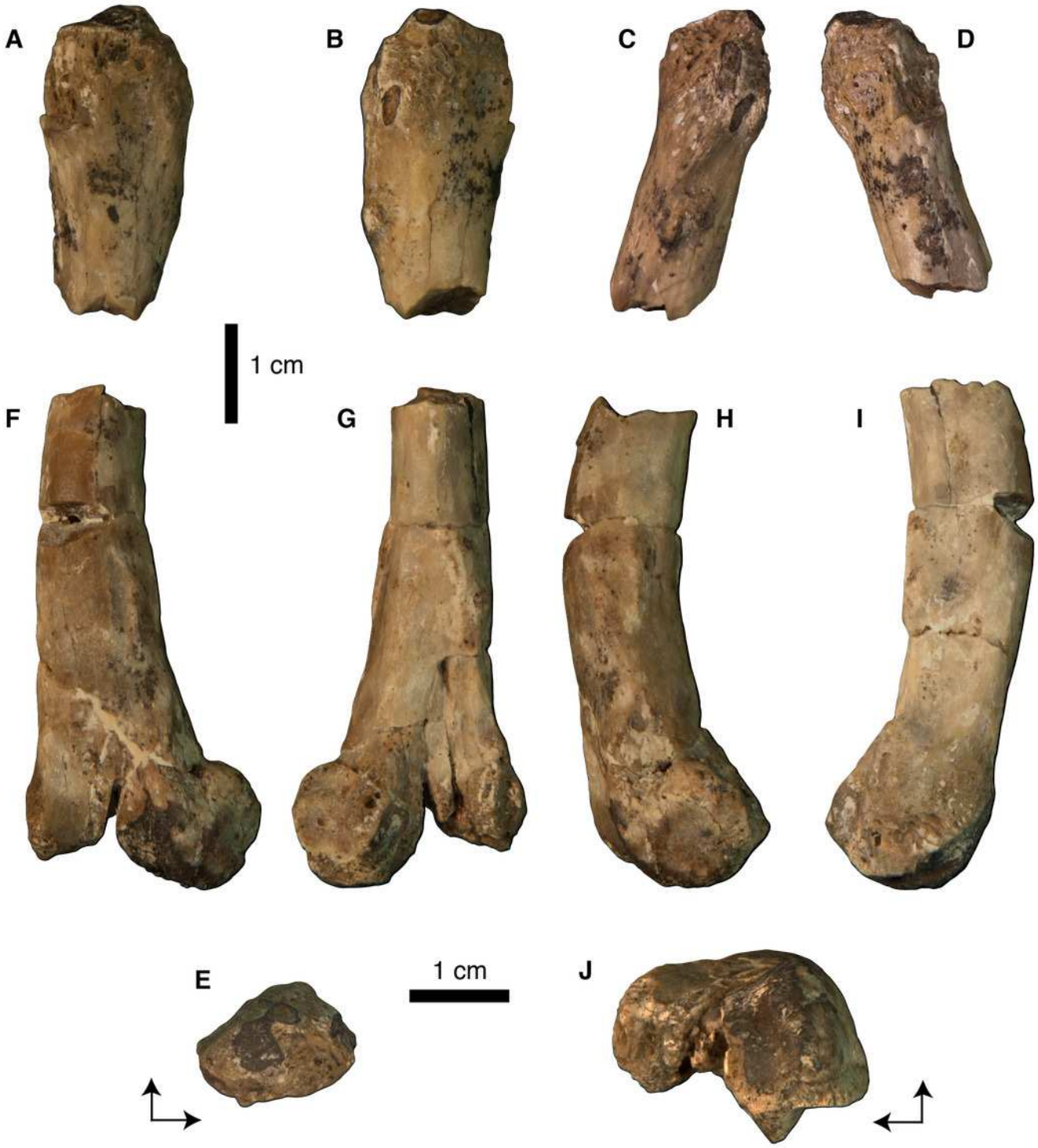
A
B
C
D
1 cm
F
G
H
I
E
1 cm
J

Figure 3(on next page)

Line drawings of left femur of *Vegavis* sp. (SDSM 78247).

(A) dorsal, (B) ventral, (C) lateral, (D) medial, (E) proximal, and (F) distal views. Arrows in E and F indicate dorsal (top of image) and medial directions. Hatching indicates worn or broken areas. Abbreviations: af, antitrochanteric face; ds, distolateral scar; fc, fibular crest; ft, fibular trochlea; ftc, fovea for insertion of tendineus m. tibialis cranialis; imi, insertion for m. iliotrochantericus; lc, lateral condyle; mc, medial condyle; msc, medial supracondylar crest; pf, proximoventral fossa; pop, popliteal fossa; ps, patellar sulcus; tfc, tibiofibular crest; tmg, tubercle for insertion of m. gastrocnemialis. Scale bar = 1 cm.

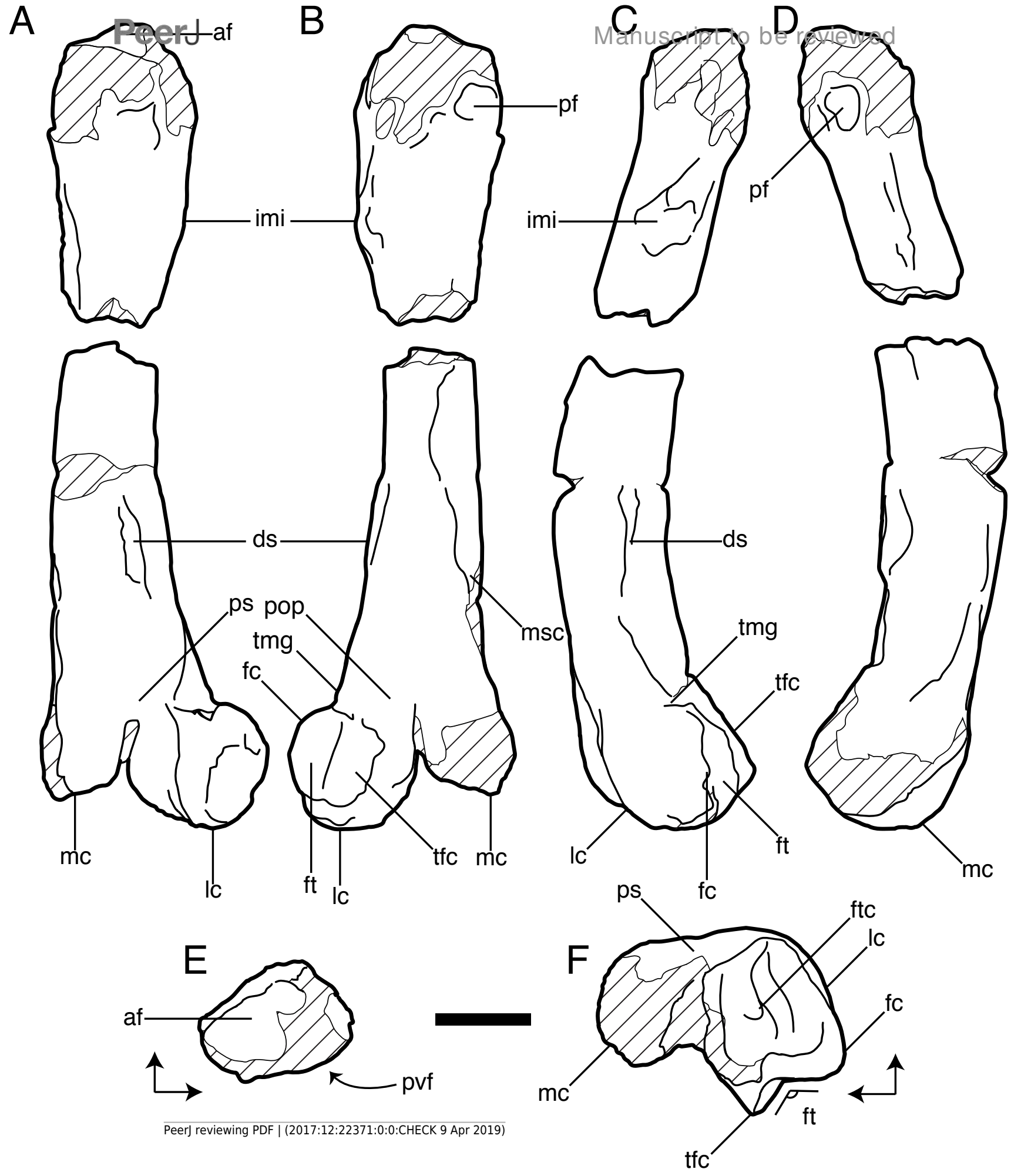

Figure 4

Comparison of left femora.

(A, E, I, M, P) *Vegavis* sp. (SDSM 78247), (B, F, J, N, Q) *Vegavis iaai* (cast of MACN-PV 19.148, reversed), (C, G, K) *Polarornis gregorii* (TTU P 9245, from Agnolín et al., 2017:fig. 1m, n, o), (D, H, L, O, R) and *Cariama cristata* (TMM M-10446), in dorsal (A–D), lateral (E–H), ventral (I–L), medial (M–O), and distal (P–R) views. Abbreviations as in Fig. 3 except: h, femoral head; is, intercondylar sulcus; le, lateral epicondyle; me, medial epicondyle; t, femoral trochanter. Scale bar = 1 cm.