

## PHYLOGENY AND TAXONOMY OF THE PATAGONIAN MIOCENE FALCON *THEGORNIS MUSCULOSUS* AMEGHINO, 1895 (AVES: FALCONIDAE)

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**ABSTRACT**—The fossil record of the family Falconidae is poor and fragmentary. Extinct representatives from South America include the early-middle Miocene (Santacrucian) *Thegornis musculosus* and *Thegornis debilis*. Both species were originally described as Falconidae and afterwards moved to Accipitridae Circinae or Buteoninae. The analysis of a very well preserved and complete specimen of *T. musculosus* with similar stratigraphic and geographic provenances of the type material (lower levels of Santa Cruz Formation, coast of Patagonia, Argentina) corroborates the validity of the genus and its falconid affinities. The skull and postcranial morphology exhibit strong resemblances with the open-savannah inhabiting *Herpetotheres* and the forest-dwelling *Micrastur* (Herpetotherinae) but differ substantially from Falconinae (Falconini plus Caracarini). Detailed comparisons with a broad arrange of falconiform taxa in a cladistic framework, confirm its phylogenetic placement within the Herpetotherinae and sister to *H. cachimans*. The ecotonal margins produced by the vanishing of humid forests that developed during changes in Patagonian plant communities throughout early Neogene times are hypothesized as a plausible scenario to understand the evolution of this basal clade of falcons.

### INTRODUCTION

THE FALCONIDAE Leach, 1820 (falcons, falconets, caracaras, and kestrels) are small to medium-sized predatory birds present in all habitats around the world except Antarctica, with most of the extant diversity concentrated in the Neotropics (Olson, 1976a, 1985; White et al., 1994). They have generally been placed alongside the other diurnal raptors included in the order Falconiformes Sharpe, 1874, i.e., the accipitrids (hawks, eagles, and kites). However, detailed morphological studies of families with a traditional systematic approach (Jollie, 1976, 1977a, 1977b, 1977c), as well as recent molecular evidence (Hackett et al., 2008), suggest that falconids are not related to accipitrids, but are actually closer to passerines, parrots, and seriemas. Amidst the controversy concerning the phylogenetic relationships of all these bird groups, it is clear that falconids constitute by themselves a monophyletic assemblage (Griffiths, 1994; Griffiths et al., 2004; Hackett et al., 2008).

The fossil record of the falconids is poor and fragmentary, providing little evidence about the purported Gondwanan origin of the basic stocks that gave rise to their main clades or subfamilies (White et al., 1994; Feduccia, 1996). Several early Eocene fossils from England and specimens from the middle Eocene Messel oil shales of Germany were primarily supposed to be falconids or accipitrids (Peters, 1992, 1994; Feduccia, 1996), but are currently considered raptorial birds of dubious identity or belonging to taxa (e.g., Messelasturidae Mayr, 2005) whose phylogenetic affinities link the Strigiformes Wagler, 1830 (owls) to Falconiformes (Mayr, 2000, 2005). The oldest falconids are known from the Eocene-Oligocene Phosphorites du Quercy in France (Mourer-Chauviré, 1982) and from the Eocene of Antarctic Peninsula (Tambussi et al., 1995; Vizcaíno et al., 1998). The South American extinct representatives include the Miocene *Badiostes patagonicus* Ameghino, 1895 from Patagonia and several Pleistocene species of caracaras are known from the West Indies (Olson, 1976b, 2008; Tonni, 1980; Cuello, 1988; Tambussi and Noriega, 1996; Suárez and Olson, 2001, 2003). Two other

taxa from the late early Miocene of Patagonia (Santacrucian Stage/Age), *Thegornis musculosus* Ameghino, 1895 and *Thegornis debilis* Ameghino, 1895, were both erected on the basis of fragments of distal tarsometatarsi and originally described as belonging to Falconidae (Ameghino, 1895). However, later revisions removed them to the Accipitridae either as Circinae (Brodkorb, 1964) or Buteoninae (Agnolin, 2006). Moreover, *T. musculosus* was transferred to the genus *Buteo* Lacépède, 1799 (Agnolin, 2006). The recent finding of a very well preserved and complete specimen herein referred to *T. musculosus*, with very similar stratigraphic and geographic provenances to those of the type material, allowed us to confirm both the validity of Ameghino's genus *Thegornis* and its original placement within the falconid family.

We performed a cladistic analysis including many representative genera of falconids and *T. musculosus* in order to establish the phylogenetic relationships of the latter. Our results support the hypothesis that *T. musculosus* is a member of a basal clade which comprises the living forest falcons of the genus *Micrastur* Gray, 1841, closely allied to the Laughing Falcon *Herpetotheres cachimans* (Linnaeus, 1758); the *Thegornis-Micrastur-Herpetotheres* group being sister to the remaining, more derived, falconines.

### MATERIALS AND METHODS

The new materials herein referred to *T. musculosus* belong to a single specimen (MPM-PV-3443), and they are housed at the paleontological collection of the Museo Regional Provincial Padre M. J. Molina, Río Gallegos, Santa Cruz Province, Argentina.

The osteological nomenclature follows Howard (1929) and Jollie (1976, 1977a, 1977b, 1977c). Baumel and Witmer's (1993) terminology is added in brackets for ambiguous anatomical terms. Comparative specimens are listed in Appendix 1.

The cladistic relationships among taxa were analyzed following the theoretical principles of phylogenetic systematics. We performed a phylogenetic analysis including 10 taxa (7

species of the most representative living genera of the falconid subfamilies and tribes, one fossil species, and two accipitrid taxa), to determine the phylogenetic position of *T. musculosus*. We obtained 66 characters from the available bony elements of specimen MPM-PV-3443 (skull, sternum, coracoid, clavicle, humerus, pelvis, femur, tibiotarsus, and tarsometatarsus; see Appendix 2 for character definitions and states).

Character polarity and rooting were established using outgroup comparisons (Nixon and Carpenter, 1993). We designated *Circus buffoni* (Gmelin, 1788) as an outgroup for the purpose of drawing the tree diagram. Analysis of our data matrix (Appendix 3) was performed with TNT v.1.1 (Goloboff et al., 2003). It consisted of 1,000 replications by random addition of sequences using TBR branch swapping, holding 10 trees per replicate with characters equally weighted and coded as non-additive. The collapsing rule utilized was the minimum length rule.

*Institutional acronyms*.—MPM-PV=Museo Regional Provincial Padre M. J. Molina; MHNT=Museu de História Natural de Taubaté; CICYTTP=Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción; BMNH=British Museum of Natural History.

#### SYSTEMATIC PALEONTOLOGY

Order FALCONIFORMES Sharpe, 1874

Family FALCONIDAE Leach, 1820

*Thegornis musculosus* is referred to the Falconidae and distinguished from the Accipitridae Vigors, 1824 by the following characters: supraorbital process of prefrontal without free superciliary bone or indication of its presence; posterior tympanic process more extended from posterior than dorsal margin of tympanic cavity; length of zygomatic process of squamosal equal to 2/5 or more of quadrate length, being absent or at least short and blunt in accipitrids (see Suschkin, 1905, p. 22); articular squamosal process for squamosal capitulum of quadrate (processus suprameaticus) sharp-pointed; basitympanic plate narrow: basitympanic process width (i.e., distance between lateral points of basitympanic plate) representing 42% of post-temporal width (measured across zygomatic processes), ranging from 45.2 to 63.5% and from 40.5 to 48% in accipitrid and falconid skulls, respectively (Jollie, 1976, p. 214); presence of delimited triangular area between sternocoracoid fossa and m. supracoracoideus scar; head of coracoid not bent medially, with clavicular facet (facies articularis clavicularis) steeply inclined forming a continuous plate in medial view, not projecting noticeably from head at its anteroventral angle (see Jollie, 1977, p. 284); processus acromialis of clavicle slightly directed dorsally rather than posteriorly; lateral fossa on extremitas omalis clavicularum shallow and obscure, not deep and well pneumatized; furculum narrowly U-shaped rather than V-shaped; lateral margin of distal portion of posterior iliac crest (crista dorsolateralis ilii) straight, not distinctly S-shaped; lateral opening isolated by ossified loop on anterior aspect of distal tibiotarsus; outer calcaneal process (crista lateralis hypotarsi) reduced; medial calcaneal process (crista medialis hypotarsi) large, extending well down the shaft as medial hypotarsal ridge (crista medialis plantaris), and rather centrally placed, being faintly marked and rather medially located in accipitrids; fossa of flexor hallucis brevis (fossa parahypotarsalis medialis) confined to medial aspect of tarsometatarsus, more centrally located in accipitrids; tuberositas m. tibialis cranialis not as protrudent; lateral margin of fossa metatarsi I lacking irregular ridge typical of accipitrids; second trochlea (trochlea

metatarsi II) more proximal than third trochlea; medial process of trochlea II thinner, less tapered, with more truncated tip, and more clearly separated from trochlear body than accipitrids; trochlea II lacking deep pit in medial view; third trochlea (trochlea metatarsi III) almost symmetrical, being asymmetric in accipitrids (not so accentuated in buteonines) due to strong inclination and very different heights of trochlear rims; fourth trochlea (trochlea metatarsi IV) narrower and strongly inclined laterally, being parallel to third trochlea or inclined medially in accipitrids.

#### Subfamily HERPETOTHERINAE Lesson, 1842

The osteological characters that refer *T. musculosus* to the Herpetotherinae and distinguish it from the rest of the Falconidae are as follows: floor of vestibule sloping up and medially as lower edge of narial aperture, being floor leveled with margin of naris in Caracarini Griffiths, 1999 and well below in Falconini; anterior end of palatines wider; orbital margins showing great extension, being longer than Falconinae; scapula straighter, much less curved; humerus proportionally shorter than Caracarini and longer than Falconini, with more pronounced curvature; bicipital crest (crista bicipitalis) shorter and somewhat less rounded in outline than Falconinae, meeting shaft more perpendicularly; lateral flaring of deltoid crest (crista deltopectoralis) moderate, more important than Caracarini, but lesser than Falconini, with margin angled at mid-length; ectepicondylar prominence (processus supracondylaris dorsalis) more laterally and distally located; entepicondyle (processus flexorius) well extended distally beyond internal condyle and laterally directed, being more parallel to shaft in Falconini, and short, not surpassing level of condyle, in Caracarini; lateral torsion of distal shaft and epiphysis of femur accentuated; joint between outer cnemial crest (crista cnemialis lateralis) and shaft of tibiotarsus incurved; proximal tibiotarsal end medially displaced, being distal inner cnemial crest (crista cnemialis cranialis) not sharply aligned with medial shaft border, but both aligned in Falconinae; lateral hypotarsal ridge (crista lateralis plantaris) slightly defined and oblique; medial process of second trochlea of tarsometatarsus less medially directed than Falconini and much more than Caracarini.

#### Genus *THEGORNIS* Ameghino, 1895

*Type species*.—The genus *Thegornis* was erected without formal designation of a type species by Ameghino (1895:353). His description included two species: *T. musculosus* appearing first (Ameghino, 1895, p. 353–355), and *T. debilis* appearing subsequently (Ameghino, 1895, p. 354–355). Ameghino's original notation was "*Thegornis musculosus* n. gen. n. sp." (Ameghino, 1895, p. 353), and "*Thegornis debilis* n. sp." (Ameghino, 1895, p. 355), thus indirectly indicating that the more complete remains of *T. musculosus* were intended as representative of *Thegornis*. Later, Richmond (1902) formally elected *T. musculosus* as type species of *Thegornis* by subsequent designation, stating "(first species mentioned)" (Richmond, 1902, p. 718). When Agnolin (2006, p. 73) transferred *T. musculosus* to *Buteo*, he synonymized *Thegornis* to *Buteo*, but arbitrarily decided to keep the generic name *Thegornis* only to designate *T. debilis*, violating article 69.1 of the ICZN (1999): "If an author established a nominal genus or subgenus but did not fix its type species, the first author who subsequently designates one of the originally included nominal species validly designates the type species of that nominal genus or subgenus (type by subsequent designation), and no later designation is valid." Agnolin's action is such a later



FIGURE 1—*Thegornis musculosus* Ameghino, 1894, BMNH-A600, and *Thegornis debilis* Ameghino, 1894, BMNH-A601. Original illustrations and photos of both holotypes and material referred to *Thegornis musculosus*, MPM-PV-3443. Distal fragments of both right and left tarsometatarsi of *T. musculosus*: 1, 4, 8, 12, anterior views; 3, 6, 9, 13, posterior views; 7, 14, distal views; 11, proximal view; 2, 5, anterior views of *T. debilis*. Scale equals 4 cm.

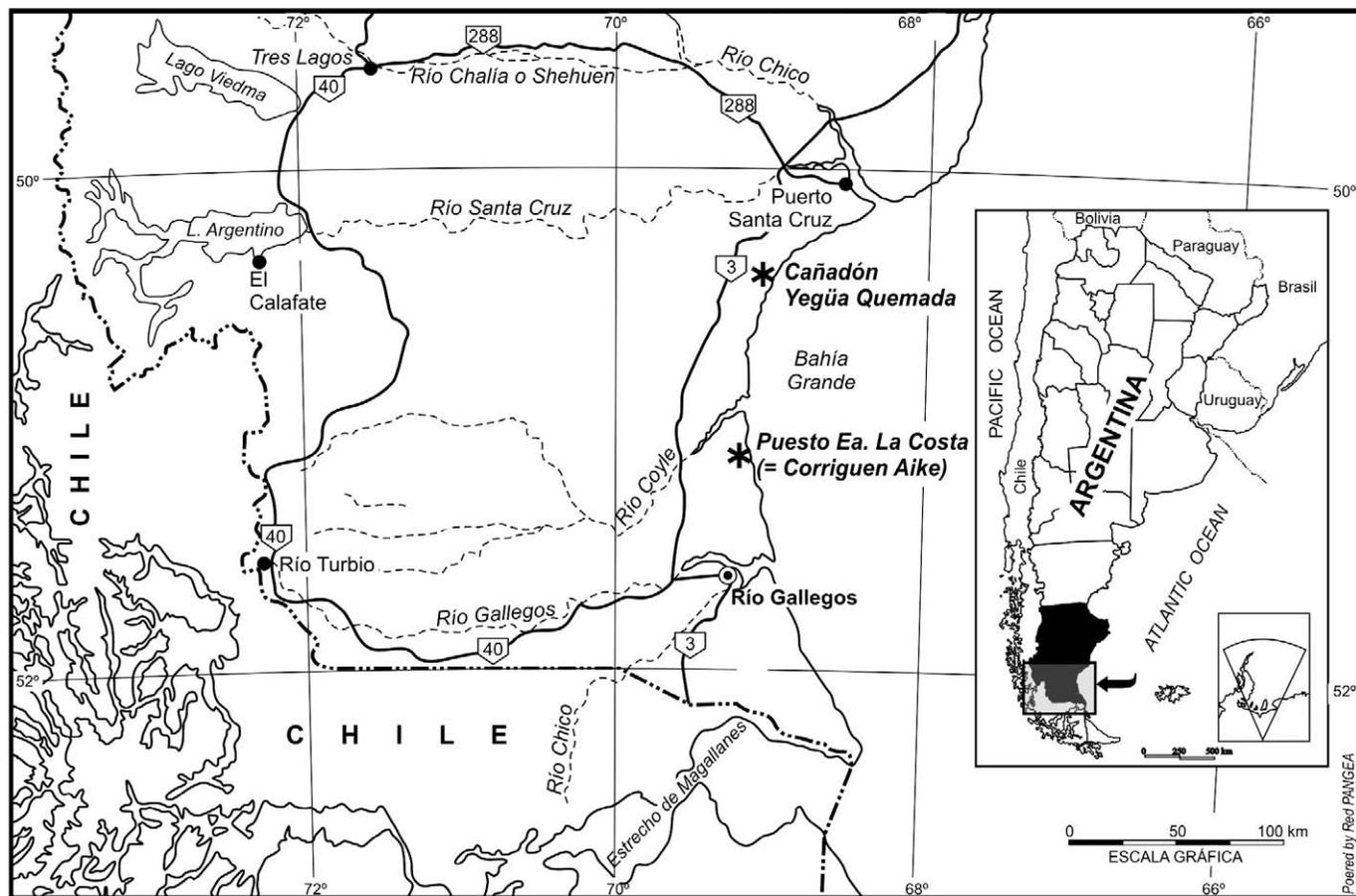


FIGURE 2—Location map showing the fossiliferous localities of Puesto Estancia la Costa (=Corriguen Aike) and Cañadón Yegua Quemada, Santa Cruz Province, Argentina.

designation of *T. debilis* as type of *Thegornis*, and thus an invalid nomenclatural act. The type species of a genus will remain the name bearer even if the name is later invalidated, thus it is impossible to transfer the name *Thegornis* to designate only *T. debilis*, since if *T. musculosus* is subsumed within *Buteo*, then *Thegornis* is also a synonym of *Buteo*. Hence, if only *T. musculosus* is included in *Buteo*, the name *Thegornis debilis* is not available, and a new generic name is mandatory for *T. debilis*.

**Included species.**—Until further refined, both *T. musculosus* and *T. debilis* must be included together within *Thegornis*. Because both species are recorded at the same locality and stratigraphic level, the difference in size relates to sexual dimorphism rather than to geographic or temporal changes, suggesting the possibility that *T. debilis* may represent a male of *T. musculosus*. This idea is in accordance with the sexual differences in size observed in *H. cachinnans*, in which males are smaller than females (Dunning, 2008). However, this hypothesis remains to be tested with the discovery of more specimens of both *Thegornis* species.

**Emended diagnosis.**—Rostrum more robust, larger, and with less upper curvature than living *Herpetotherinae*; narial aperture nearly rounded; supraorbital process of prefrontal elongated; orbital margins enlarged; fossae musculus temporalis (Livezey and Zusi, 2006) large and well extended towards sagittal plane above a strong crista nuchalis transversa; prominentia cerebellaris globose; basipterigoid processes absent; corpus scapulae straight, with sharply ridged margo caudalis and markedly grooved facies lateralis; head (caput

humeri) protrudent; crista deltopectoralis largely flared, abruptly angled; fossa m. brachialis transversely wide, proximally shortened, disto-medially enlarged and excavated; tuberculum lig. collateralis ventralis of ulna bulged; fossa iliocaudalis very deep; cross-section of femoral shaft elliptical; crista cnemialis cranialis broad, well ridged, not aligned to medial border of shaft; tendinal groove (sulcus extensorius) of tibiotarsus similar in depth to those of extant *herpetotherines* but longer; diminute lateral opening isolated between ossified loop and distal shaft margin; crista medialis hypotarsi large, well extended distally as in *Micrastur* and shorter than *Herpetotheres*; sulcus extensorius of tarsometatarsus limited by sharp shaft ridges, intermediate between the deeper and longer of *Micrastur* and shallower but shorter of *Herpetotheres*; cross section of midshaft H-shaped but not as marked as in *Micrastur*; anterior lateral border of shaft elevated as a crest reaching the distal foramen; outer posterior metatarsal ridge distally low, giving distal shaft a rather triangular cross-section; fossa metatarsi I large and deep; trochlea II slightly grooved; medial process of trochlea II thin, distinct (less pointed than *Micrastur*), and medially oriented.

*THEGORNIS MUSCULOSUS* Ameghino, 1895

Figures 1, 4–8.5

**Holotype.**—BMNH-A600. Distal fragment of right tarsometatarsus, housed at the British Museum of Natural History (Fig. 1.1, 1.3, 1.4, 1.6).

**Referred material.**—MPM-PV-3443. Cranium broken at the base of rostrum; distal fragment of rostrum (beak); one

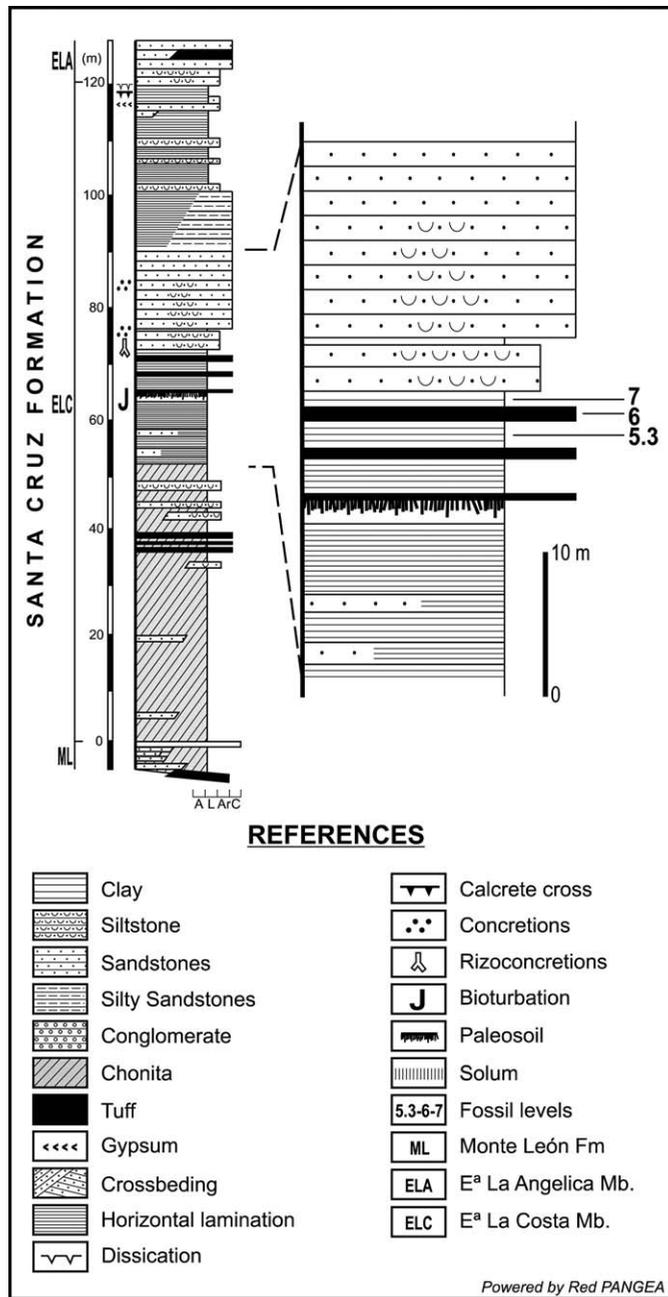


FIGURE 3—Stratigraphic profile of the Santa Cruz Formation.

cervical, two thoracic, and two caudal vertebrae; fragment of right pelvis; fragment of preacetabular ilium fused to anterior synsacrum; complete left femur; proximal end of right femur; complete left tibiotarsus plus left fibula; proximal end of right tibiotarsus plus right fibula; distal end of left tarsometatarsus; right tarsometatarsus without trochlea II; right and left metatarsals I; right digit I; phalanx 2 and unguis phalanx of left digit II; phalanx 1, 2, 3, and unguis of right digit III; phalanx 3 and unguis of left digit III; phalanx 2, 3, 4, and unguis of right digit IV; unguis phalanx of left digit IV; sternum; right humerus; left humerus lacking distal end; proximal fragment of left coracoid; proximal end of right coracoid; proximal fragment of left scapula; right clavicle (furcula); proximal fragment of right radius; left radius; left ulna lacking distal end; distal end of right ulna; phalanx 1 of right digit major (III).

*Locality and horizon.*—Puesto Estancia La Costa (=Corriguen Aike), Santa Cruz Province, Argentina. Tauber’s Fossiliferous Level 6, Estancia La Costa Member, Santa Cruz Formation (Tauber, 1997a, 1997b) (Figs. 2, 3).

*Correlation between Ameghino’s type locality and the new finding site.*—The type specimens of *T. musculosus* (BMNH-A600), *T. debilis* (BMNH-A601), and *Badiostes patagonicus* (BMNH-A602) were collected by Carlos Ameghino in 1892–1893, and described by his brother Florentino in 1895, who sold them to the Natural History Museum (then the British Museum of Natural History) in 1896, as part of a larger collection of fossil birds from Patagonia (Torcelli, 1935, p. 640, 641, letters 1180 and 1181).

The type specimen of *T. musculosus* is labeled as “Early Miocene: Santa Cruz Fm. Argentina: Santa Cruz: Tagua Quemada.” There are no records of a locality “Tagua Quemada” in the reports of Carlos Ameghino (see Marshall, 1976), but a catalogue handwritten by Florentino Ameghino and kept at the Museo Argentino de Ciencias Naturales records a specimen of *T. musculosus* collected by Carlos Ameghino during his field trips of 1892–1893 at Yegua Quemada from the Santacrucian beds there exposed. The description of this specimen agrees anatomically with the type specimen of *T. musculosus*. Therefore it seems highly probable that the reference to “Tagua Quemada” is a *lapsus calami* and we propose Yegua Quemada as new type locality of *T. musculosus*. This locality is situated north of the Coyle River, in the Corpen Aike Department, Santa Cruz Province, and approximately 90 km north from Puesto La Costa, where the new specimen MPM-PV-3443 was collected (Fig. 2). There is only one stratigraphic study of Yegua Quemada—albeit unfortunately still unpublished (Parras et al., 2005)—describing only the marine deposits of the early Miocene Monte León Formation, a widespread unit underlying the Santa Cruz Formation. At Yegua Quemada, the outcrops above the Monte León Formation include shell beds of the oyster *Crassostrea orbigny*, a species characteristic of the lowermost beds of the Santa Cruz Formation (Parras and Griffin, 2009). The lithology of the levels carrying the oyster beds and that of the Santacrucian beds with mammals are indistinguishable, a fact already noted by Ameghino (1900–1902) who included the marine levels at the base of his “Formación Santacruciana” (see Parras and Griffin, 2009). This suggests a tentative correlation of the Santa Cruz Formation at Yegua Quemada with the lower beds of the Estancia La Costa member at the beach exposures south of the Coyle River (Kay et al., 2008), suggesting some temporal range for *T. musculosus*.

The type specimen of *T. debilis* is labeled as “Santa Cruz: Corriguen-kaik” and also agrees with a specimen recorded in Florentino Ameghino’s handwritten catalogue. Tauber (1991, 1996, 1997b) proposed that his Puesto La Costa Locality corresponds to Carlos Ameghino’s Corriguenkaik or Corriguen Aike Locality (see Marshall, 1976) (Fig. 2). Although there are brief stratigraphic descriptions of this locality (Tauber, 1991, 1996), the information available does not allow us to infer from which level the type specimen of *T. debilis* was collected. However, it may come from the middle beds of the Estancia La Costa Member of the Santa Cruz Formation, the only levels outcropping at the beach platform in Puesto Estancia La Costa (Fig. 3). For a detailed discussion on the stratigraphic provenance of Carlos Ameghino’s collection in the Atlantic coast of the Santa Cruz Province see Tauber (1997a).

*Description.*—The cranium of *T. musculosus* (Fig. 4.1–4.6) exhibits the overall shape typical of the falconiforms, showing

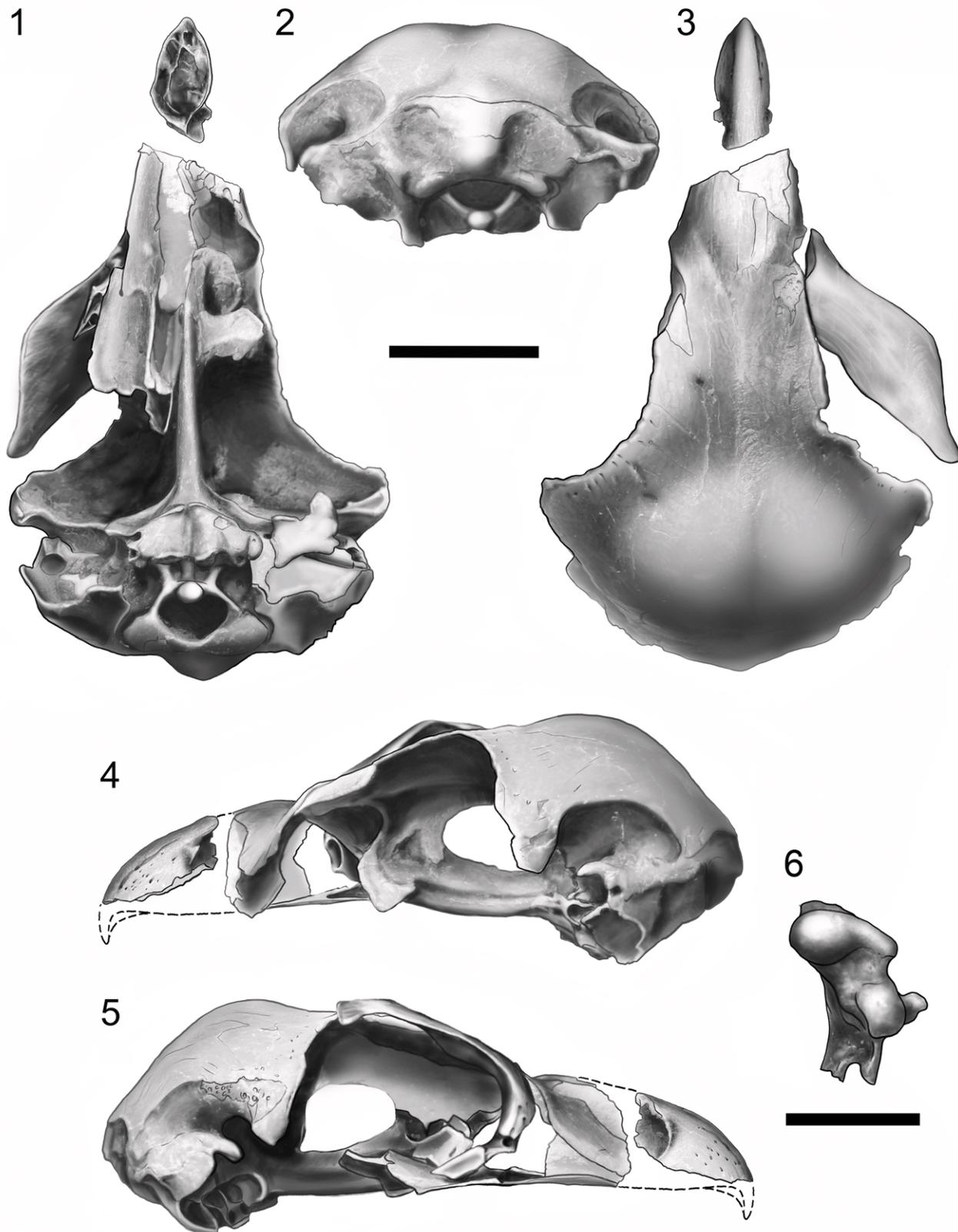


FIGURE 4—*Thegornis musculosus* Ameghino, 1894, MPM-PV-3443. 1–5, skull, scale=2 cm: 1, ventral; 2, posterior; 3, dorsal; 4, 5, lateral views; 6, quadrate bone in ventral view, scale=1 cm.

the conspicuous bulges of the frontal bones (cerebral swellings) and the median depression from brow to occiput. Notwithstanding the badly damaged state of preservation, the rostrum of the fossil specimen can be roughly reconstructed.

The upper curvature of the preserved part of the bill resembles that of *Milvago* Spix, 1824 (Fig. 4.4, 4.5). The cross section through the tip of the rostrum is also intermediate between the very high and laterally compressed of *Micrastur semitorquatus*

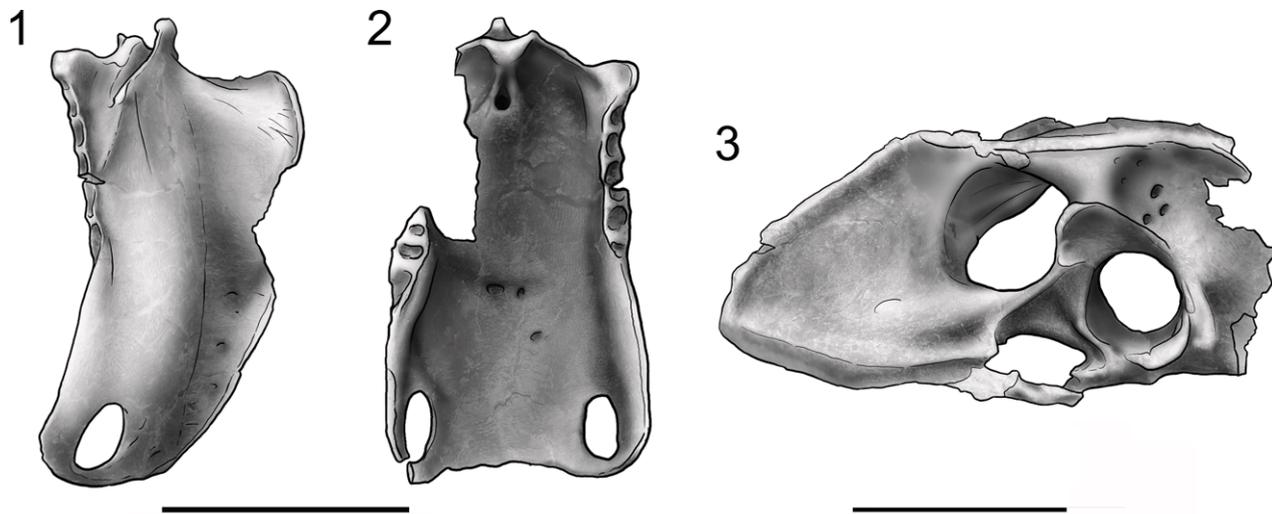


FIGURE 5—*Thegornis musculosus* Ameghino, 1894, MPM-PV-3443. 1, 2, sternum, scale=4 cm: 1, lateral view; 2, dorsal view; 3, pelvis in lateral view, scale=2 cm.

(Vieillot, 1817a) and *Herpetotheres cachinnans* and the more depressed of *Falco* Linnaeus, 1758, resembling that of *Micrastur ruficollis* (Vieillot, 1817a). The tomial margins of the premaxillae are simple and continuous, rather straight, without grooves and the sigmoid outline of the hook. Only the dorsoposterior corner of the left ovoid-shaped narial aperture, margined by the nasal bone, is preserved.

The frontonasal hinge is simple, with the presence of a fissure between the nasal and frontal process of the premaxilla. The frontal process of nasal contacts with the prefrontal but is not fused. It flares laterally as in *Micrastur*, less markedly than

in *Herpetotheres* (Fig. 4.3). The antorbital process of the prefrontal (os prefrontale) is characterized by a narrow, dorsolateral tear-duct notch. It contacts ventrally over a large part of its length with the lateral ethmoid (os ectethmoidale). The shape of the ventral portion of this process is somewhat broader than in *Micrastur* but thinner than in *Herpetotheres*. The incisura delimited between both bones, which connects the orbital and nasal cavities, shows an intermediate size, being hardly larger than in *Herpetotheres* but smaller than in *Micrastur*. The supraorbital process of the prefrontal is well developed and elongated (Fig. 4.3). Accordingly, the orbital

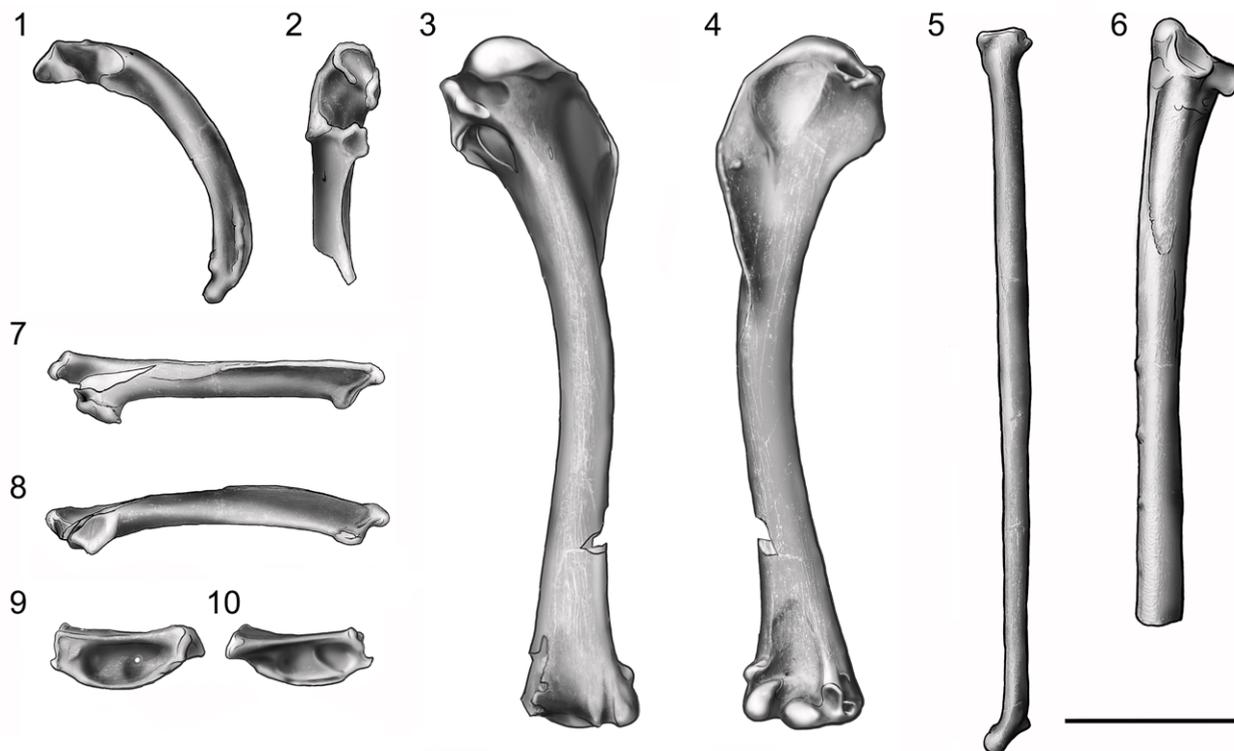


FIGURE 6—*Thegornis musculosus* Ameghino, 1894, MPM-PV-3443. 1, left scapula in dorsal view; 2, proximal end of right coracoid in dorsal view; 3, right humerus in anconal view; 4, right humerus in palmar views; 5, left radius in anconal view; 6, left ulna in palmar view; 7, left scapula in dorsal view; 8, left scapula in internal view; 9, phalanx 1 of right digit major (III) in external view; 10, phalanx 1 of right digit major (III) in internal view. Scale=3 cm.

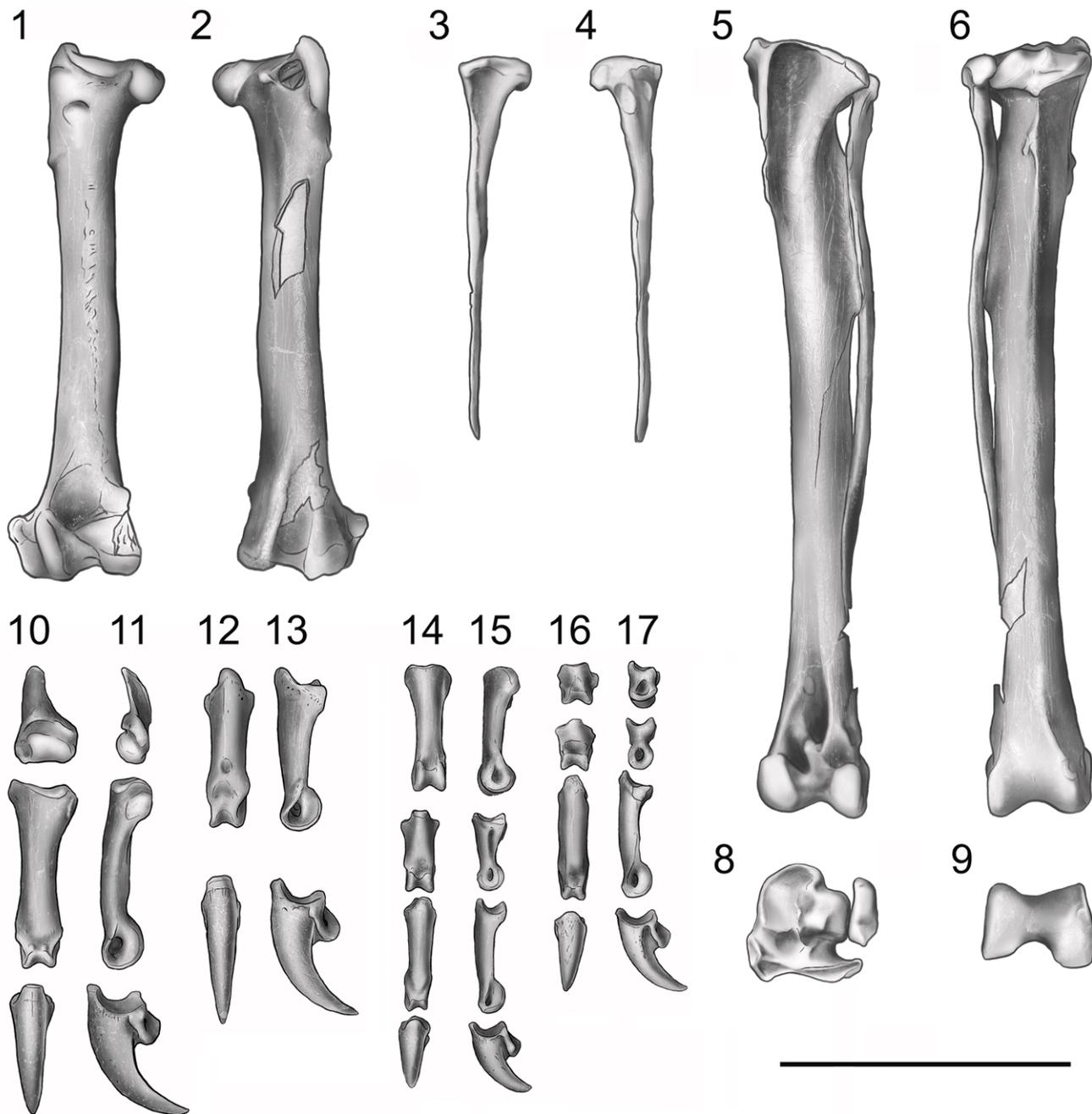


FIGURE 7—*Thegornis musculosus* Ameghino, 1894, MPM-PV-3443. 1, 2, left femur in posterior and anterior views, respectively; 3, 4, left fibula in lateral and medial views, respectively; 5–8, left tibiotarsus in anterior, posterior, proximal, and distal views, respectively; 9, 10, right metatarsal I and digit I in dorsal and lateral views, respectively; 11, 12, phalanx 2 and unguis of left digit II in dorsal and lateral views, respectively; 13, 14, phalanx 1, 2, 3, and unguis of right digit III in dorsal and lateral views, respectively; 15, 16, phalanx 2, 3, 4, and unguis of right digit IV in dorsal and lateral views, respectively. Scale=5 cm.

margins show a great extension, contacting for a short distance with the inner margin of the supraorbital process of the prefrontal. The apex of the postorbital process is broad as in *Herpetotheres*, being thinner and more pointed in *Micrastur*. The foramen of the interorbital septum is subelliptical as in *Herpetotheres*, being more quadrangular in the species of *Micrastur*, mainly the posterior border which tends to be vertically straight. However, this character seems to be ontogenetically quite variable.

The posterior tympanic process is similar to that observed in *Herpetotheres* and *Micrastur* (Fig. 4.4, 4.5), i.e., intermediate

in development and anteriorly curved, being rather reduced in *Milvago* and *Falco*, whereas it is conspicuous and pointed in *Caracara* Merrem, 1826. As a result of its presence, the caudal tympanic margin has an angle at the level of the head of the quadrate and also at the convergence between the squamosal and exoccipital (processus paroccipitalis). Viewed posteriorly, the tympanic margin and the exoccipital process width delimit a rounded outline (Fig. 4.1, 4.2). The dorsal part of the tympanic rim (os squamosum) is flared. The cerebellar prominence (prominentia cerebellaris) is conspicuous and globose, bordered laterally by deep depressions on exoccipitals

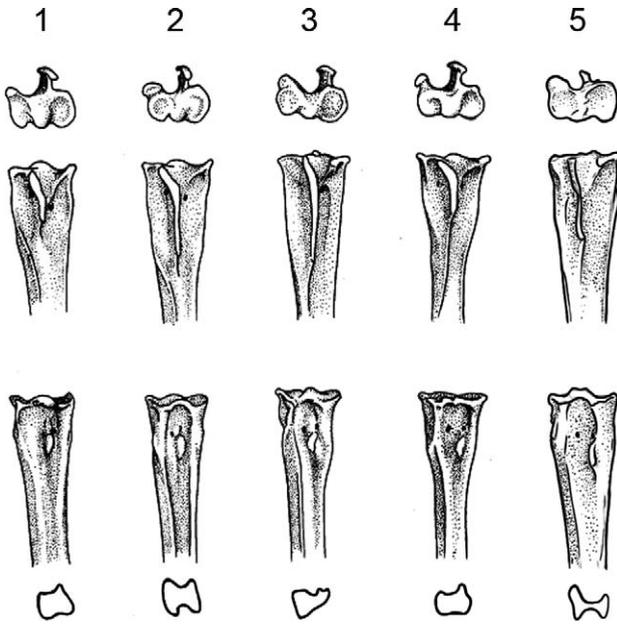


FIGURE 8—Proximal ends of tarsometatarsi of: 1, *Caracara plancus*; 2, *Micrastur semitorquatus*; 3, *Herpetotheres cachinnans*; 4, *Falco mexicanus*; 5, *Thegornis musculosus* Ameghino, 1894; 5, MPM-PV-3443 in proximal, posterior, medial, anterior, and shaft cross-section views. Modified from Jollie (1977b).

(Fig. 4.2). The caudal view of the skull resembles that of *Herpetotheres*, differing from *Micrastur* whose temporal fossae are smaller, shorter, and more laterally located, with a faint development of the crista nuchalis.

In ventral view, the quadrate is triangular and resembles the configuration found in *Herpetotheres*. The outer articular condyle (condylus lateralis) is large and globose, running posteriorly to join the caudal condyle (condylus caudalis), and showing a median curve between them which gives the surface a kidney-shaped appearance. This surface tends to be constricted anteroposteriorly in falconines. The medial articular surface (condylus medialis) is rather small and oval (Fig. 4.6). A well developed choanal ridge is delimited by the palatines. The basitympanic processes (proc. lateralis parasphenoidalis) at the sides of the basitemporal plate (lamina parasphenoidalis), as well as the pointed spine-like alasparsphenoid processes at the base of the parasphenoidal rostrum, are very well developed in *T. musculosus* (Fig. 4.1); similar to those of *Herpetotheres*, *Micrastur*, *Caracara*, and *Milvago*. The basipterigoid processes are absent, being only present as distinct spines in *Herpetotheres* and *Micrastur* within the living species of falconids.

**Sternum.**—The sternum of *T. musculosus* is similar in shape to that of *Herpetotheres*, i.e., more squared than that rectangular of *Micrastur* (Fig. 5.1, 5.2). The ventral manubrial spine (spina externa rostri) in *T. musculosus* is short, blunt, and triangular like in *Herpetotheres*, compared with the thin and elongated spine which is typical of the remaining falconids. There are short and separate lateral processes like in *H. cachinnans* and *M. ruficollis*, somewhat more joined in *M. semitorquatus*, whereas they are placed closer to the midline merging in a single medial dorsal spine in *Milvago*, *Caracara*, and *Falco*. The coracoid sulci (sulcus articularis coracoideus) are long and overlap each other considerably like in *Herpetotheres*. The dorsal margins of these sulci have distinct coracoid pads. The sterno-coracoid process (processus cranio-lateralis) is short and laterally projected like in

*Herpetotheres*, similar to the orientation of *Caracara* but longer; whereas it is large and more cranially directed in *Micrastur*, *Milvago*, and *Falco*. The sterno-coracoid fossa is similar to that of *Herpetotheres*, confined below the anterior half of the costal margin, whereas it extends somewhat more posteriorly in *Falco*. The posterior margin of the sternum is square and has a pair of fenestrae. The keel (carina sterni) is thin, roughly triangular in outline, with the anterior margin jutting slightly forward at its apex, and tapering to its terminus on the posterior margin. Viewed posteriorly, the cross section of the sternum of *T. musculosus* is similar to that of *M. semitorquatus*, with the dorsal surface more concave than in *H. cachinnans*, *M. ruficollis*, caracarines, and falconines.

**Coracoid.**—The preserved portion of the shaft is more robust than in *Falco*, but less stout and less robust than in *Caracara*, *Milvago*, and *Herpetotheres*, very similar to the condition observed in the compared species of *Micrastur* (Fig. 6.2). Below the clavicular facet there is a small fossa which does not have pneumatic openings. The procoracoid process is well developed, with its tip curved abruptly dorsally enclosing the triosseal canal (sulcus m. supracoracoidei). In proximal view of head, this sulcus is rather rounded as in *Herpetotheres* and *Micrastur*, whereas it is ovoid in *Falco*, *Caracara*, and *Milvago*.

**Scapula.**—The overall shape of the scapula resembles those of *Herpetotheres* and *Micrastur* because it is straight along its length (Fig. 6.7, 6.8). The furcular articulation (facies articularis clavicularis) and the glenoid facet (facies articularis humeralis) are very well developed as in *Herpetotheres* and *Micrastur*, being the former articular surface proportionally larger than those of *Caracara*, *Milvago*, and *Falco*. The acromion of *T. musculosus* is less protrudent cranially than those of Caracarini, similar to blunt acromion of *Herpetotheres* and *Micrastur*. The neck and blade (corpus scapulae) are more robust and dorso-ventrally broader than in *Caracara*, similar to *Herpetotheres*, whereas *Falco* shows the slimmest configuration. The margo caudalis is markedly ridged. There is a shallow groove ventrally on half the width of the facies lateralis. This concavity extends from the middle portion of the blade to the apex (extremitas caudalis). Ridge and groove are both faintly developed and restricted to the caudal third of the scapular length in *Herpetotheres*, *Micrastur*, and *Falco*, but they are completely absent in *Caracara* and *Milvago*. The apex of the scapula of *T. musculosus* is anomalously truncated, exhibiting a knobby aspect due probably to a scared fracture produced in life.

**Clavicle.**—The head of the clavicle ends in a round knob (processus acromialis) which is directed slightly dorsally (Fig. 6.1). The lateral fossa on the extremitas omalis clavicularae is shallow and obscure, being only irregularly marked with pneumatic openings in *Falco*. The coracoid articularity pad (facies articularis acrocoracoidea) is large. Just below this articulation surface, *T. musculosus* and *Falco* have a procoracoid process and notch poorly indicated, being well developed in *Herpetotheres* and *Micrastur*, but completely lacking in *Caracara*. The shaft curves slightly, forming a moderate angle with the proximal end, similar to that of *Herpetotheres*, less marked than in *Micrastur*; whereas it is less angled in caracarines and *Falco*. The hypocleidium (apophysis furculae) is indistinct, with a small surface of articulation.

**Humerus.**—The humerus of *T. musculosus* resembles those of *Herpetotheres* and *Micrastur* in overall morphology; however, the curvature of shaft is similar to that of *Herpetotheres*, but lesser than in *Micrastur* (Fig. 6.3, 6.4). The head (caput humeri) is hardly more protrudent proximally

than in *Herpetotheres* and *Micrastur*, more than in Falconini, similar to the protrusion exhibited by *Caracara* and *Milvago* but more inclined anconally. The head has a well-defined anconal border limiting the capital groove (incisura capitis). The internal tuberosity (tuberculum ventrale) is similar to those of herpetotherines, less acuminate than in Caracarinini and Falconini. The external tuberosity (tuberculum dorsale), as well as the attachment for the tendon of m. supracoracoideus, does not exhibit important differences among the compared genera. The bicipital surface (intumescencia humeri) is less bowed and smaller than in *Caracara*, *Milvago*, and *Falco*. The deltoid crest delimits a broad and concave surface anconally. The external tricipital groove (sulcus scapulotricipitalis) is deeper than in *Herpetotheres*, similar to that of *Caracara* and *Falco*. Contrarily, the olecranal fossa (fossa olecrani) is shallower than in *Herpetotheres*, *Caracara*, and *Falco*. The attachment for the anterior articular ligament (tuberculum supracondylare ventrale) is smaller than in *Caracara* and *Herpetotheres*, with a comparatively similar surface than in *Micrastur* and *Milvago*. The external condyle (condylus dorsalis) is similar to the observed in living herpetotherines, more globose than in *Caracara*, *Milvago*, and *Falco*. Contrarily, the internal condyle (condylus ventralis) is more elongated in latero-medial extension and less rounded than in the latter, of similar shape than in *Herpetotheres* and *Micrastur*.

*Ulna*.—The shaft is robust. Nine pairs of anconal and inner papillae of secondaries can be observed on the preserved fragment of the left ulna, which lacks the distal portion of shaft and the corresponding distal end (Fig. 6.6). The olecranon is broad and blunt as in *Herpetotheres*, *Micrastur*, *Caracara*, and *Milvago*, whereas it is more acuminate in *Falco*. The impression of brachialis anticus (impressio brachialis) is deep and conspicuous, less distally extended than in *Falco* and *Micrastur*.

On the preserved distal epiphysis of the right ulna, it can be observed the subelliptical dorsal border of the external condyle (condylus dorsalis ulnae) which is similar to that of *Herpetotheres*, less rounded than in *Micrastur* and much more rounded than in Falconini. Caracarinines seems to present an intermediate condition between those of herpetotherines and falconines, but this character also shows intraspecific variation among taxa.

*Radius*.—The shaft is robust and straight, with both epiphyses broadened (Fig. 6.5).

*Pelvis*.—In dorsal view, the lateral outline or margin of the distal portion of the posterior iliac crest is straight, i.e., parallel to the synsacrum; whereas it is slightly (*Caracara*, *Milvago*) or strongly outcurved (*Falco*) in the remaining falconids compared (Fig. 5.3). In correlation with the orientation of these crests, the pelves of *T. musculosus*, *Herpetotheres*, *Micrastur*, and in a lesser extent those of the Caracarinini, are narrower than those of the Falconini. This crest is strongly raised over the dorsal surface where the ilium (ala postacetabularis ilii) meets the synsacral shield, being moderately raised in *Herpetotheres*; whereas in *Micrastur*, *Caracara*, *Milvago*, and *Falco*, it coincides exactly with the angle between the ala postacetabularis ilii and the lamina infracristalis ilii. Consequently, the fossa iliocaudalis is very deep in *T. musculosus*, moderately depressed in *Herpetotheres*, and shallow in *Micrastur*, *Caracara*, *Milvago*, and *Falco*.

In lateral view, the fused plate of the ilium and ischium (ala ischii) tapers to a truncated posterior margin (processus terminalis ischii) without any indication of a notch (Fig. 5.3). The aboved mentioned plate is shorter antero-posteriorly but

dorso-ventrally taller than in *Micrastur*, *Caracara*, *Milvago*, and *Falco*, due to the marked slope or downward angling of the posterior portion of the ilium. This proportion resembles that of *Herpetotheres*. The shape of the iliosquadic fenestra (foramen ilioischadicum) resembles that of *Herpetotheres*. Its size is subequal to that of the obturator foramen. A similar proportion is also observed in *Herpetotheres*, whereas the iliosquadic fenestra is clearly larger than this foramen in *Micrastur*.

*Femur*.—Proximal end showing a well-developed trochanteric ridge (crista trochanteris), similar to that of the extant herpetotherines, more prominent anteriorly than in *Falco* but less than in *Caracara* and *Milvago* (Fig. 7.1, 7.2). There is a large, deep, and rounded pneumatic foramen just medial to the trochanteric ridge, similar to the foramina of *Herpetotheres* and *Micrastur*; whereas these openings are shallower in *Falco* and caracarinines, being smaller in *Falco* and elliptical in *Caracara*. However, this character seems to be quite variable among different specimens. The head is proportionally similar in size to that of *Herpetotheres*, i.e., bigger than in the remaining compared taxa.

The shaft is robust and antero-posteriorly depressed. The external and fibular condyles, together with the fibular groove (trochlea fibularis), are more laterally displaced than in *Caracara*, *Milvago*, and *Falco*. This orientation is consequence of the lateral torsion of both the distal portion of shaft and its epiphysis. The popliteal fossa is similar in depth to those of *Micrastur* and *Herpetotheres*, shallower than in the remaining falconids, with the exception of *Falco peregrinus* where it is shallower.

The epicondylus lateralis is larger than in the caracarinines, similar to those of *Herpetotheres* and *Micrastur*, with *Falco* showing the most reduced development.

*Tibiotarsus*.—The overall morphology of the tibiotarsal bone of *T. musculosus* is similar to that of *Herpetotheres*, being somewhat more robust and relatively shorter than the remaining genera compared with the exception of *Falco* (Fig. 7.5, 7.6). The proximal epiphysis has a slight medial displacement and, additionally, this relative displacement is reinforced by the pronounced incurvation of the shaft at the base of the outer cnemial crest. This configuration resembles *Micrastur* and *Herpetotheres*, although it is somewhat less displaced in them. The inner cnemial crest is strong, with broadened and well ridged margins (Fig. 7.8). The fibular crest (crista fibularis) is similar to those of *Micrastur*, conspicuous, and slightly more laterally expanded than in *Herpetotheres*, but much more than in the caracarinines and falconines. The lateral border of the tendinal groove is limited by a raised ridge, more pronounced in *Micrastur* than in *Herpetotheres* and caracarinines, but less than *Falco* (Fig. 7.5). The posterior intercondylar sulcus (trochlea cartilaginis tibialis) is broader and shallower than in *Micrastur*, similar in deepness to *Herpetotheres* (Fig. 7.9). The posterior condylar borders are not very extended proximally (i.e., shorter than in *Micrastur* and Falconinae) and subparallel, as in living herpetotherines, whereas they are smoothly convergent proximally in Falconinae (Fig. 7.5). An ossified loop on the anterior aspect of the distal end is formed by a spinelike ossification which fuses with the lateral margin of the shaft, isolating a lateral opening. This lateral opening is present in falconids with different degrees of development (Suschkin, 1905; Jollie, 1976, p. 224). Thus, it is represented by a small hole (*Herpetotheres*), a pit with perforations (*Micrastur*), or a well-developed opening (*Caracara*, *Milvago*, *Falco*). In *T. musculosus* this character resembles the condition observed

in *Herpetotheres*, i.e., the presence of a reduced depression exhibiting a diminute perforation on its surface (Fig. 7.5). A second osseous loop develops over the tendon of the m. extensor digitorum longus to form the supratendinal bridge (pons supratendineus), delimiting a medial opening distally. This bridge is narrow and oblique in *T. musculosus*, similar to that of *Micrastur*, whereas it is broader and more transverse in *Herpetotheres*. Consequently, the medial opening is more elliptical and proximo-distally elongated in *T. musculosus* and *Micrastur*, but more rounded and horizontally placed in *Herpetotheres*. It is broader and oblique in *Caracara*, *Milvago*, and *Falco* (Fig. 7.5).

*Fibula*.—It is very similar to those of other falconids used in comparison, but looks robust. It lacks other important features to be noted (Fig. 7.3, 7.4).

*Tarsometatarsus*.—The overall morphology of this bone strongly resembles those of *Herpetotheres*, sharing other important features with *Micrastur* (Fig. 1.4–1.13). The outer calcaneal process of *T. musculosus* is reduced, similar in shape and size to those of *Herpetotheres* and *Micrastur*. The extension of the medial calcaneal process, which continues as the medial hypotarsal ridge (Fig. 1.9, 1.11), is similar to that of *Micrastur*, intermediate between those very long of *Herpetotheres* (where it continues distally as a smooth ridge lateral to the median margin) and *Falco* (where it continues distally with the medial margin), and the shortest ridge of *Caracara* and *Milvago*. In the species of *Micrastur* compared, this ridge extends for approximately a fourth of the total tarsometatarsal length, varying between a third and almost a half of this length in *Herpetotheres*. The outer cotylar surface (cotyla lateralis) is just slightly higher than the inner (cotyla medialis), as in *Micrastur* and *Herpetotheres*, whereas *Caracara* and *Milvago* have the outer cotyla lower than the inner. In *Falco* this character is variable, having the cotylae at the same height (*F. mexicanus* Schlegel, 1850, *F. sparverius* Linnaeus, 1758) or the outer higher (*F. peregrinus* Tunstall, 1771).

In anterior view, the intercotylar prominence (eminentia intercotylaris) is broad and low, as in *Micrastur* and *Herpetotheres*, being narrow and more elevated in *Caracara* and *Milvago* and rather flat in *Falco*. The tuberositas m. tibialis cranialis is prominent and situated just distal to the inner proximal foramen on the medial side of the fossa infracotylaris dorsalis. This fossa is continuous with the anterior metatarsal groove (sulcus extensorius) (Fig. 1.8, 1.10). The depth of the fossa in *T. musculosus* is intermediate between the very deep and distally extended fossa of *Micrastur* which has strong and elevated borders, and that of *Herpetotheres* which is shallower and has lower borders. These borders are increasingly less marked in an ordered sequence including *Caracara*, *Milvago*, and *Falco*. In accordance, the shaft is grooved for a greater part of its length in *T. musculosus* and *Micrastur*, intermediate in depth and extent of grooving in *Herpetotheres*, followed by the caracarinids, with the shallower and shorter groove in *Falco*.

The cross section of the tarsometatarsal midshaft of *T. musculosus* shows a rather tetragonal form (H-shaped), similar to that found in *Micrastur*, with an important anterior and posterior grooving but not so deep as in the latter (Fig. 8.5). The remaining genera of falconids compared exhibit a rather flat posterior surface of shaft, having a nearly triangular (*Herpetotheres*) or square cross section (*Caracara*, *Milvago*, *Falco*). The distal portion of the outer posterior metatarsal ridge, at the level of the end of the medial hypotarsal ridge, is as low in *T. musculosus* as in *Herpetotheres*; but it extends as a

raised ridge somewhat more distally in *Micrastur*; whereas it furthermore remains as an elevated ridge beyond the level of the fossa metatarsi I in *Buteo* (Fig. 1.9, 1.11).

The adductor digiti II impression is very well developed, as in *Herpetotheres* and *Micrastur*, more faintly marked than in *Falco* and the caracarinids. The tendinal impression of this muscle is also clearly marked, surpassing the metatarsal scar (fossa metatarsi I) proximally and distally, whereas its extension can be traced as far as the proximal end of this scar in most falconids (Jollie, 1976, p. 268). This tendon is usually ossified in two needle-like structures that are preserved in the new specimen of *T. musculosus*. The fossa metatarsi I extends more proximally than in Caracarinids and *Falco*, but less than in *Micrastur* (Fig. 1.9, 1.11).

The second trochlea has a distinctively formed articulatory body, showing a slight median groove on its articular surface (Fig. 1.12, 1.13). However, the articular surface of the body of the trochlea II in *T. musculosus*, as well as in living herpetotherines, is less developed than in some Buteonine accipitrids (e.g., *Buteo*). In fact, this difference can be clearly appreciated in distal view when comparing their antero-posterior depths. Moreover, this feature is also evident in medial view: approximately the dorsal half of the inner side of the trochlea III can be observed above the dorsal border of trochlea II in *T. musculosus*, *Herpetotheres*, and *Micrastur*; whereas only the most dorsal trochlear border of the former raised above the latter in *Buteo*, showing how distinctly shaped is the inner trochlea in each group. We believe that the superficial resemblance, probably due to convergence, of the trochlea II of *T. musculosus* with that of buteonines led prior authors to mistake their assignments (Brodtkorb, 1964; Agnolin, 2006). Indeed, the trochlea II of buteonines is not typical of most accipitrids, and that of herpetotherines is not clearly representative of those observed in the remaining falconids. The trochlea II of *T. musculosus* presents a smooth depression in medial view, as in *Herpetotheres* and *Micrastur* (Jollie, 1976, p. 270). The outer rim of the trochlea III is somewhat more ventral or plantar than the inner, as in *Micrastur* and *Herpetotheres* (1.12, 1.13), whereas both ridges have similar heights in *Caracara*, *Milvago*, and *Falco*.

The articular surface of the trochlea IV is intermediate between the larger and broader trochlea of *Herpetotheres* and the thinner one of *Micrastur*. When viewed distally, it is clearly inclined laterally as in living herpetotherines, exhibiting a quite different orientation from that of *Buteo* where it parallels trochlea III. The lateral ridge of the fourth trochlea has a well developed process or wing which extends ventrally as in *Micrastur*, *Herpetotheres*, and most accipitrids; whereas this wing is shorter in *Caracara*, *Milvago*, and *Falco* (Fig. 1.12, 1.13).

*Foot*.—The digits of *T. musculosus* can be partially reconstructed based on the preserved elements of both the right and left feet as follows: a complete digit I; digit II, lacking the phalanx 1; a complete digit III; digit IV, lacking the phalanx 1 (Fig. 7.10–7.17). The foot of *T. musculosus* is typical of the falconids in having long, strong and sharp unguis phalanges, and a short basal phalanx of the third digit. The strengthening of the claws and the shortening of basal segments of the toes have been interpreted as a specialization for grasping (Jollie, 1976, p. 227).

#### CLADISTIC ANALYSIS

Parsimony analysis of our data set (Appendix 3) results in the production of only one most-parsimonious tree of 109 steps in length (MPTs), consistency index (CI) of 0.936, and

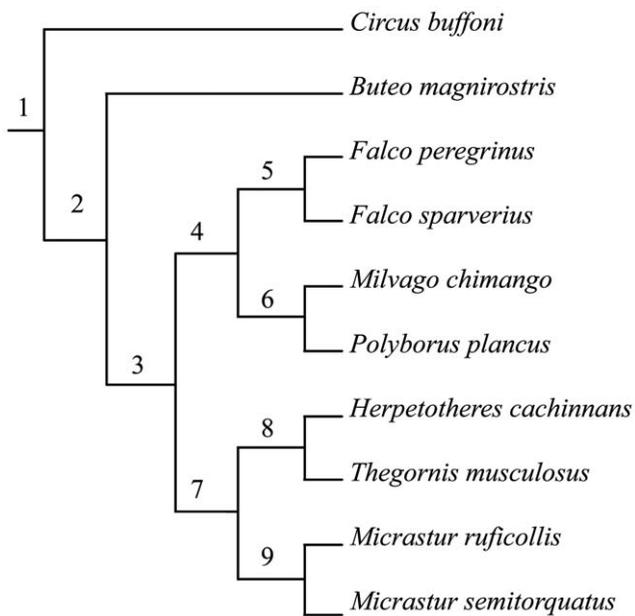


FIGURE 9—Cladogram obtained with TNT program. Numbers above branches indicate the different nodes.

retention index (RI) of 0.952 (Fig. 9). The topology of the tree is congruent with those obtained by previous cladistic analyses considering only extant genera of Falconidae (Griffiths, 1999; Griffiths et al., 2004).

The clade including the species of *Falco* (tribe Falconini) and the caracaras (tribe Caracarini) is strongly supported by seven synapomorphies, exhibiting a sister group relationship between them (Fig. 9, Node 4). This grouping is consistent with other phylogenetic studies defining the subfamily Falconinae on the basis of morphological and molecular data (Griffiths, 1999; Griffiths et al., 2004).

The Herpetotherinae clade was also recovered in our analyses, defined as a well-supported group containing the species of *Micrastur* plus the clade including *H. cachinnans* and *T. musculosus* (Fig. 9, Node 7). This group is supported by 11 exclusive synapomorphies (2[0], 8[0], 24[0], 26[1], 27[0], 32[1], 33[0], 41[0], 44[0], 45[0], 49[1]). Within it, *M. semitorquatus* and *M. ruficollis* appear weakly defined by only one synapomorphy (65[1]) as sister group of *H. cachinnans* plus *T. musculosus* (Fig. 9, Node 9). This latter clade presents six synapomorphies (4[0], 15[1], 28 [1], 29[1], 36[1], 38 [0]) (Fig. 9, Node 8), with *H. cachinnans* defined by six autapomorphies (1[0], 47[1], 50[1] 52[2], 53[1], 62[1]), and *T. musculosus* by two (35[1], 40[0]).

#### DISCUSSION

*Taxonomy and systematics of Thegornis.*—The morphology of the cranium of specimen MPM-PV-3443, together with other diagnostic features of the limb bones (v.gr. characters of the humerus, the tibiotarsus, and tarsometatarsus), clearly indicate its falconid affinity. The holotype of *Thegornis musculosus* (tarsometatarsus, BMNH-A600) is identical in shape and measurements to the same element in MPM-PV-3443, allowing the reference of the whole skeleton to *T. musculosus*. Thus, we reject both the modern placement of *T. musculosus* in the accipitrid genus *Buteo* and the assignment of *T. debilis* as the unique species of *Thegornis* (Agnolin, 2006). Agnolin (2006) mistakenly referred *Thegornis* to *Buteo* based on comparisons with *Buteo magnirostris* Gmelin, 1788, which

has been repeatedly placed in the monotypic genus *Rupornis* Kaupp, 1844 (Raposo et al., 2009).

*Thegornis musculosus* exhibits strong resemblances with the living species of herpetotherines (*Micrastur* and *H. cachinnans*) and differs substantially from falconines and caracarines. Some osteological characters of *T. musculosus* show a rather intermediate condition between those observed in the compared species of *Micrastur* and *H. cachinnans*. These facts indicate that *T. musculosus* could represent a morphotype linking the forest falcon clade with the lineage leading to the modern Laughing Falcon, which would accord well with our understanding of the history of paleoenvironments in the early Miocene of southern Patagonia (see below). *Thegornis debilis*, also known from a distal end of a tarsometatarsus, is more fragmentary but clearly smaller than the holotype of *T. musculosus* (Table 1).

*Paleoenvironments and evolution of herpetotherines.*—Changes in Patagonian plant communities throughout early Neogene times were recently analysed by Barreda and Palazzesi (2007) based on available paleobotanical and palynological information. These authors postulated that the late Oligocene-early Miocene floras in extra-Andean Patagonia were characterized by the occurrence of shrubby-herbaceous elements alternating with the previously widespread forests of Nothofagaceae, Podocarpaceae, and Araucariaceae. During the early Miocene, distinctive floristic elements of the Chaco Domain increased in diversity and abundance due to warm climates that allowed their southward dispersal (Barreda and Palazzesi, 2007, p. 44). The middle-late Miocene records show an expansion of the xerophytic-adapted flora coupled with the demise of the last megathermal and humid taxa, but riparian or gallery forests remained across extra-Andean Patagonian regions until about the middle Miocene (Barreda and Palazzesi, 2007, p. 42). Grass records were scarce during early Miocene, but there was a major expansion of grass-dominated communities in southern South America from late Miocene onward (Barreda & Palazzesi, 2007, p. 44). The presence of abundant Azollaceae water ferns in some levels, gallery forests, and grasslands interspersed with xerophytic vegetation during the middle-late Miocene of Patagonia, is consistent with the existence of flooded savannas or savannas with lotic water bodies. Thus, a contrast between coastal salt environments occupied by xerophytic associations and more forested inland environments is supposed to have developed.

This early-middle Miocene paleoenvironmental reconstruction, characterized by changing and rather contrasting habitat conditions, seems to be a good scenario to understand the evolution of the herpetotherine clade. All Herpetotherinae, extant and extinct, are strictly Neotropical, ranging from Mexico to northern Argentina (Ferguson-Lees and Christie, 2006). All living species of Herpetotherinae included in the genus *Micrastur* are inhabitants of humid and wet tropical forests, most often at the interior of primary forest (*M. plumbeus* Sclater, 1918; *M. gilvicolis* Vieillot, 1817b; *M. mirandollei* Schlegel, 1862; *M. buckleyi* Swann, 1917; *M. mintoni*, Whittaker, 2002), but the two widespread species (*M. ruficollis* and *M. semitorquatus*) also occur at forest edge habitats, second-growth forests with dense understorey and mangroves (Bierregaard, 1994). *Herpetotheres cachinnans*, the remaining and unique monotypic genus of the subfamily, is common in tropical and subtropical zones at forest edges and open forests, mixed palm savanna and forest, being always observed near large clearings if nesting in closed primary forests. Taking into account the habitat preferences above mentioned and the phylogenetic relationships postulated among members of this basal clade, it is plausible to think that an ancestral herpetotherine form, probably a strict forest dweller,

TABLE 1—Comparison of measurements between *Thegornis musculosus*, BMNH-A600 and MPM-PV-3443; *Thegornis debilis*, BMNH-A601; *Micrastur semitorquatus*, MNHT-1463, MNHT-601; *M. ruficollis*, MNHT-1124, MNHT-1147; and *Herpetotheres cachinnans* MNHT-624, MNHT-1125). All measurements are in mm. Missing data are indicated by (-).

	<i>T. musculosus</i> BMNH-A600	<i>T. musculosus</i> MPM-PV-3443	<i>T. debilis</i> BMNH-A601	<i>M. semitorquatus</i> MNHT-1463-601	<i>M. ruficollis</i> MNHT-1124-1147	<i>H. cachinnans</i> MNHT-624-1125
<b>Skull</b>						
Width through postorbital processes	-	51.0	-	37.5/37.8	28.3/28.2	47.0/46.0
Skull base width through otic region	-	20.0	-	37.1/35.6	27.0/26.4	42.8/41.2
<b>Tibiotarsus</b>						
Total length	-	130.64	-	111.3/104.1	71.2/67.6	98.5/97.9
Proximal width	-	20.10	-	13.1/11.2	7.8/7.6	13.5/12.5
Distal width	-	17.5	-	11.6/11.5	6.8/6.8	12.2/12.2
<b>Tarsometatarsus</b>						
Proximal width	-	17.6	-	12.7/11.2	7.0/6.8	12.3/12.4
Distal width	21.0	20.5	14.0	12.4/11.3	6.6/6.8	14.2/13.3
Least shaft width	9.0	9.0	6.0	5.0/4.5	3.8/4.0	5.9/5.9
Least shaft depth	8.0	7.4	-	-	-	-
Length scar metatarsal I	15.0	15.2	-	-	-	-
Greatest width scar metatarsal I	4.0	4.15	-	-	-	-
Hypotarsal crest length	-	27.3	-	22.3/21.0	12.4/13.2	26.3/18.0
Total length	-	95.04	-	90.0/84.0	61.2/57.8	63.7/64.0
<b>Humerus</b>						
Total length	-	120.80	-	79.2/76.9	48.7/46.2	86.6/85.2
Distal width	-	22.10	-	14.9/14.3	9.2/9.0	15.6/15.4
Proximal width through tuberosities	-	25.0	-	16.3/15.2	10.0/9.5	17.8/17.4
<b>Radius</b>						
Total length	-	126.3	-	75.8/71.3	48.3/46.2	91.3/90.5
<b>Sternum</b>						
Length	-	71.2	-	57.5/56.6	33.8/32.5	57.0/56.3
Width through attachment last rib	-	40.3	-	28.0/26.2	17.5/18.4	34.4/33.3
<b>Femur</b>						
Total length	-	90.92	-	-/69.4	46.0/46.5	64.4/63.2
Proximal width	-	21.85	-	15.0/13.8	7.8/7.6	13.8/13.6
Distal width	-	21.75	-	15.2/14.4	8.8/8.6	14.6/14.0
Width midshaft	-	10.8	-	-/6.7	4.0/3.8	6.6/7.0
Depth midshaft	-	7.54	-	-/6.3	3.5/3.8	6.2/6.8

gave rise to *Thegornis musculosus* at the ecotonal margins of the gradually vanishing wet and humid forested communities. A next, more speculative, evolutionary step would be that, in association with the suggested Miocene trend of sustained warming and increasing aridity of habitats, an *Herpetotheres*-like descendant adapted to more open Chacoan conditions arose from among the ancestral *Thegornis*-like forms. The wide distribution of *H. cachinnans* (Mexico to northern Argentina) might provide a useful test of this hypothesis: if phylogeographic studies show a northward expansion of *H. cachinnans*, support would be added to a southern *Herpetotheres* origin from *Thegornis*-like ancestors.

Living *Micrastur* forest-falcons display little osteological variation, and illustrate the fact that species level differentiation might arise without concomitant dramatic morphological changes in the group. Indeed, the taxonomy of *Micrastur* has been greatly enhanced by the recognition of species and/or subspecies after minor differences in specimens and evident differences in vocalizations were studied (Schwartz, 1972; Whittaker, 2002).

Future studies on the natural history and the phylogeny of falconids, together with a more thorough analysis of Tertiary vertebrate communities, will illuminate the herpetotherine evolutionary scenarios herein proposed.

ACKNOWLEDGMENTS

We thank H. Alvarenga (MNHT), P. Tubaro, and C. Kopuchian (MACN) for access to the comparative material of living species, S. Chapman who kindly sent us photographs of the type specimens deposited in the BMNH, and J. González for the illustrations, Dirección de Patrimonio Cultural of Santa Cruz Province for permission for the field work, and Museo Regional Provincial Padre M. J. Molina (Río Gallegos) for assistance for the field work, S. L. Olson, H. James, and anonymous reviewer for their constructive comments. Grants PICT 26219, PIP 1054, UNLP N474 (to SFV), and PICT 392 (to JIN) supported this research.

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- ACCEPTED 23 JUNE 2011
- APPENDIX 1—Specimens used for osteological comparisons and phylogenetic reconstruction.
- Micrastur semitorquatus*, MHNT 601, 1463; *M. ruficollis*, MHNT 1147, 1124; *Milvago chimango*, MHNT 675; *M. chimachima*, MHNT 745, MACN 430223; *Polyborus plancus*, MHNT 725, CICYTTP-ZV-AFAL-103, 104; *Herpetotheres cachinnans*, MHNT 1125, 624, MACN 54484, 26903; *Falco peregrinus*, MHNT 708; *F. mexicanus*, MHNT 842; *F. femoralis*, MHNT 605; *F. sparverius*, MHNT 52, CICYTTP-ZV-AFAL 101; *F. tinnunculus*, MHNT 1348; *F. rufigularis*, MHNT 951; *Buteo magnirostris*, MHNT 755; *B. swainsoni*, MHNT 809, MACN 1566, 18137, 23600; *B. jamaicensis*, MHNT 449, MACN 54481; *B. polyosoma*, MHNT 788; *B. platypterus*, MHNT 553; *B. lineatus*, MHNT 441; *B. albicaudatus*, MHNT 1869; *Busarellus nigricollis*, MHNT 885; *Heterospizias meridionalis*, MHNT, 312; *Rostrhamus sociabilis*, MHNT 667; *Buteogallus urubitinga*, MHNT 959; *Spizaetus tyrannus*, MHNT 1023; *Haliaeetus vocifer*, MHNT 1935; *H. leucocephalus*, MHNT 520; *Harpia harpyja*, MHNT 711; *Geranoaetus melanoleucus*, MHNT 918; *Aquila chrysaetos*, MHNT 514; *Leucopternis albicollis*, MHNT 1781.
- APPENDIX 2—Description of characters used for phylogenetic analysis.
0. Robustness and size of the rostrum: robust, vaulted, and large (0); robust but of moderate size (1); stubby and short (2); weak and short (3).
  1. Cross section through the tip of the rostrum: very high and laterally compressed (0); moderate in height and compression (1); low and depressed (2).
  2. Floor of the vestibule: slopes up and inward as the lower margin of the naris (0); leveled with the lower margin of the naris (1); below the lower margin of the naris (2).
  3. Tomial margins: simple and continuous (0); with grooves and sigmoid outline (1).
  4. Outer articular surface of quadrate: large and kidney-shaped, with its long axis running posteriorly (0); small and constricted anteroposteriorly (1).
  5. Ventral portion of the antorbital process of prefrontal: thin (0); intermediate in thickness (1); thick (2).
  6. Supraorbital process of the prefrontal: short (0); large (1).
  7. Free superciliary bone of the supraorbital process: present or with an indication of its presence (0); completely absent (1).
  8. Extension of orbital margins: great (0); moderate (1); small (2).
  9. Posterior tympanic process: extended from the dorsal margin of the tympanic cavity rather than the posterior (0); well extended from the posterior rather than the dorsal margin of the tympanic cavity (1).
  10. Size and shape of the posterior tympanic process: reduced (0); moderate in size and anteriorly curved (1); conspicuous and pointed (2); small, pointed (3).
  11. Articular process of the squamosal: well developed and sharp-pointed (0); absent, or short and blunt if present (1).
  12. Zygomatic process of the squamosal: absent or short (0); long (1).
  13. Basitympanic process at the sides of the basitemporal plate: vestigial or absent (0); very well developed (1).
  14. Basiparasphenoid plate width: broad (0); narrow (1).
  15. Lateral process of sternum: absent or well lateralized if present (0); short, separated and located near midline (1); vestigial or nearly merged toward the midline in a single medial dorsal spine (2).
  16. Ventral manubrial spine: short, blunt, and triangular (0); thin and elongated (1).
  17. Scarless triangular area delimited between the sternocoracoid fossa and the m. supracoracoideus scar: absent (0); distinct (1).
  18. Coracoid head: Bent markedly forward (0); not bent forward (1).
  19. Procoracoid process: reduced (0); well developed (1).
  20. Clavicular facet: projected noticeably from the head (0); steeply inclined forming a continuous plate (1).
  21. Clavicular head: ending in a pointed extreme and directed backward (0); ending in a round knob and directed slightly upward (1).
  22. Furculum shape (anterior view): V-shaped (0); U-shaped (1).
  23. Internal tuberosity: small, pointed, and protrudent (0); large, but slightly prominent anconally (1); large and protrudent (2).
  24. Bicipital crest: short, meeting shaft more perpendicularly (0); long, meeting shaft obliquely (1).
  25. Bicipital surface: reduced, slightly bowed (0); large, markedly bowed (1).
  26. Lateral flaring and margin of deltoid crest: strong, with margin angled at mid-length (0); moderate, with margin angled at mid-length (1); moderate, with continuous or not angled margin (2).
  27. Location of the ectepicondylar prominence: accentuated lateral and distal location (0); more medially and proximally placed (1).
  28. Brachial depression: transversally narrow, well elongated proximally, with its disto-medial border deeply excavated (0); transversally broadened, proximally shortened, with shallow excavation of its disto-medial border (1).
  29. Attachment of the anterior articular ligament: small (0); intermediate (1); large (2).
  30. External condyle: globous, shortened (0); elongated proximo-distally (1).
  31. Internal condyle: elongated in latero-medial extension (0); rounded (1).
  32. Entepicondyle: short, not surpassing the internal condyle distally (0); long, extending beyond the internal condyle and laterally directed (1); long, extending beyond the internal condyle and parallel to shaft (2).
  33. Curvature of humeral shaft: strong (0); moderate (1).
  34. Margin of the posterior iliac crest in dorsal view: S-shaped (0); straight (1); outcurved (2).
  35. Fossa iliocaudalis: superficial (0); very deep (1); moderately deep (2); shallow (3).
  36. Ala ischii: elongated antero-posteriorly, dorso-ventrally low, with very strong downward angling (0); short antero-posteriorly, dorso-ventrally tall, with marked downward angling (0); elongated antero-posteriorly, dorso-ventrally low, with moderate posterior slope (1).

37. Iliioischadic foramen size: similar to the obturator foramen (0); markedly larger than the obturator margin (1).
38. Femoral head size: large (0); small (1).
39. Trochanteric ridge: large (0); moderate (1); small (2) (*Falco*).
40. Cross-section of shaft: depressed antero-posteriorly, markedly elliptical (0); rather circular (1).
41. Lateral torsion of distal shaft and epiphysis: strong (0); moderate (1).
42. Popliteal fossa: shallow (0); deep (1).
43. Epicondylus lateralis: large (0); moderate (1); reduced (2).
44. Alignment of distal inner cnemial crest to medial border of tibiotarsal shaft: not aligned, but laterally placed (0); not aligned, but medially placed (1); aligned (2).
45. Joint between outer cnemial crest and shaft: incurved (0); rather straight (1).
46. Development of lateral opening distal to ossified loops on the anterior end of tibiotarsus: absent (0); a small hole (1); a pit with perforations (2); a conspicuous opening (3).
47. Supratendinal bridge developed over m.extensor digitorum longus: narrow and oblique (0); broad and more transverse (1); broad and oblique (2).
48. Outer calcaneal process: well developed (0); reduced (1).
49. Lateral hypotarsal ridge: not developed or, rather vertical, if insinuated (0); slightly defined or clearly marked, but oblique (1).
50. Size, relative position, and distal extension of medial calcaneal process (plus the medial hypotarsal ridge): small or faintly marked, medially placed, and very short in distal extent (0); conspicuous, centrally placed, very long, extending as a smooth ridge lateral to median shaft margin (1); conspicuous, centrally placed, very long, continuing distally with median shaft margin (2); conspicuous, centrally placed, long, moderate in distal extension (3); small, centrally placed, short, reduced distal extension (4).
51. Location of fossa for flexor hallucis brevis on plantar aspect of shaft: central (0); confined to medial aspect (1).
52. Borders of anterior metatarsal groove: not elevated (0); both sharp, elevated, very well marked (1); sharp (the outer), more rounded and lower (the inner) (2); both lower and less marked (3).
53. Distal extension of sulcus extensorius: great (0); intermediate (1); reduced (2).
54. Cross section of tarsometatarsus at midshaft: Triangular, with concave posterior surface (0); H-shaped, well grooved on anterior and posterior aspects (1); triangular, with rather flat posterior surface (2); square, with flat posterior surface (3); intermediate between markedly H-shaped and triangular (4).
55. Adductor digit II impression: well developed (0); less marked (1).
56. Lateral margin of fossa metatarsi I: forming an irregular ridge (0); uniformly margined (1).
57. Proximal extension of fossa metatarsi I: very well extended (0); extended (1); less extended (2).
58. Medial process of inner trochlea: broadened, rather fused with trochlear body, tapering at tip (0); thin, clearly separated from trochlear body, more truncated at tip (1).
59. Orientation of medial process of inner trochlea: well directed medially (0); moderate medial orientation (1); more plantarly orientated (2).
60. Second trochlea (anterior view): projected more distally than third trochlea (0); retracted more proximally than third trochlea (1).
61. Third trochlea: asymmetric (0); almost symmetrical (1).
62. Wing on lateral ridge of fourth trochlea: very well developed (0); moderately developed (1); less developed (2).
63. Orientation of fourth trochlea (distal view): parallels third trochlea or slightly inclined medially (0); strongly or slightly inclined laterally (1).
64. Proportion between length/robustness of shaft: very long and markedly slender (0); moderate length and robustness (1); short and rather robust (2).
65. Depth of fossa infracotyleris dorsalis: shallow or intermediate in depth, with low borders (0); very deep, with strong and elevated borders (1).

## APPENDIX 3—Character taxon matrix used for phylogenetic analysis.

Circus\_buffoni  
111110001031000000000000100100000100011111000102000000000200000010

Buteo\_magnirostris  
111110001031000000000000100100000100011111000102000000000200000010

Thegornis\_musculosus  
110001110110111101111111001011001011100100001010113110401111110120

Micrastur\_semitorquatus  
110010110110111211111111001000001012211110001020113110101011110101

Micrastur\_ruficollis  
110010110110111211111111001000001012211110001020113110101011110101

Herpetotheres\_cachinnans  
100002110110111101111111001011001012100110001011111121201111111120

Caracara\_plancus  
01101201212011121111112112102110123201011112132104132311212112110

Milvago\_chimango  
311012012100111211111112112100110123201011112132104132311212112110

Falco\_sparverius  
222110111100111211111112110102112123211211122132102132311210112120

Falco\_peregrinus  
222110111100111211111112110102112123211211122132102132311210112120