

A stem falconid bird from the Lower Eocene of Antarctica and the early southern radiation of the falcons

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Abstract *Antarctoboenus carlinii* nov. gen. nov. sp. is a large-sized falconiform bird from the La Meseta Formation (Lower Eocene) at Seymour (Marambio) Island, West Antarctica. The holotypical tarsometatarsus was originally assigned to Falconidae and its affinities to Polyborinae were pointed out. Detailed osteological and comparative analyses of the Antarctic specimen allowed recognition of the new taxon as a member of stem group Falconidae, i.e. it is supposed to belong to the early radiation of the falconiform lineage. *Antarctoboenus carlinii* is distinguished from members of crown group Falconidae by having a very shallow sulcus extensorius, a large foramen vasculare distale, an undistinguishable tendinal attachment for the m. adductor digiti II, and short trochlea metatarsi II, among its main diagnostic characters. Purported phylogenetic relationships between *A. carlinii* and Polyborinae are based on plesiomorphic characters retained in the tarsometatarsus of the latter clade. Our conclusions reinforce the hypothesis

about the Neotropical or Austral origin of Falconidae supported by previous molecular phylogenies.

Keywords Fossil bird · Falconiformes · Paleogene · Seymour Island · Stem lineage · *Antarctoboenus carlinii*

Zusammenfassung

Ein der Stammgruppe Falconidae angehörender Vogel aus dem Untereozän der Antarktis und die frühe südliche Radiation der Falken

Antarctoboenus carlinii nov. gen. nov. sp. ist ein großer falkenartiger Vogel aus der La Meseta Formation (Untereozän) auf der Seymour-Insel (Isla Marambio) in der Westantarktis. Der Holotyp-Tarsometatarsus wurde ursprünglich den Falconidae (Falkenartigen) zugeordnet, und seine Ähnlichkeiten mit den Polyborinae (Geierfalken) wurden hervorgehoben. Detaillierte osteologische und vergleichende Analysen des Antarktis-Exemplars ermöglichten es, das neue Taxon als ein Mitglied der Stammgruppe Falconidae anzuerkennen, d.h. es gehört vermutlich der frühen Radiation der Falconiformes-Abstammungslinie an. *Antarctoboenus carlinii* unterscheidet sich von den Mitgliedern der Kronengruppe Falconidae durch mehrere diagnostische Merkmale, u.a. einen sehr flachen sulcus extensorius, ein großes foramen vasculare distale, einen undeutlichen Sehnenansatz für den m. adductor digiti II und kurze trochlea metatarsi II. Angebliche phylogenetische Beziehungen zwischen *A. carlinii* und Polyborinae basieren auf plesiomorphen Merkmalen, die im Tarsometatarsus der Polyborinae erhalten sind. Unsere Schlussfolgerungen stärken die Hypothese eines Neotropen- oder Austral-Ursprungs der Falconidae, die auch von bisherigen molekularen Stammbäumen gestützt wird.

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Introduction

The avian family Falconidae constitutes a group of small to medium-sized diurnal raptors whose monophyly is strongly supported (e.g. Griffiths et al. 2004; Wink and Sauer-Gürth 2004; Fuchs et al. 2015). It is accepted that the family radiation comprised three major clades, generally recognized at subfamilial rank: *Herpetotherinae*, *Polyborinae*, and *Falconinae* (Griffiths 1999; Griffiths et al. 2004; Fuchs et al. 2011, 2012, 2015; Noriega et al. 2011). The *Herpetotherinae* includes the Forest Falcons of the genus *Micrastur* and the monotypic *Herpetotheres cachinnans* commonly known as Laughing Falcon. The *Polyborinae* comprises the Caracaras (i.e. *Caracara*, *Phalcoboenus*, *Ibycter*, *Daptrius*, and *Milvago*) and the Spot-winged Falconet *Spizapteryx circumcincta*. Finally, the *Falconinae* includes the Old World Falconets *Microhierax* and the Pygmy-falcons *Polihierax*, together with true falcons and allies belonging to the genus *Falco*.

With the exception of the almost worldwide distribution of *Falco* and the Afro-Asian range of *Polihierax* and *Microhierax*, the remaining diversity of falconids is concentrated in the Neotropics (Olson 1976; White et al. 1994; Ferguson-Lees and Christie 2001; Fuchs et al. 2015). This fact led to the consideration that most of their evolutionary history occurred in South America and that the *Falconinae* had derived from primitive neotropical forms (Olson 1976; Ericson 2012). However, the scarce paleogene fossil record for the group does not bring conclusive evidence to support the purported Neotropical or Austral origin of its main clades (White et al. 1994; Feduccia 1996).

Tambussi et al. (1995) reported the presence of a probable *Polyborinae* at Lower Eocene deposits in Antarctica (Fig. 1) in a brief abstract, but although it constituted a relevant finding because of its geographic provenance and age, the material has never been thoroughly analyzed, nor figured or formally described. Herein, we make an exhaustive revision and comparative study of the Antarctic specimen, proposing a new phylogenetic position of this taxon with respect to extant and extinct falconid lineages.

Materials and methods

Institutional abbreviations

BMNH	British Museum of Natural History, London, UK
CFA-OR	Ornithological Collection, Fundación de Historia Natural “Félix de Azara”, Buenos Aires, Argentina

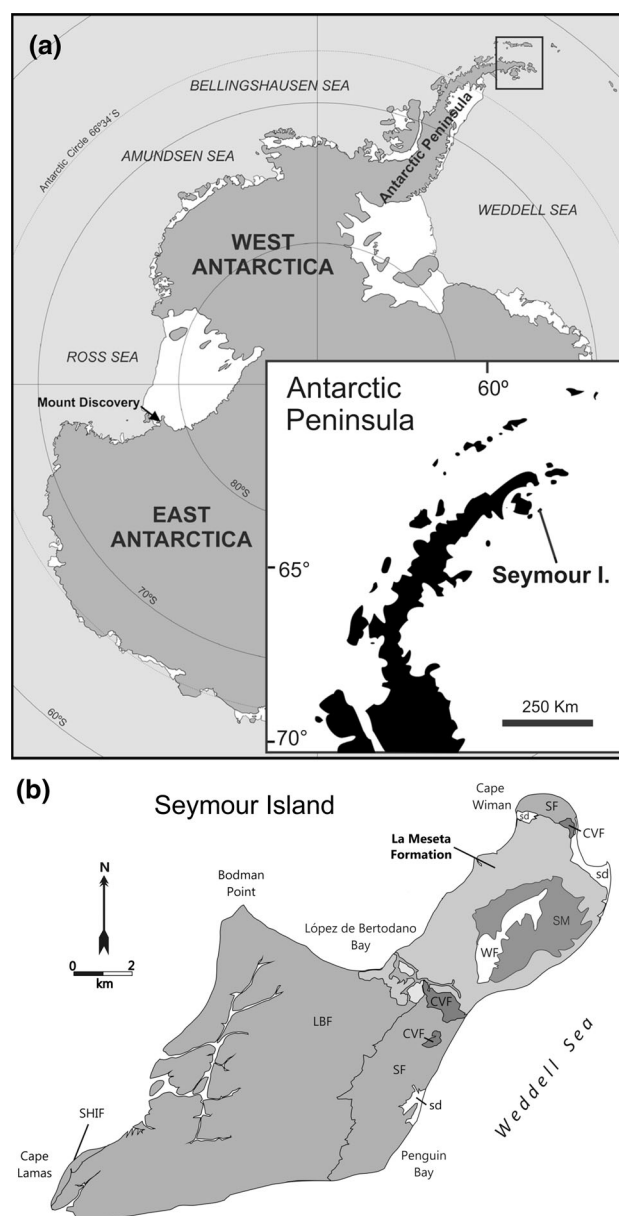


Fig. 1 **a** Geographical location of Seymour Island in Antarctic Peninsula (West Antarctica). **b** Geological map of Seymour Island indicating the outcrops of La Meseta Formation. Other stratigraphic units are also indicated: *CVF* Cross Valley Formation, *LBF* López de Bertodano Formation, *SF* Sobral Formation, *SM* Submeseta Formation, *WF* Weddel Formation, *sd* surficial deposits

MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MHNT	Museu de História Natural de Taubaté, Taubaté, Brazil
MLP	Museo de La Plata, La Plata, Argentina
MPM-PV	Paleontological Collection, Museo Regional Provincial “Padre M. J. Molina”, Río Gallegos, Santa Cruz, Argentina

Comparisons included the following living species deposited at CFA-OR, MACN, and MHNT collections: *Accipiter striatus*, *Rupornis magnirostris*, *Buteo polyosoma*, *Parabuteo unicinctus*, *Cariama cristata*, *Chunga burmeisteri*, *Micrastur ruficollis*, *M. semitorquatus*, *Herpetotheres cachinnans*, *Spizapteryx circumcincta*, *Polyborus plancus*, *Milvago chimango*, *M. chimachima*, *Phalcoboenus albogularis*, *P. australis*, *Polihierax semitorquatus*, *Falco mexicanus*, *F. rusticolus*, *F. peregrinus*, *F. tinnunculus*, *F. columbarius*, *F. femoralis*, and *F. sparverius*. Holotypical specimens and additional materials of the following extinct falcons were also compared: *Thegornis musculosus* (BMNH-A600, MPM-PV-3443; Santa Cruz Formation, Lower Miocene, Santa Cruz Province, Argentina; see Ameghino 1895; Noriega et al. 2011), *T. debilis* (BMNH-A601; Santa Cruz Formation, Lower Miocene, Santa Cruz Province, Argentina; see Ameghino 1895; Noriega et al. 2011), and *Badiostes patagonicus* (BMNH-A602; Santa Cruz Formation, Lower Miocene, Santa Cruz Province, Argentina; see Ameghino 1895; Noriega et al. 2011). Data from other Miocene taxa as *Pediohierax ramenta* and *Falco hezhengensis* were extracted from their published descriptions and figures (Wetmore 1936; Becker 1987; Li et al. 2014).

The measurements are in millimeters and were taken with a Vernier caliper of 0.01 mm of resolution. Osteological nomenclature follows Baumel and Witmer (1993).

Results

Systematic palaeontology

Class Aves LINNAEUS 1758
 Order Falconiformes SHARPE 1874
 Family Incertae sedis
 Genus *Antarctoboenus* nov.

Type species *Antarctoboenus carlinii*

Diagnosis Large-sized falconiform bird, similar to *Polyborus plancus* in overall dimensions. The following characters distinguish it from other extinct or extant taxa of the crown group Falconidae: (1) distal end of sulcus extensorius very shallow; (2) dorsal opening of the foramen vasculare distale large; (3) tendinal attachment for m. adductor digiti II undistinguishable; (4) trochlea metatarsi II short (i.e. distally not exceed the half of trochlea metatarsi III); (5) medial divergence of trochlea metatarsi II weak; (6) in plantar view, incisura intertrochlearis lateralis well developed proximally; (7) in distal view, incisurae intertrochlearis medialis et lateralis wide.

Additionally, the new taxon is characterized by the following combination of features: (1) shaft narrowed (vs. shaft broadened in *Herpetotheres*, *Thegornis*, and large-sized *Falco* spp.); (2) cross-section of the tarsometatarsal midshaft squared (vs. triangular in *Herpetotheres*; “H” shaped in *Thegornis* and *Micrastur*); (3) dorsal surface of shaft flattened, without cristae (vs. medial crista developed in *Herpetotheres*; both medial and lateral cristae developed in *Micrastur* and *Thegornis*); (4) crista plantaris medialis not prominent and projected nearly vertical towards the proximal end (vs. both cristae plantare medialis et lateralis strongly developed in Herpetotherinae; crista plantaris medialis more laterally projected in Falconinae); (5) absence of bony channel for m. extensor brevis digiti IV at the level or above the dorsal opening of the foramen vasculare distale (evident due to the presence of two foramina on the dorsal surface; vs. channel normally present in Polyborinae and Falconinae); (6) plantar opening of the foramen vasculare distale large and proximally located (vs. reduced and more distally positioned in *Herpetotheres*, *Thegornis*, *Spizapteryx*, *Pediohierax*, and Falconinae; reduced and more proximal in *Micrastur*); (7) fossa metatarsi I poorly defined, relatively wide, shallow, and distally located (vs. narrow and more proximal in *Micrastur*; deeper in *Herpetotheres* and *Thegornis*; wider and well defined in *Polyborus* and *Phalcoboenus*); (8) absence of a wide indentation on medial surface (vs. present in Herpetotherinae); (9) area of insertion of m. abductor digiti II on trochlea metatarsi II reduced (vs. large, continuous with the sulcus extensorius in Herpetotherinae, as well as in Falconinae, but less marked); (10) canalis interosseus distalis totally ossified, i.e. distal notch absent (vs. canalis absent or incomplete in *Herpetotheres* and Falconinae, i.e. distal notch present); (11) fossa supratrochlearis plantaris relatively deep (vs. shallow in Herpetotherinae); (12) trochlea metatarsi IV short (vs. more distally extended in most falconids, except in *Falco* where it is even shorter); (13) in dorsal view, proximomedial constriction (fovea lig. collateralis) above trochlea metatarsi II absent (vs. present in Herpetotherinae, *Pediohierax* and Falconinae); (14) articular plantar surface of trochlea metatarsi III elongated (vs. short and wide in Herpetotherinae and Falconinae); (15) trochlea metatarsi III not directed medially in dorsal view (vs. markedly directed medially in *Thegornis*, *Micrastur*, and Falconinae; weakly inclined in *Herpetotheres*); (16) in plantar view, lateral rim of trochlea metatarsi IV more distally projected than medial rim (vs. similar projections of both rims in Polyborinae and Falconinae); (17) in distal view, trochlea metatarsi IV laterally oriented, with lateral rim widened and plantarly shortened (vs. trochlea more dorsally oriented with lateral ridge narrow and plantarly extended in *Polihierax* and Herpetotherinae).

Derivatio nominis *Antarctic walker*, from *Antarcto*, in reference to Antarctica, and *boenus* derived from the Greek “baino”, to walk, in reference to the presumed plesiomorphic condition of the holotypical tarsometatarsus shared with the extant ground-dwelling polyborines (i.e. *Phalcoboenus*).

Species *Antarctoboenus carlinii* nov. Figure 2a–c.

Holotype MLP 95-I-10-8, distal end of left tarsometatarsus. Collected by Sergio Santillana during the Antarctic Summer Campaign of 1995.

Type locality IAA 2/95 locality, Seymour (Marambio) Island, Antarctic Peninsula, West Antarctica. The material comes from the *Cucullaea* I Allomember (level 35 in Montes et al. 2013) of the La Meseta Formation (Marenssi et al. 1998; Fig. 1a, b).

Age Middle Ypresian, Early Eocene. Strontium dating yielded ages of 52.8–49 million years ago for the level 35 of the *Cucullaea* I Allomember in the type locality (Montes et al. 2013).

Diagnosis as for the genus

Derivatio nominis in honor of Dr. Alejandro Ricardo Carlini (1963–2010), leader of the Argentine research program on reproductive and feeding ecology in Antarctic pinnipeds.

Measurements Distal width 22.2, midshaft width 9.4.

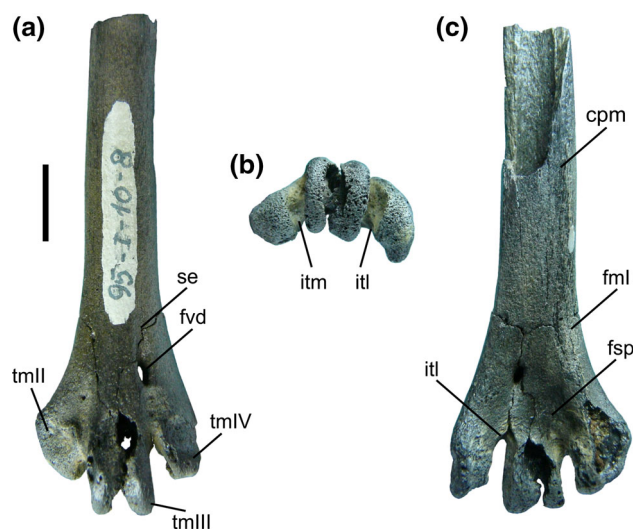


Fig. 2 *Antarctoboenus carlinii* nov. gen. nov. sp. from the Lower Eocene of Antarctic Peninsula. **a** Distal end of left tarsometatarsus, MLP 95-I-10-8, holotype, dorsal view. **b** Idem, distal view. **c** Idem, plantar view. *cpm* crista plantaris medialis, *fml* fossa metatarsi I, *fsp* fossa supratrochlearis plantaris, *fvd* foramen vasculare distale, *itl* incisura intertrochlearis lateralis, *itm* incisura intertrochlearis medialis, *se* sulcus extensorius, *tmII* trochlea metatarsi II, *tmIII* trochlea metatarsi III, *tmIV* trochlea metatarsi IV. Scale bar 10 mm

Description and comparisons

As in *Micrastur*, Polyborinae, the extinct *Pediohierax* and basal Falconinae (e.g. *Polihierax* spp., “*tinnuculus*” group of *Falco*), the shaft of *Antarctoboenus carlinii* is narrow, and considering the preserved fragment of bone, it seems to have been elongated, differing from the broadened and shorter of *Herpetotheres*, the allied Miocene Patagonian genus *Thegornis*, and some large-sized *Falco* spp. (e.g. *F. rusticolis*, *F. peregrinus*, *F. mexicanus*). The tarsometatarsal specimen is broken at midshaft, exhibiting a square cross-section as in Polyborinae and Falconinae. Contrarily, the midshaft presents a triangular cross-section due to reduction of the lateral surface of the bone in *Herpetotheres*, whereas the dorsal and plantar surfaces are strongly grooved, giving the shaft the typical H-shaped cross-section in *Micrastur* and *Thegornis* (see Jollie 1976, Fig. 140e; Noriega et al. 2011, Fig. 8). The dorsal surface of the preserved shaft in *Antarctoboenus* is flattened as in Polyborinae and Falconinae, differing from the development of a medial crest present in *Herpetotheres*, and of both medial and lateral ones in *Micrastur* and *Thegornis*. Crista plantaris medialis is not very prominent as shown in Polyborinae and Falconinae. This crest projects nearly vertical towards proximal end as it can be observed in Polyborinae and *Pediohierax* in plantar view, and does not incline laterally as in Falconinae. On the contrary, both crista plantaris medialis et lateralis are well developed in Herpetotherinae, delimiting a deep sulcus flexorius.

On the dorsal surface, the distal portion of the sulcus extensorius in *Antarctoboenus* is very shallow, being only slightly marked when joining the foramen vasculare distale; whereas this sulcus is somewhat more conspicuous in Polyborinae and Falconinae, exhibiting its major development in Herpetotherinae (Fig. 3a).

The canalis interosseus distalis which contains the tendon of m. extensor brevis digiti IV (Baumel and Witmer 1993:113) is usually bordered distally by a bony channel at the level or above the dorsal opening of the foramen vasculare distale (Jollie 1976; Fig. 3a, ceIV). Thus, the distal end of the tarsometatarsus can show two adjacent lateral foramina, one above the other. Notwithstanding its variability, this condition is common in most Polyborinae and Falconinae (Becker 1987), being absent in Herpetotherinae and *Antarctoboenus*. Additionally, the dorsal opening of the foramen vasculare distale in *Antarctoboenus* is larger than in any other known falconid (Fig. 3a 1). Similarly, the large plantar opening and the proximal location of this foramen in *Antarctoboenus* resembles the condition observed in Polyborinae (excepting *Spizapteryx*), contrasting with the reduced and distally placed opening of the remaining falconids (only in *Micrastur* this foramen is as proximal as in Polyborinae, but it is very small). Plantarily,

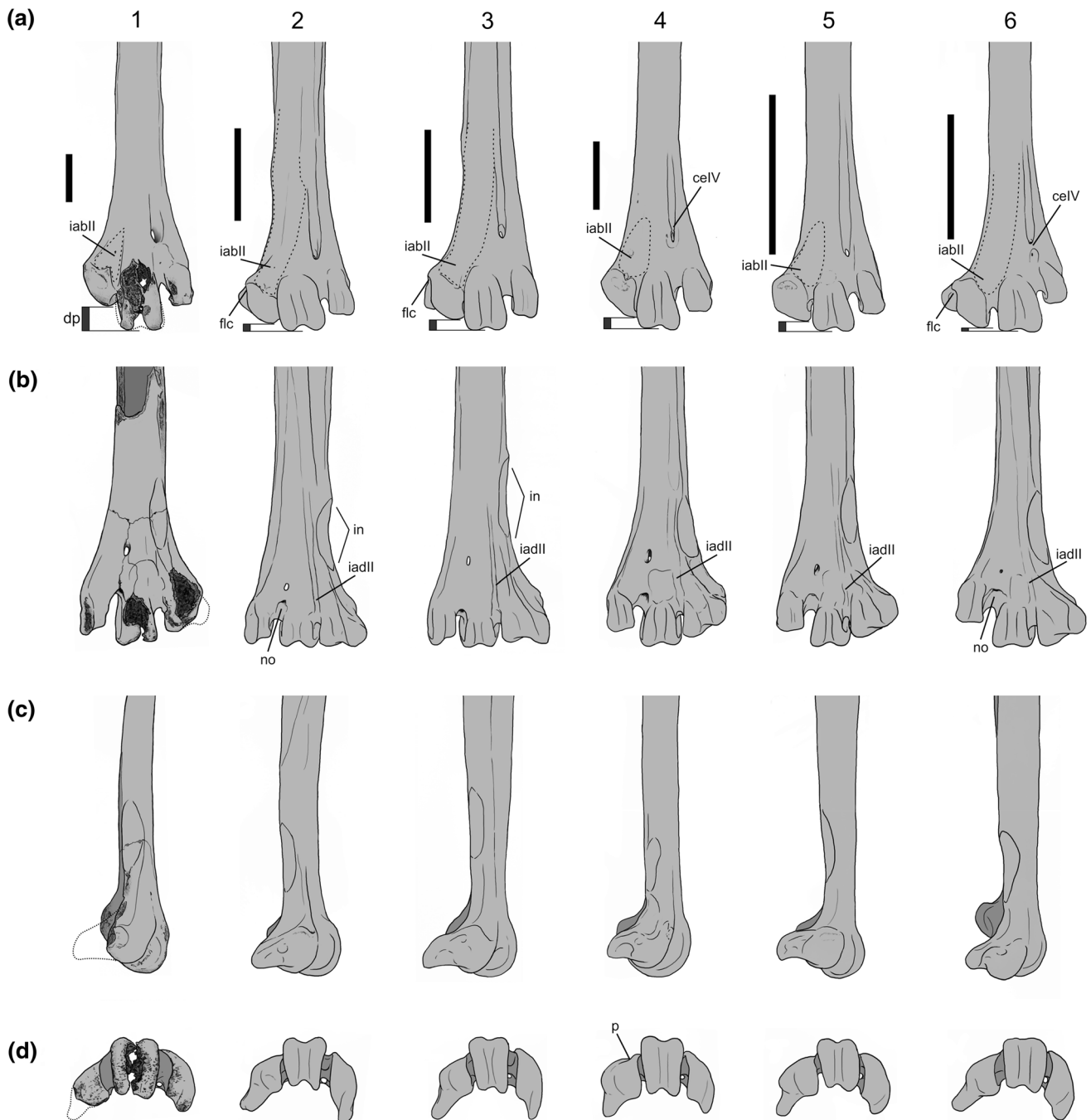


Fig. 3 Comparative tarsometatarsal morphology of *Antarctoboenus carlinii* nov. gen. nov. sp. and representatives of the major extant falconid lineages. **a** Distal end of left tarsometatarsus in dorsal view. **b** Idem, plantar view. **c** Idem, medial view. **d** Idem, and distal view. 1 *Antarctoboenus carlinii*, MLP 95-I-10-8, holotype. 2 *Herpetotheres cachinnans*, MACN 54484. 3 *Micrastur semitorquatus*, CFA-OR-498.

4 *Polyborus plancus*, CFA-OR-027-2. 5 *Spizapteryx circumcincta*, MACN 23601. 6 *Falco femoralis*, MACN 54810. *celV* canalis for m. extensor brevis digiti IV, *fic* constriction (fovea lig. collateralis), *iabII* insertion area of m. abductor digiti II, *iadII* impressio m. adductor digiti II, *in* indentation, *no* notch of the canalis interosseus distalis, *p* pit. Scale bar 10 mm

the tendinal impression of the adductor digiti II is indistinguishable in *Antarctoboenus*, differing from the weak, but well defined attachment of Polyborinae and Falconinae, and the large and deep mark of Herpetotherinae (Jollie 1976; Noriega et al. 2011; Fig. 3b, iadII). As in

Polyborinae and Falconinae, the fossa metatarsi I in *Antarctoboenus* is larger and more distal than in *Micrastur*. In *Herpetotheres* and *Thegornis* the fossae exhibit similar widths and positions than that of *Antarctoboenus*, but are more excavated. This fossa in *A. carlinii* resembles that of

Falconinae, *Pediohierax* and the small Polyborinae (e.g. *Milvago*, *Spizapteryx*), whereas in *Polyborus* and *Phalcoboenus* it is better defined and larger. Concerning the development of the fossa metatarsi I, *Antarctoboenus* also shares with Polyborinae and Falconinae the absence of a large indentation on the medial surface of the bone, which is also typical of the Herpetotherinae (excepting *Thegornis*), being more pronounced and elongated in *Micrastur* than in *Herpetotheres* (Fig. 3b, in). In these latter taxa, this indentation exhibits a medial projection at its proximal part, which is clearly observable in dorsal and plantar views.

In dorsal view, the area for attachment of m. abductor digiti II on trochlea metatarsi II in *A. carlinii* is reduced or proximodistally shortened (not continuous with the sulcus extensorius) and does not surpass laterally the midline of shaft, resembling the overall generalized morphology of Polyborinae. Contrarily, in Herpetotherinae this area is large and slightly concave (Fig. 3a, iabII), surpassing the midline of shaft laterally and extending largely towards the proximal end to join the wide and deep sulcus extensorius. This condition is similar, but less marked in *Falco*, where the muscular attachment and the sulcus extensorius are shallower than in Herpetotherinae. Additionally, the distal surface of this attachment area above trochlea metatarsi II is smooth in Falconinae and Herpetotherinae, whereas in *Antarctoboenus* and Polyborinae it presents rugosities and/or conspicuous pits (in *Polyborus* and *Phalcoboenus*, with a well-marked pit above dorsal surface of trochlea in distal view; Fig. 3 d4, p; see also Jollie 1976, Fig. 142Ab).

On the plantar surface, *Antarctoboenus* shares with *Micrastur*, *Thegornis*, Polyborinae, and *Pediohierax*, a canalis interosseus distalis completely ossified along its whole extent, with its distal opening situated above the incisura intertrochlearis lateralis or a little bit more proximoplantarly. On the contrary, *Herpetotheres* and Falconinae have a canalis briefly (Jollie 1976) or not ossified (e.g. some *Falco* spp., *Polihierax semitorquatus*), exhibiting a proximally extended plantar notch (Fig. 3b, no) and its distal opening opens on plantar surface. *Antarctoboenus* presents a fossa supratrochlearis plantaris relatively deep as in Polyborinae and Falconinae and different to the condition found in Herpetotherinae.

The distal projection of trochlea metatarsi II is smaller than that of trochlea metatarsi III compared to any other known falconid. In dorsal view, trochleae metatarsorum II and IV extend distally to the same level, not surpassing half the length of trochlea metatarsi III. In the remaining falconids, the trochlea metatarsi II projects more distally than trochlea IV, largely beyond half the length of trochlea III. Besides, only some species of *Falco* have the trochlea metatarsi IV shorter than that of *A. carlinii*. In dorsal view, the slight medial divergence of trochlea II in *A. carlinii*

seems to be unique within falconiforms. Although the medio-plantar rim of trochlea metatarsi II is lost in the holotype, the presence of a wing or process emerging from the articular body can be inferred from the preserved base observed in medial and plantar views. Beyond its smaller size, the overall shape of trochlea II is similar to that of Polyborinae because its articular body lacks the proximo-medial constriction (Fig. 3a, flc) dorsally observed in Herpetotherinae, *Pediohierax*, and Falconinae. This constriction is always clearly notable when the fovea lig. collateralis can be seen dorsally. Thus, the medio-plantar process of the trochlea II in *A. carlinii* and the Polyborinae is plantarly directed and avoids the visibility of the fovea lig. collateralis, whereas the constriction seems to be well developed when the medio-plantar process of the trochlea is more medially projected.

Although *Antarctoboenus* has the trochlea metatarsi III partially eroded, its plantar articular surface seems to be elongated as in Polyborinae, *Pediohierax*, and Falconinae, differing from the very short and wide trochlea present in Herpetotherinae. As in Polyborinae, in dorsal view, this trochlea is not medially inclined as in Falconinae, Herpetotherinae, and *Thegornis*. In distal view, plantar rims of trochlea metatarsi III are rounded, not pointed as in other falconids, but this state could be due to weathering. In plantar view, the lateral rim of trochlea metatarsi IV projects more distally than the medial one in *A. carlinii*, as in Herpetotherinae, whereas both rims have similar projections in Polyborinae and Falconinae. In distal view, trochlea metatarsi IV is more laterally oriented in *A. carlinii* than in Herpetotherinae, as in Polyborinae and Falconinae (excepting *Polihierax*), and the plantar process of its lateral rim is shorter than in the latter.

In plantar view, *Antarctoboenus carlinii* differs from other falconids by having an incisura intertrochlearis lateralis deeper (extending more proximally than the proximal end of trochlea metatarsi III), whereas, in distal view, both incisurae are wider than those of other falcons.

Discussion and conclusions

Because of similarities in habits and morphology, members of the family Falconidae have been traditionally grouped within the order Falconiformes (e.g. sensu Wetmore 1960) together with raptors belonging to Accipitridae (hawks and allies) and other diurnal birds of prey (i.e. Cathartidae, Sagittariidae, and Pandionidae). However, anatomical studies (Jollie 1976, 1977a, b, c) have shown that similarities between falcons and hawks are not due to close phylogenetic relationship, but mainly to convergence. Recent molecular phylogenies agreed with this arrangement (e.g. Ericson et al. 2006; Hackett et al. 2008;

McCormack et al. 2013; Yuri et al. 2013), giving support to a new clade (i.e. Australaves; see Ericson 2012; Jarvis et al. 2014), which includes falcons and allies together with seriemas (Cariamiformes), parrots (Psittaciformes), and passerine birds (Passeriformes). Our comparative analysis demonstrates that *Antarctoboenus carlinii* shares with Falconidae and differs from Accipitridae (auct. Accipitri-formes) in the following characters (see also Jollie 1976; Noriega et al. 2011; Cenizo and Tassara 2013): (1) absence of irregular crest above the distolateral margin of fossa metatarsi I; (2) trochlea metatarsi II more proximally positioned than trochlea III; (3) medial process of trochlea metatarsi II slimmer, less conical, with blunt apex, more plantarly directed and clearly separated from trochlear body; (4) plantar articular surface of trochlea metatarsi II weakly grooved; (5) more slight depression (fovea lig. collateralis) above medial surface of trochlea metatarsi II; (6) trochlea metatarsi III more symmetrical; (7) trochlea metatarsi IV narrower and well directed laterally.

In the current phylogenetic context, Falconidae constitutes the unique extant family included within the order Falconiformes (see Remsen et al. 2008, SACC Proposal #290, 2008). However, some analyses have recovered a sister relationship between the Falconidae and Cariamidae (Ericson et al. 2006; Ericson 2008; Wang et al. 2012), even has been proposed the inclusion of Cariamidae in Falconiformes (Ericson 2012). In this sense, *Antarctoboenus carlinii* shares with Falconidae and differs from Cariamidae in several characters including: (1) more elongated fossa metatarsi I and situated further distally; (2) absent sulcus for musculus extensor hallucis longus on the medial surface of the distal shaft; (3) trochlea metatarsi II with a large medial projection on the plantar surface and much wider than the trochlea metatarsi IV; (4) in distal view, trochleae metatarsorum arranged in arch; (5) dorsoplantarly shorter trochlea metatarsi III.

The palaeontological record of Falconidae is especially meager during Paleogene times and early assignments are most dubious (Mayr 2009). This is the case for *Parvulivenator watteli* from the Lower Eocene of England based on a distal end of tarsometatarsus and some associated phalanges (Harrison 1982) and of a second specimen referred to the same taxon (Mayr 2005) that was later discarded as a raptor and proposed to represent a coliform bird (Mayr 2005, 2009). *Stintonornis mitcheli*, also from Lower Eocene deposits of England and referred to a purported Falconidae, is represented by a third distal tarsometatarsus (Harrison 1984). Mourer-Chauviré (2006) also pointed out the presence of still undescribed falconids from the Upper Eocene and Lower Oligocene of the Phosphorites du Quercy in France. Finally, *Masillaraptor parvunguis* is a lower Middle Eocene taxon from Messel (Germany) known by two largely complete specimens

(Mayr 2006) and originally related to Polyborinae (Peters 1988, 1991). Unfortunately, the trochleae metatarsorum in both specimens of *M. parvunguis* are very poorly preserved precluding any comparison with *A. carlinii*. Further, the phylogenetic affinities of *Masillaraptor* are difficult to establish because it shares a combination of homoplastic characters with Accipitridae and Falconidae, i.e. two unrelated raptor lineages (see Mayr 2006, 2009). Thus, evidence of Paleogene falconid fossils outside South America are best regarded as unconfirmed.

Neogene fossils (Fig. 4) include the tiny extinct falcon *Pediohierax ramenta* from the Middle Miocene of Nebraska which was postulated as the sister taxon of Falconinae (Becker 1987). In South America, the earliest records of falcons come from Early Miocene of Patagonia and include three taxa. *Badiostes patagonicus* was originally described as an owl (Ameghino 1895), but later transferred to Falconidae (Wetmore 1922; Lambrecht 1933; Brodkorb 1964) and its affinities proposed to be with Polyborinae (Olson 1985). *Thegornis musculosus* and *T. debilis* are the other two valid species recently revised and included within the Herpetotheriinae as the sister taxon of *H. cachinnans* (Noriega et al. 2011). Other scattered or fragmentary specimens referred to falconids have been mentioned for the Early to Late Miocene of Patagonia (Tonni 1980; Chiappe 1991), but unfortunately they have not yet been described. The first undoubted records of Polyborinae (i.e. *Milvago* sp.) were reported from the Late Miocene of Central Argentina (Cenizo et al. 2012) and Late Pliocene of Chile (Emslie and Guerra Correa 2003).

The holotypical specimen of *Antarctoboenus carlinii* was cited for the first time in a short communication, assigned to Falconidae and its affinities to Polyborinae pointed out (Tambussi et al. 1995). Although the Antarctic specimen had never been properly described nor compared, its relationship with Caracaras was uncritically accepted and sustained throughout two decades (e.g. Tambussi and Acosta Hospitaleche 2007; Tambussi and Degrange 2013; Reguero et al. 2013). Moreover, the material was never illustrated until recently (Tambussi and Acosta Hospitaleche 2007; Reguero et al. 2013). Tambussi and Acosta Hospitaleche (2007:607) stated that specimen MLP 95-I-10-8 “exhibits a morphology similar to living polyborines in having the trochlea for the second digit shorter and wider than the trochlea for the digit four, bearing a plantarly projection” (see also Tambussi and Degrange 2013). However, these similarities between *A. carlinii* and the Polyborinae seem to be faintly supported from a phylogenetic point of view. The plantar projection of trochlea metatarsi II and its greater width than trochlea IV are generalized characters not only within Polyborinae, but in all falconids. On the other hand, the Polyborines, as well as all falconids (including the extinct *Thegornis* and

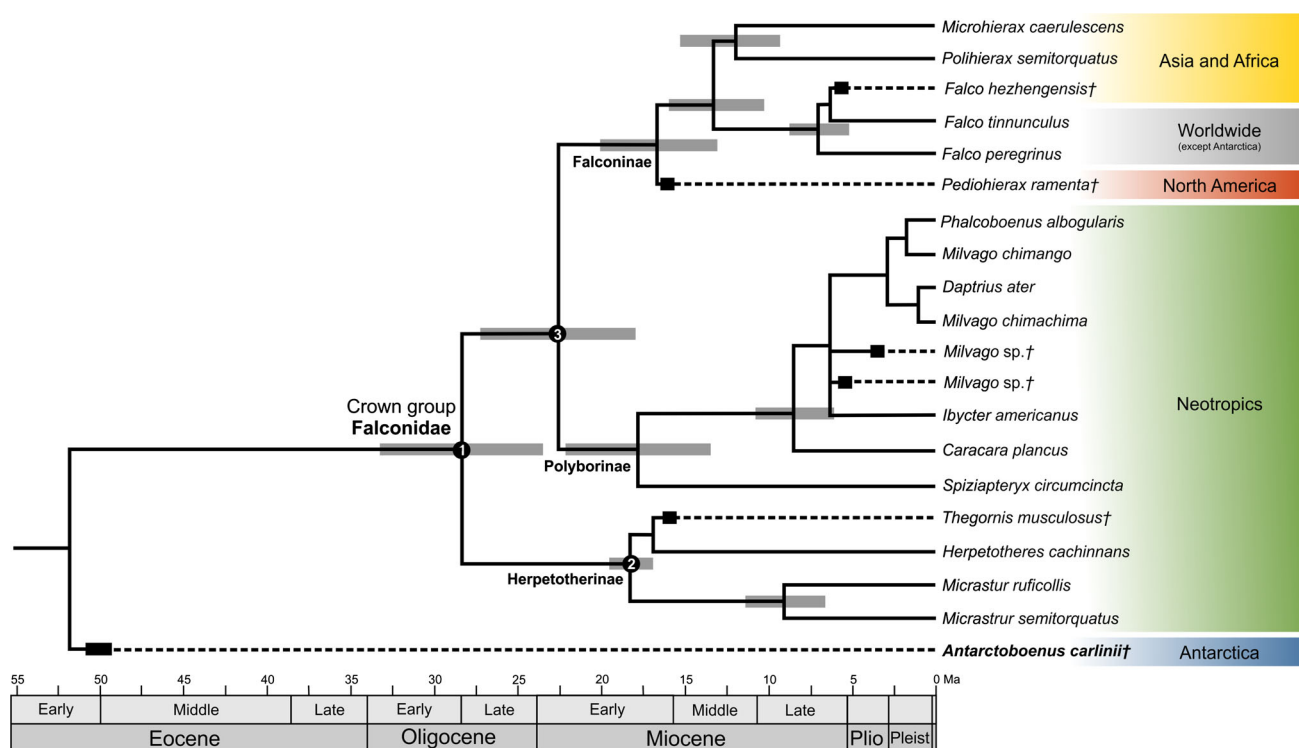


Fig. 4 Geographical range, temporal distribution, and phylogenetic affinities of extant and fossil falconid birds. The internal nodes are supported by the following presumably derived features: (1) well-defined sulcus extensorius, impression of m. adductor digiti II present, trochlea metatarsi II distally projected beyond half the trochlea III, strong medial divergence of trochlea metatarsi II; (2) cross-section of midshaft not squared, developed crista dorsalis medialis, prominent cristae plantaris medialis et lateralis, wide and deep impression of m. adductor digiti II, shallow fossa supratrochlearis plantaris; (3) sulcus extensorius generally closed distally by a bony canal on the dorsal opening of foramen vasculare distale, medial and lateral ridges of

trochlea metatarsi IV distally projected at the same level. Backbone phylogeny of extant taxa after Fuchs et al. (2015), inferred from mitochondrial and nuclear sequence data. Affinities of extinct taxa *Thegornis*, *Pediohierax*, and *Falco hezhengensis* were taken from osteological phylogenies performed by Noriega et al. (2011); Becker (1987); and Li et al. (2014), respectively, and we follow the taxonomic criteria of Cenizo et al. (2012) and Emslie and Guerra Correa (2003) for the fossil specimens of *Milvago* sp. The temporal distribution of fossil taxa (*dagger*) is indicated by *black squares*. *Grey bars* indicate divergence times estimates for the primary lineages within the extant Falconids according to Fuchs et al. (2015)

Pediohierax) present a trochlea metatarsi II longer (i.e. more distally extended) than trochlea metatarsi IV. Contrarily, both trochleae have similar distal spreadings because the trochlea metatarsi II is remarkably shorter in *A. carlinii*. Indeed, Mayr (2009) was the first to notice this striking morphological difference.

From the above-cited features and our remaining detailed descriptions, it can be inferred that *A. carlinii* has very close affinities to the crown group Falconidae; however, several derived characters of the latter are absent in *A. carlinii* (e.g. sulcus extensorius well developed, trochlea metatarsi II more distally extended than trochlea IV, dorsal opening of the foramen vasculare distale reduced, impression of tendon del m. adductor digiti II well-marked; Fig. 4).

With the exception of the diagnostic characters described above, the morphology of *A. carlinii* is more similar to that of Caracaras than to any other falconid. In accordance with our hypothesis, previous authors had pointed out that

tarsometatarsal morphology in Polyborinae is possibly very close to the primitive condition found in the family (Jollie 1976, 1977c; Olson 1976; Becker 1987). We think that the original relationships postulated between *A. carlinii* and Polyborinae are based on plesiomorphic characters retained in the tarsometatarsus of the latter clade.

Fuchs et al. (2015) stated that the Antarctic specimen described herein could potentially constitute a stem Falconidae if their divergence time analyses were correct (i.e. this fossil would be too ancient to belong to the crown group if the oldest estimate for the first Falconidae split was at 34.8 million years ago; Fig. 4).

In sum, we consider that *A. carlinii* represents the most primitive falconiform taxon until now known and belongs to the early evolutive radiation of this raptorial lineage. Our interpretation, although being exclusively based on anatomical characters, contradicts prior inferences about the systematic assignment and concomitant phylogenetic affinity of the Antarctic specimen (Tambussi et al. 1995;

Tambussi and Acosta Hospitaleche 2007; Tambussi and Degrange 2013), reinforcing the hypothesis about the Neotropical or Austral origin of Falconidae as suggested by molecular phylogenies (Ericson et al. 2006; Ericson 2012; Fuchs et al. 2015).

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