New insights about *Hinasuri nehuensis* (Aves, Rheidae, Palaeognathae) from the early Pliocene of Argentina

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Hinasuri nehuensis Tambussi was a robust, extinct rheid bird from the early Pliocene of Buenos Aires province, Argentina. This paper revisits the femoral morphology of *H. nehuensis* and provides an updated osteological description together with new insights into its palaeobiology. Size estimates and a comparison of standardized measurements relative to *Rhea americana* demonstrate that *H. nehuensis* had an above-average body mass. The femoral dimensions of *H. nehuensis* were also proportionately greater than those of *R. americana*, but its reconstructed musculature is otherwise very similar. This suggests that *H. nehuensis* had powerful proximal muscles consistent with its enlarged size. This could have been an advantage for avoiding predators and to tolerate the seasonally harsh environments of the Pampean region during the Pliocene–Pleistocene.

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RHEIDAE is today represented by two species: *Rhea americana* and *Pterocnemia pennata*, which are the largest flightless birds in South America (Folch 1992). These species are cursorial and possess elongate, massive hindlimbs with powerful musculature (Folch 1992, Picasso 2010, 2014). Several extinct rheids have been discovered in Paleogene and Neogene deposits of Argentina and Brazil. Indeterminate pedal phalanges (Tambussi 1995) are known from the lower Eocene Las Flores Formation (Río Chico Group) of Patagonia, Argentina (Raigemborn *et al*. 2010, Woodburne *et al*. 2014). The Brazilian material includes *Diogenornis fragilis* Alvarenga, 1983 from Itaboraian sediments considered to be early Eocene in age (Woodburne *et al*. 2014); however, this taxon might be more closely related to casuariids (Alvarenga 2010). The Argentinian Neogene record incorporates *Opisthodactylus patagonicus* Ameghino, 1891 and *Opistodactylus* sp. from the Miocene Santa Cruz and Chinchinales formations of Patagonia (Ameghino 1891, Agnolin & Chafrat 2015). Another undetermined species of *Opistodactylus* occurs in the upper Miocene (Huayquerian) of Tucumán province in northwestern Argentina (Noriega & Vezzosi 2011). *Pterocnemia* is present in the upper Miocene Cerro Azul Formation of the Pampean region (Cenizo *et al*. 2012), and *Pterocnemia mesopotamica* has been described recently from the Miocene Ituzaingó Formation of the Mesopotamian region, and Aisol Formation of Mendoza province (Agnolin & Noriega 2012). Pliocene (early Pliocene: Deschamps *et al*. 2012, Tomassini *et al*. 2013) Pampean taxa are represented by *Heterorhea dabbenei* Rovereto, 1914 and *Hinasuri nehuensis* Tambussi, 1995 from the Monte Hermoso Formation of Buenos Aires province, Argentina. *Hinasuri nehuensis* is documented from a single left femur that is characteristically robust. This taxon was described as part of a revision of extinct Rheidae from Argentina (Tambussi 1995), but several aspects of its morphology were not thoroughly dealt with. The holotype femur (MLP 86-VI-21-1) is, however, well preserved and nearly complete, allowing estimation of body mass based on mid-shaft circumference (Campbell & Marcus 1992) and a reconstruction of musculature based on closely related taxa (Bryant & Seymour 1990); in particular the hindlimb of *Rhea americana* (Picasso 2010).

This study revisits the femoral morphology of *Hinasuri nehuensis* in order to: (1) provide an updated detailed anatomical description; (2) attempt a reconstruction of the muscles of the femur; and (3) estimate body mass of the species and assess its palaeobiological implications.

Materials and methods

Osteological and myological terminology follows Baumel *et al*. (1993). Body mass was estimated

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Authors	*a*	*b*	R^2	Method	Body mass estimation of *H. nehuensis*
Dickison (2007)	0.625	2.46	0.89	Ordinary least square	35.77 kg
Campbell & Marcus (1992, table 3, subgroup "LL")	–0.14	2.44	0.95	Ordinary least square	38.25 kg

Table 1. Parameters of selected allometric equations, log y = log a + $b$log x (expressed as linear functions of log-transformed data), were y = body mass, x = femur circumference, a = intercept, b = slope, R^2 = correlation coefficient.

(Table 1) using the measurement parameters and allometric equations of Campbell & Marcus (1992) and Dickison (2007). These models contrasted a heterogeneous dataset of ratites together with species of Ciconiidae, Aramidae, Phoenicopteridae, Ardeidae, Plataleidae, Cochleridae, Scopidae, Rallidae, Gruidea, Otididae and Burhinidae; and an allometric series of ratites, respectively. The proportions of MLP 86-VI-21-1 were also compared across eight standardized femoral measurements (taken with a 300 mm, 0.01 mm precision digital caliper: Fig. 1) from a sample of the extant Greater Rhea, *Rhea americana* (n=9; Table 2). Arithmetic mean, standard deviation and 95% confidence intervals were calculated for both species samples. Qualitative observations were based on examples of the Greater Rhea (specimens of Table 2) and Lesser Rhea, *Pterocnemia pennata* (MLP-O-662, MLP-PV-411, MACN 01, 04).

Institutional abbreviations. MLP-PV, Colección de la División Paleontología Vertebrados Museo de La Plata, Buenos Aires, Argentina; MLP-O, Colección Ornitológica de la División Zoología Vertebrados del Museo de La Plata, Buenos Aires, Argentina; MLP-PV, Colección Anexa de la División Paleontología Vertebrados, Museo de La Plata, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

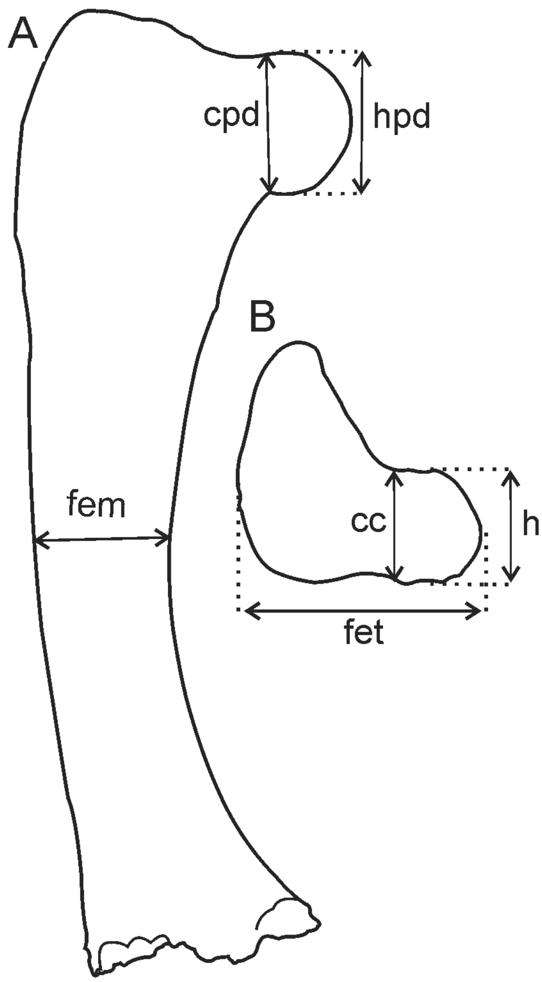

Fig. 1. Schematic drawing of femur of *Hinasuri nehuesnsis* showing the femoral measures taken. **A**, Caudal view; **B**, proximal view of the proximal end. Abbreviations: Fet = latero-medial width of proximal femoral end, between laterally surface of trochanter and caput femoris; Hc = cranio-caudal width of caput femoris; Hpd = proximo-distal width of caput femoris; Cc = cranio-caudal width of collum femoris; Cpd = proximo-distal width of collum femoris; Fem = latero-medial diameter of corpus femoris; Fed = antero-posterior diameter of corpus femoris (not shown); Cir = circumference of corpus femoris (not shown).

Systematic palaeontology

PALAEOGNATHAE Pycraft, 1900
RHEIFORMES (Forbes, 1884)
RHEIDAE Bonaparte, 1849

Hinasuri nehuensis Tambussi, 1995

Referred material. MLP 86-VI-21-1 (Fig. 2A–E).

Updated description. MLP 86-VI-21-1 lacks only the extremitas distalis, trochanter femoris and a small portion on the proximal region of the shaft (Fig. 2A, B). The shaft is otherwise curved in cranial view (Fig. 2A). The spherical caput femoris has a wide facies articularis acetabularis, and shallow and irregular fovea ligamentus capitis (Fig. 2B–D). The trochanter femoris is not preserved, but the end of the crista trochanterica is present (Fig. 2B), and has a rim that gradually merges into the femoral shaft. A short and wide collum femoris and part of the facies articularis antitrochanterica are evident in proximal view (Fig. 2C); the latter is broad cranially but narrows towards the caudal end. Rugosities mark the impressiones obturatoriae and impressiones trochanteris proximally (Fig. 2A, E). The corpus femoris has a convex

	MLP 876	MLP 877	MLP 879	MLP 880	MLP 881	MLP 273	MLP 650	MLP 666	MLP 903
Fet	51.83	50.63	48.43	47.60	47.75	47.49	53.29	57.32	46.55
Fem	25.80	22.13	24.65	17.39	20.29	21.47	24.90	27.04	20.59
Fed	24.93	25.37	22.70	21.14	24.14	24.05	21.26	20.12	20.94
Hpd	22.65	25.50	21.81	20.33	22.05	26.03	25.49	27.01	23.15
Hlm	23.87	23.90	20.83	20.70	22.50	22.61	23.13	27.37	23.39
Cc	19.81	22.88	23.20	19.65	23.41	25.56	24.37	26.33	19.62
Cpd	22.78	21.82	20.03	17.18	20.65	21.06	20.32	23.85	23.10
Cir	76.00	75.00	68.00	62.00	72.00	74.00	72.00	80.00	68.00

Table 2. Femur measurements (mm) of *Rhea americana* specimens

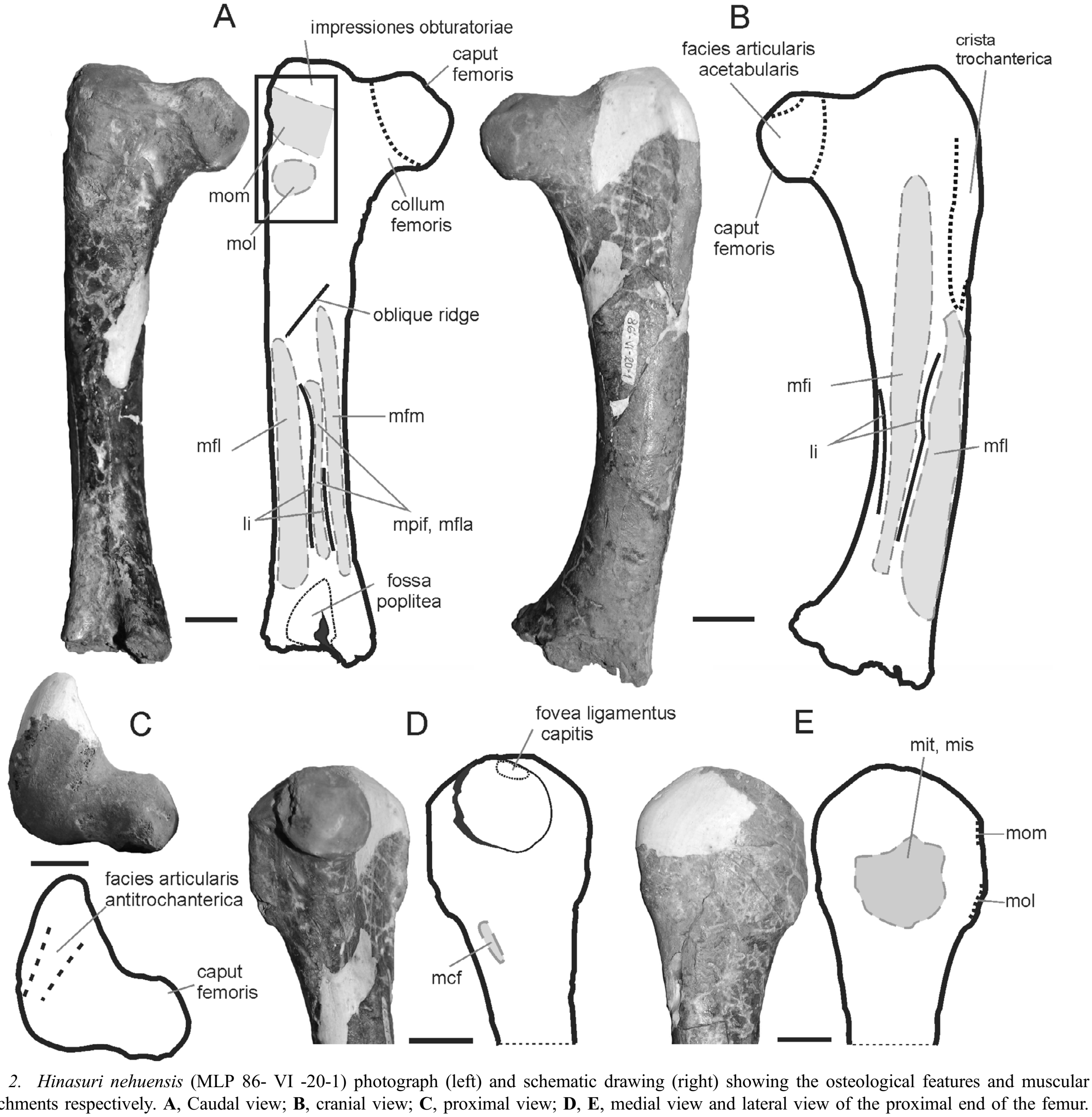

Fig. 2. Hinasuri nehuensis (MLP 86- VI -20-1) photograph (left) and schematic drawing (right) showing the osteological features and muscular attachments respectively. **A**, Caudal view; **B**, cranial view; **C**, proximal view; **D**, **E**, medial view and lateral view of the proximal end of the femur. Abbreviations: li = linea intermuscularis; mom = muscle obturatorius medialis; mol = muscle obturatorius lateralis; mfl = muscle femortibialis lateralis; mfi = muscle femorotibialis intermedius; mfm = muscle femorotibialis medialis; mpif = muscle puboischiofemoralis; mfla = muscle flexor cruris lateralis; mcf = muscle caudofemoralis; mis = muscle ischiofemoralis; mit = muscles iliotrochanterici (caudalis, cranialis, medialis). Scale bar = 20 mm.

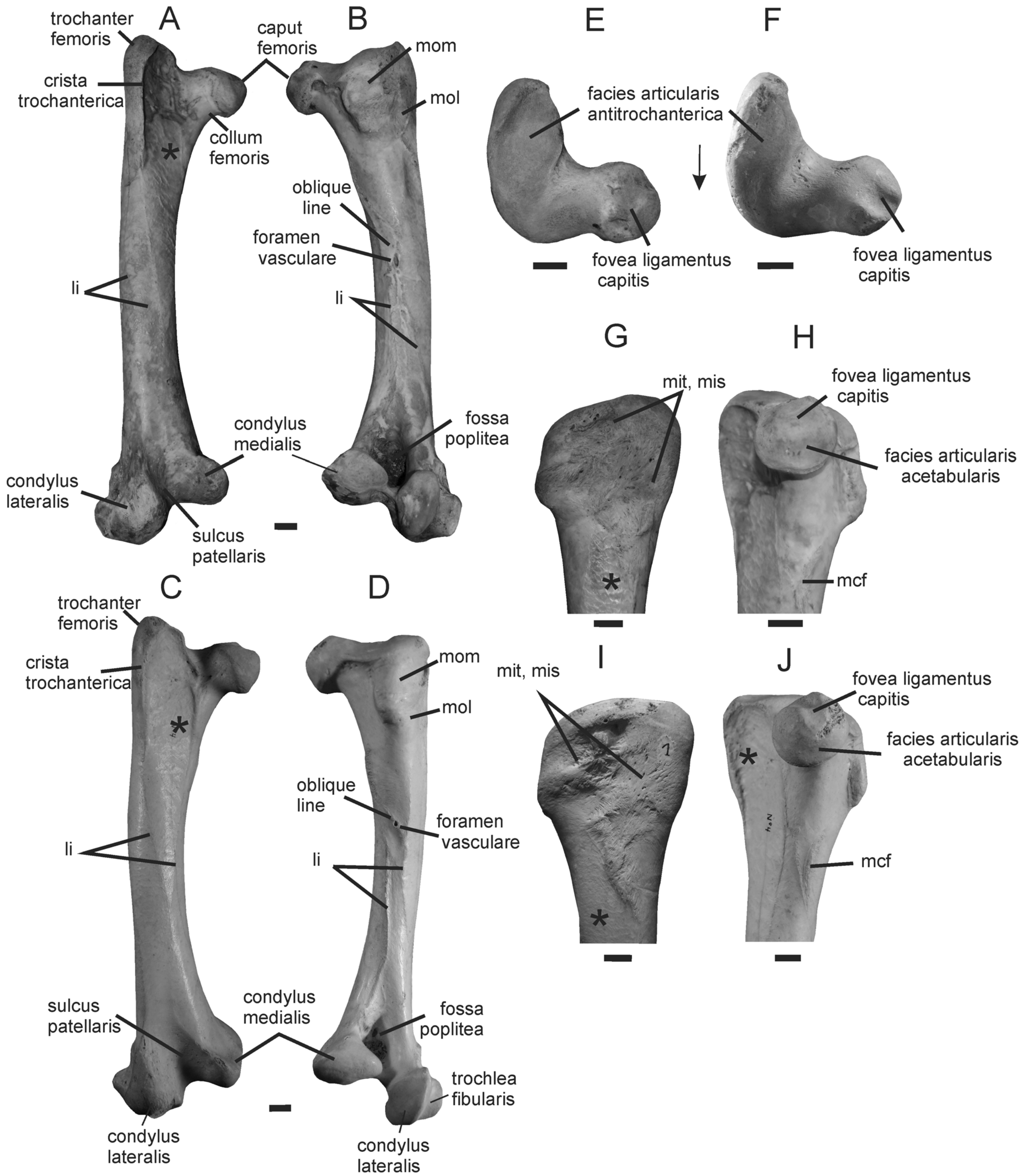

Fig. 3. Femur of *Rhea americana* (A, B, E, G, H, MLP 903) and *Pterocnemia pennata* (C, D, F, I, J, MACN 1, 4). **A**, **C**, Frontal view; **B**, **D**, Caudal view; **E**, **F**, Proximal view of the femoral head and trochanter; **G**, **I**, Lateral aspect of the proximal region; **H**, **J**, Medial aspect of the proximal region. Arrows indicates cranial aspect. Abbreviations: li = linea intermuscularis; mom = muscle obturatorius medialis; mol = muscle obturatorius lateralis; mcf = muscle caudofemoralis; mis = muscle ischiofemoralis; mit = muscles iliotrochanterici (caudalis, cranialis, medialis). Asterisks (*) indicate smooth/ripple bone surface associated with attachment of *femorotibialis* muscle group (see text). Scale bar = 10 mm.

facies cranialis, whereas its facies caudalis is flattened. Several lineae intermusculares are present; there are paired medial and lateral ridges in the facies cranialis (Fig. 2B). Two lineae intermusculares are observable in the facies caudalis (Fig. 2A). They are proximodistally oriented and merge with the shaft distally. Finally, a short oblique ridge (Fig. 2A) can be distinguished caudally. A portion of the fossa poplitea is visible at the distal end (Fig. 2A).

Comparisons (Fig. 2A–E) with extant species (Fig. 3A–J) reveal numerous morphological similarities: a wide and short collum femoris (Fig. 3A–F); spherical caput femoris with a wide facies articularis acetabularis and irregular contour of the fovea ligamentum capitis (Fig. 3H–J); and overall structural compatibility in the crista trochanterica (Fig. 3A, B), corpus femoris and the muscular impressions of the lineas intermuscularis (Fig. 3A–D), iliotrochanterici and obturatoriae (Fig. 3G, I). The caudal portion of the crista trochanterica in MLP 86-VI-21-1 (Fig. 2B) and those of the facies articularis antitrochanterica (Fig. 2C) are also virtually identical (Fig. 3A, C, E, F).

Reconstruction of musculature. The impressiones obturatoriae are conspicuous broad scars that mark the m. obturador medialis tendon attachment (Fig. 2A, E). Adjacent to this is a blunt protrusion for the m. obturatorius lateralis (Fig. 2A, E). In medial view, a rough protuberance supported the m. caudofemoralis (Fig. 2D). Laterally, the extremita proximalis bears a broad, roughened depression (Fig. 2E) for the mm. iliotrochanterici (=m. i. caudalis, m. i. cranialis, m. i. medialis) and m. ischiofemoralis. Insertions for the m. iliofemoralis externus and m. iliofemoralis internus could not be identified in either MLP 86-VI-21-1 or specimens of *R. americana*. On the corpus femoris, the lineae intermusculares demarcates the boundary between components of the mm. femorotibialis (=m. f. lateralis, m. f. medialis and m. f. intermedius). The m. femorotibialis medialis and m. f. intermedius attach to the caudal and medial surfaces of the shaft (Fig. 2A, B); the m. femorotibialis lateralis inserts on the lateral surface (Fig. 2B). In caudal view (Fig. 2A), the osseous area between the lineae intermusculares corresponds to the site of attachment of the m. flexor cruris lateralis (pars accessoria) and m. puboischiofemoralis; however, their delineations could not be distinguished.

Femoral dimensions and estimated body mass. The femur of *H. nehuensis* was proportionately larger than that of *Rhea americana* (Fig. 4, Table 3), with all dimensions falling outside confidence intervals (Table 3). The body mass of *H. nehuensis* (Table 1) was calculated at 38.25 kg using the Campbell & Marcus (1992) equation, versus 35.77 kg from Dickison (2007).

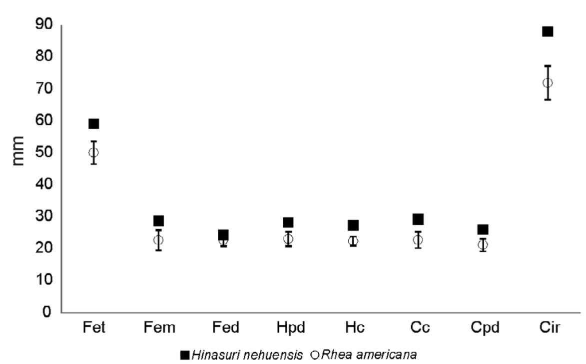

Fig. 4. Scatter plot showing the measurements of *Hinasuri nehuensis* and the mean and standard deviation for measurements of *Rhea americana*. Abbreviations: Fet = latero-medial width of proximal femoral end, between lateral surface of trochanter and caput femoris; Hc = cranio-caudal width of caput femoris; Hpd = proximo-distal width of caput femoris; Cc = cranio-caudal width of collum femoris; Cpd = proximo-distal width of collum femoris; Fem = latero-medial diameter of corpus femoris; Fed = antero-posterior diameter of corpus femoris (not shown); Cir = circumference of corpus femoris (not shown).

		Fet	Fem	Fed	Hpd	Hc	Cc	Cpd	Cir
H. nehuensis		59.05	28.7	24.35	28.29	27.3	29.27	26.08	88
R.americana	**M**	50.10	22.70	22.74	23.06	22.40	22.76	21.20	71.89
(*n* = 9)	**SD**	3.53	3.11	1.94	2.24	1.40	2.55	2.00	5.30
	IC	2.71	2.39	1.49	1.72	1.08	1.96	1.54	4.08
		(47.39–52.81)	(20.30–25.09)	(21.24–24.23)	(21.34–24.78)	(21.32–23.48)	(20.80–24.72)	(19.66–22.74)	(67.81–75.96)

Table 3. Femur measurements (mm) of *Hinasuri nehuensis* and the mean (M), standard deviation (SD) and 95% interval of confidence (IC) and their confidence limits between brackets. Abbreviations: Fet = latero-medial width of proximal femoral end; Fem = latero-medial diameter of corpus femoris; Fed = antero-posterior diameter of corpus femoris; Hc = cranio-caudal width of caput femoris; Hpd = proximo-distal width of caput femoris; Cc = cranio-caudal width of collum femoris; Cpd = proximo-distal width of collum femoris; Cir= circumference of corpus femoris.

Discussion

Muscular reconstruction in fossils is problematic because there is no direct relationship between bone relief and muscular attachment (McGowan 1979, Bryant & Seymour 1990, Hutchinson 2001, Petermann & Sander 2013). Nevertheless, the compatible femoral morphology of *H. nehuensis* and *R. americana* infers massive proximal muscles and large body mass in the former extinct taxon.

The insertion points of eight muscles or muscle groups were identified, out of the 15 that have their attachment at the proximal end and shaft of the femur in *Rhea americana* (Picasso 2010). Those muscles with tendinous attachments, such as the m. obturatorius medialis, m. o. lateralis, mm. iliotrochanterici (=m. i. caudalis, m. i. cranialis, m. i. medialis) and the m. ischiofemoralis, are associated with roughened areas and scars, some of them remarkably prominent (e.g., the m. obturatorius lateralis). Other muscle insertions were more depressed (e.g., the mm. iliotrochanterici). Poor definition of the m. ischiofemoralis, mm. iliotrochanterici, m. iliofemoralis internus and m. i. externus might be a consequence of the small size of these muscles, as evidenced by *R. americana* (Picasso 2010). The mm. femorotibiales are likewise indistinct, but can be positioned approximately by the lineas intermuscularis (Hutchinson 2001). These also have a fleshy origin in extant birds (George & Berger 1966) and are thus associated with smooth bone (Bryant & Seymour 1990, Hutchinson 2001, Petermann & Sander 2013). Insertion of the m. caudofemoralis is partly fleshy and tendinous in *R. americana* (Picasso 2010); the corresponding scar is rugose in both this taxon and *Hinasuri nehuensis*.

Hinasuri nehuensis was a large member of the Rheidae. Its body mass estimate of 35 kg is substantially greater than the average of 23 kg for *Rhea americana* (Davies 2000, Dunning 2008). Body size affects many aspects of an animal's life, including structure, ecology and physiology, which can vary substantially between small- and large-bodied species and/or individuals (Maurer *et al*. 1992, Purvis & Orme 2005). Large size offers advantages for predator avoidance and increased tolerance to environmental change via the capacity to obtain nutrients from poorer quality aliment (Maurer *et al*. 1992, Purvis & Orme 2005). These factors might have similarly influenced body mass increase in *H. nehuensis*, which lived at a time of increasingly extreme temperatures and decreased precipitation in the Pampean region during the Pliocene–Pleistocene (Rabassa *et al*. 2005). The coeval occurrence of cariamid birds and myrmecophagid anteaters (Tonni 1974) in the early Pliocene indicates conditions resembling those of the Chacoan Province today (Tonni 1974); this is characterized by grassland savannas and steppes with xerophytic forests and seasonally semi-arid climates with harsh summers (Morrone 2001, Werneck 2011). The size of *H. nehuensis* would have likewise been beneficial for escaping all but the largest carnivorous mammals, including *Parahyaenodon argentines*, which is preserved in the Monte Hermoso Formation (see Forasiepi *et al*. 2007, Tomassini *et al*. 2013).

Disclosure statement

No potential conflict of interest was reported by the authors.

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