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NEUROCRANIAL AND BRAIN ANATOMY OF A LATE MIOCENE EAGLE (AVES, ACCIPITRIDAE) FROM PATAGONIA

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ABSTRACT—The neurocranial fragment from the Late Miocene (Huayquerian SALMA, 9,0 to 6,8 Ma) of Estancia La Pastosa new locality, Puerto Madryn Formation, Patagonia, Argentina, is described. This is the first available fossil skull of Accipitridae in South America. Features as the elongated-triangular shape of the cranial roof, vast separation between the processus postorbitalis and between both fossae temporalis, and narrow and acuminate outline of the fossa temporalis allow to assign the fossil to Accipitridae Vieilloit, 1816. The well-preserved cavum cranii allowed construction of an endocast that partially reflects brain anatomy. The latter is very similar to those of extant and fossil species of Accipitridae. This fossil eagle is the only predator recorded at this new Miocene locality thus far.

INTRODUCTION

The extant Accipitridae (eagles, buzards, kites) Vieilloit, 1816 are a conspicuous family of Falconiformes Sharpe, 1874 with widespread distribution, and whose fossil record is known from the Eocene of Europe and America (Olson, 1973; Mayr, 2005). In Argentina, fossil Accipitridae have been known since the Eocene, represented by only a few postcranial fragments (Tonni, 1980; Tambussi and Noriega, 1996; Agnolin, 2006). The Late Miocene neurocranial fragment MPEF-PV- 2523 presented here, found in sediments of Patagonia (Chubut Province, Argentina) can be assigned to Accipitridae. The fossil belonged to a large bird and constitutes the first skull remain available for this family in South America. It has long been recognized that findings of fossil birds are less frequent than those of other vertebrates, and skull remains are particularly scarce, hence the particular importance of this fossil. Likewise, the available paleoneurological information about birds has come from few known natural endocasts, and mostly through indirect data obtained from neurocranial remains. The remarkable preservation of the cavum cranii of the neurocranial fragment MPEF-PV- 2523 allowed the construction of an endocast and permitted to study the brain anatomy. The goals of this contribution are to provide an anatomical description of MPEF-PV- 2523 and the endocast obtained, and compare it with other known bird endocasts.

GEOLOGICAL SETTING

The locality Estancia La Pastosa (S 42° 49.373′, W 63° 48.917′) is situated in the marine Puerto Madryn Formation that overlies the Early Miocene to earliest Middle Miocene Gaiman Formation (Scasso et al., 2001). The age of Puerto Madryn Formation is early Late Miocene based on radiometric data (9.4 Ma, Zinsmeister et al., 1981; 10.0 ± 0.3 Ma, Scasso et al., 2001).

The new site is situated on a high coastal cliff, 25 km southwest of Punta Delgada, Península Valdés, Chubut Province, Argentina (Fig. 1). Puerto Madryn Formation corresponds to a marine transgression along the western coast of Patagonia during the Paleogene/Neogene and is known for its abundant marine invertebrate (Del Río et al., 2001) and vertebrate fauna (Acosta Hospitaleche et al., 2007; Dozo et al., 2002). More precisely, MPEF-PV- 2523 was found in sediments of the upper levels of Puerto Madryn Formation, formed by interbedded sandstones and mudstone with ripple marks in the more sandy sectors. The fossils were found in an intraformational lens-shaped conglomerate linked to the regressive phases of the Miocene sea, transitional to continental environments. The continental tetrapods recovered from the site have confirmed a Huayquerian age (Late Miocene, between 8 and 10 Ma) (Dozo et al., 2007). The presence of Dendrocygninae anseriforms (Acosta Hospitaleche et al., 2007) and Hydrochoeridae rodents (Vucetich et al., 2005) is in agreement with a continental aquatic environment.

The Estancia La Pastosa locality seems to show a scenario similar to that of Rincón Chico locality, a nearby site of similar age and sedimentary environment which contains a rich vertebrate fossil assemblage, with terrestrial and aquatic continental fauna (Dozo et al., 2002, 2007).

MATERIALS AND METHODS

The fossil material MPEF-PV- 2523 is deposited in the collection of MPEF-PV and skulls used for comparisons belong to the collections of MLP, MLP-PV-OR and MACN (see Institutional Abbreviations below). Anatomical terminology follows Baumel et al. (1993) unless otherwise indicated; vernacular names are listed in the anatomical abbreviations section. Endocasts were made for MPEF-PV- 2523 and the extant *Geranoaetus melanoleucus* skull for comparison, using President Plus Jet (light body) Coltène silicone rubber. Measurements were taken using Vernier calipers with 0.01mm increments. For comparison, skulls of
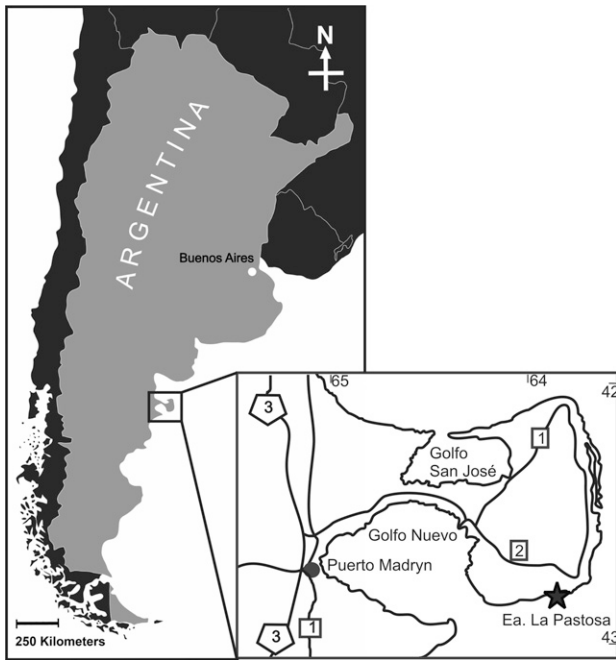
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FIGURE 1. Sketch map of Península Valdés showing geographical position of the Estancia La Pastosa locality where the fossil (MPEF-PV-2523) was discovered.

the following extant species of Accipitridae and Falconidae were studied. Accipitridae: *Astur palumbarius*: MLP 578; *Buteo albicaudatus*: MLP 575, 576; *Buteo jamaiquensis*: MACN 26597; *Buteo magnirostris*: MLP -PV-OR 691, 362; *Buteo polyosoma*: MLP -PV-OR 691, 692; *Circus cinereus*: MLP-PV-OR 690*; Geranoaetus melanoleucus*: MACN 23603, MLP 622, 623, MLP-PV-OR 696, 843; *Heterospizias meridionalis*: MACN 18248; *Ictinia plumbea*: MACN 1565a. Falconidae: *Falco femoralis*: MLP 404; *Falco peregrinus*: MLP 638; *Falco sparverius*: MACN 68441, 68598, 54489, MLP 54, 55, 56; *Falco tinnunculus*: MLP 640; *Milvago chimachima*: MACN 68438, 54485; *Milvago chimango*: MLP 60, 271, 638; *Milvus regalis*: MLP 627; *Polyborus plancus*: MACN 54350, MLP 580, 581, MLP-PV-OR 311; *Polihierax semitorquatus*: MACN 54483.

Institutional Abbreviations—**MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Sección Ornitología Buenos Aires, Argentina; **MLP**, Museo de La Plata, Buenos Aires, Argentina; **MLP-PV-OR**, Museo de La Plata, La Plata, Buenos Aires, Argentina Avian skeletal collection of the División Paleontología Vertebrados; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

Anatomical Abbreviations—**ac**, auricula cerebelli; **b**, bulges of frontal bones; **c**, cerebellum; **cnt**, crista nuchalis transversa; **cqs**, cotyla quadratica squamosi; **crt**, crista temporalis; **ct**, cavum tympanicum; **cv**, crista vallecularis; **dp**, depressio frontalis; **em**, eminentia sagittalis; **fc**, fossa cerebelli; **fcm**, fossa cranii media; **fcr**, fossa cranii rostralis; **fm**, foramen magnum; **fs**, frontal sulcus; **ft**, fossa temporalis; **fv**, vascular foramina; **ht**, hemispherium telencephali; **ies**, impressio eminentia sagittalis; **mae**, attachment area of musculus adductor mandibulae externus; **pc**, prominentia cerebellaris; **pp**, processus postorbitalis; **ps**, processus squamosalis; **rc**, recessus columellae; **rtc**, recessus tympanicus caudalis; **rtd**, recessus tympanicus dorsalis; **rtr,** recessus tympanicus rostralis; **ro**, rete ophthalmicum; **rog**, groove related to rete ophthalmicum; **sd**, sinus sagittalis dorsalis; **so**, sinus occipitalis; **sof**, supraoccipital fossa; **sr**, supraforaminal ridge; **ssd**, sulcus sinus sagittalis dorsalis; **st**, sinus transversus; **sts**, sinus transversus

mark; **tm**, tectum mesencephali; **v**, vallecula; **vcd**, vena cerebralis dorsorostralis; **vcc**, vena cerebralis dorsocaudalis.

Vernacular Names—auriculae cerebelli (flocculus), bulbus olfactorius (olfactory bulbs), cavum cranii (cranial cavity),cavum tympanicum (middle ear region), cotyla quadratica squamosi (quadrate articular facet for the squamosal), crista nuchalis transversa (nuchal crest) cristae temporalis (temporal crest), depressio frontalis (front depression), eminentia sagittalis (sagital eminetia or wulst), fissura interhemisferica (interhemispheric fissure), fossa temporalis (temporal fossa), hemispherium telencephali (cerebral hemispheres), processus postorbitalis (postorbital process), processus squamosalis (squamosal process), prominentia cerebellaris (cerebelar prominence), recessus tympanicus caudalis (posterior tympanic recess, sensu Saiff, 2006), recessus tympanicus dorsalis (upper tympanic recess, sensu Saiff, 2006), recessus tympanicus rostralis (presphenoids sinus, sensu Saiff, 2006), sinus sagittalis dorsalis (dorsal sagittal sinus), sinus transversus (transversal sinus), tectum mesencephali, (optic lobe)

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
NEOGNATHAE Pycraft, 1900
FALCONIFORMES Sharpe, 1874
ACCIPITRIDAE Vieilloit, 1816
Indeterminate genus and species
Figs. 2–4

Referred Material—MPEF-PV- 2523

Measurements—Length from supraforaminal ridge to anterior border of frontal bones 50.90 mm; width between remains of postorbital processes 51.20 mm.

DESCRIPTION

MPEF-PV-2523 comprises a partial skull roof and remains of lateral, occipital, orbital regions (facies orbitalis of os mesethmoidale, frontale, and laterosphenoidale are preserved), cavum tympanicum, and the cavum cranii (Fig. 2A–C). It is nearly triangular in shape in dorsal view (Fig. 2A) and the shallow fossae temporalis can be barely distinguished from this view.

Neurocranium Dorsal, Ventral, and Lateral anatomy

The fossil preserves the posteriormost portion of the os frontale which bears a shallow depression, the depressio frontalis (Fig. 2A). The os frontale has two cerebral bulges (sensu Jollie, 1976) separated by a shallow groove (here named frontal sulcus). In lateral view (Fig. 2B), the dorsalmost region of the fossa temporalis (the right is better preserved) of MPEF-PV-2523 presents a narrow and acuminate outline. The cristae temporalis are well defined (Fig. 2B); the area between them and the fossa temporalis is the place for attachment of musculus adductor mandibulae externus. This area has a flat surface and rounded outline (Fig. 2B). Only the proximal portion of the left processus squamosalis (sensu Pascotto et al., 2003) is preserved, whose ventral part houses the subcircular cotyla quadratica squamosi (Fig. 3). The processi postorbitalis (Fig. 2B) are represented by their proximal parts, both present and widely separated from each other.

The occipital region (Fig. 2C) presents two concave and excavated areas on the os supraoccipitale, named supraoccipital fossae (sensu Pycraft, 1902) where the musculus splenius capitis is inserted. They are separated by the prominentia cerebellaris, which is strongly convex and dorsoventrally elongated. Only the lateral and dorsal margins of the foramen magnum have been preserved, and there are no remnants of the occipital condyle. The supraforaminal ridge (sensu Pycraft, 1902) are well marked. The noticeable crista nuchalis transversa is continuous, semicir-
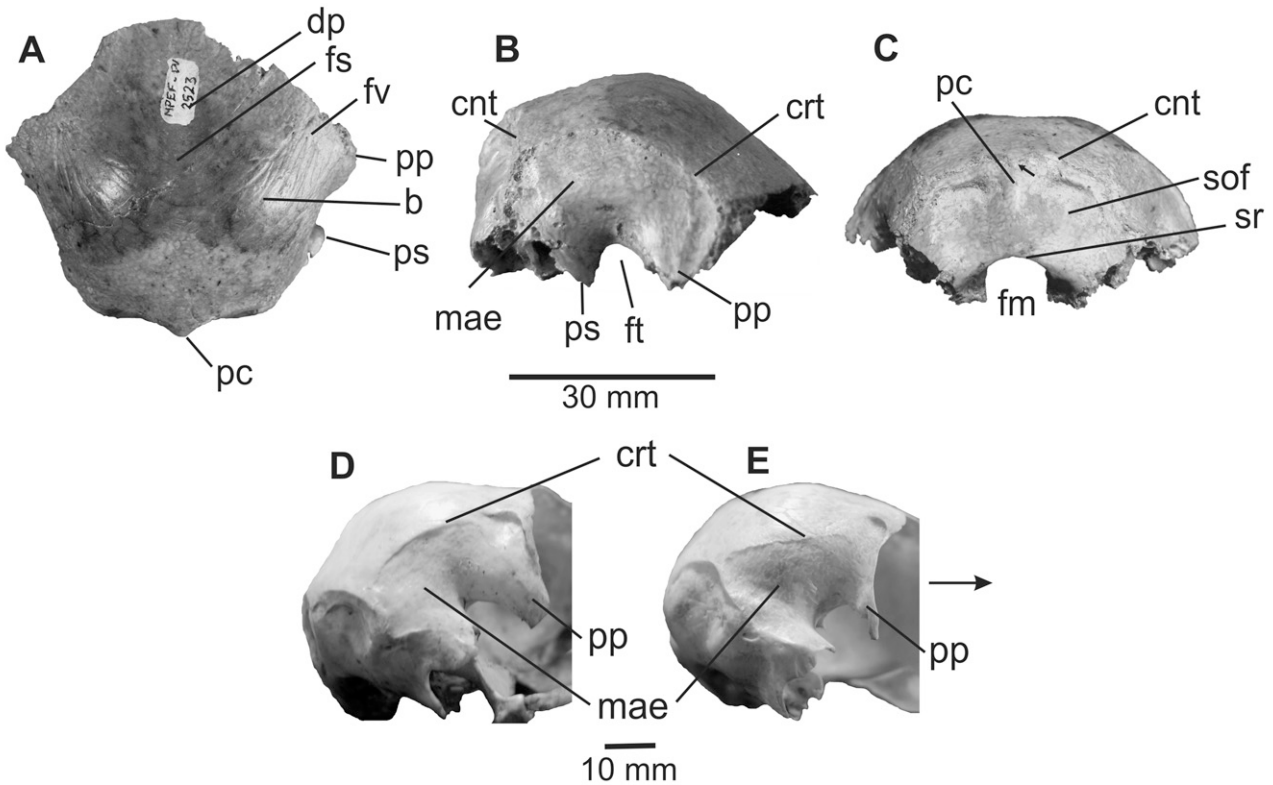
FIGURE 2. **A**, **B** and **C**, Accipitridae specimen MPEF-PV- 2523. **A**, dorsal view; **B**, lateral view; **C**, posterior view, arrow indicates location of the notch of crista nuchalis; **D** and **E**, posterior lateral view of extant Accipitridae and Falconidae specimens. **D**, *Geranoaetus melanoleucus*: MLP-PV-OR 696; **E**, *Falco sparverius* MLP-PV-OR 638, compare the area of attachment for musculus adductor mandibulae externus among B, D, and E. Arrow indicate anterior portion of the skull.

cular in shape and bearing a notch (Fig. 2C). This accident corresponds with the cranial pars of the musculus biventer cervices, which would have been well developed in the fossil specimen. Both crista nuchalis and crista temporalis converge at the level of the processus squamosalis.

In ventral view, the rostralmost region of the orbit (Fig. 3) bears the sulci nervus olfactorii and the one of the foramina nervus olfactorii (the right) (not show in the figure). A shallow oval depression located at the caudalmost area of the orbit (Fig. 3), would correspond (according to its position) to the rete ophthalmicum, a vascular network present in extant birds that functions as a brain cooling system (Midtgärd, 1984). The depression continues rostrally as a well marked and sinuous groove that extends toward the sulcus nervus olfactorii without reaching it. This groove would indicate the position of the vena and arteria supraorbitalis, which perforate the supraorbital margin of the os frontale at multiple locations, determining corresponding vascular foramina (Baumel, 1993) (Fig. 2A).

The anatomical interpretation of the cavum tympanicum (Fig. 4) is difficult to make due to the incomplete preservation and the worn condition of these region. It appears as a great circular recess with three depressions. According to our interpretation, these depressions could correspond to the recessus columellae and remains of the recessi pneumatici paratympanici. The latter are defined according to Baumel (1993) as air-filled evaginations of the tympanic cavity with multiple foramina divided by depressions that enclose the cavum tympanicum in birds. The remains of these spaces in the fossil are located anteriorly and posteriorly to the recessus columellae. The recessus tympanicus dorsalis and recessus tympanicus rostralis are located anteriorly to the recessus collumelae, whereas the recessus tympanicus caudalis is located caudally to the latter structure.

Cavum Cranii and Endocast Anatomy

Cavum Cranii—The preserved cavum cranii (Fig. 3A–C) includes both broad fossae cranii rostralis that house the impressio eminentiae sagittalis (Fig. 3A, B). These fossae are shallow elliptical concavities, with the major axis oriented rostrocaudally. The crista vallecularis is a low, rounded and weak crest separating the impressio eminentiae sagittalis of the fossa cranii
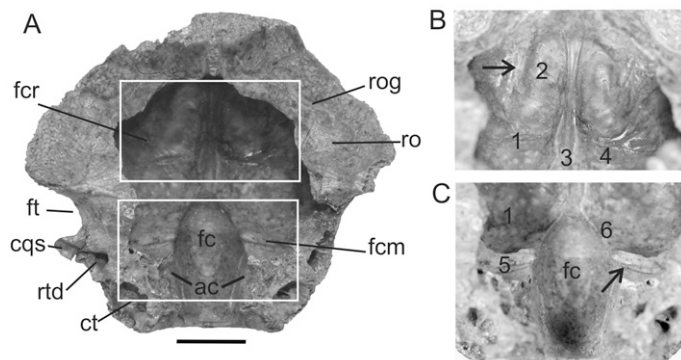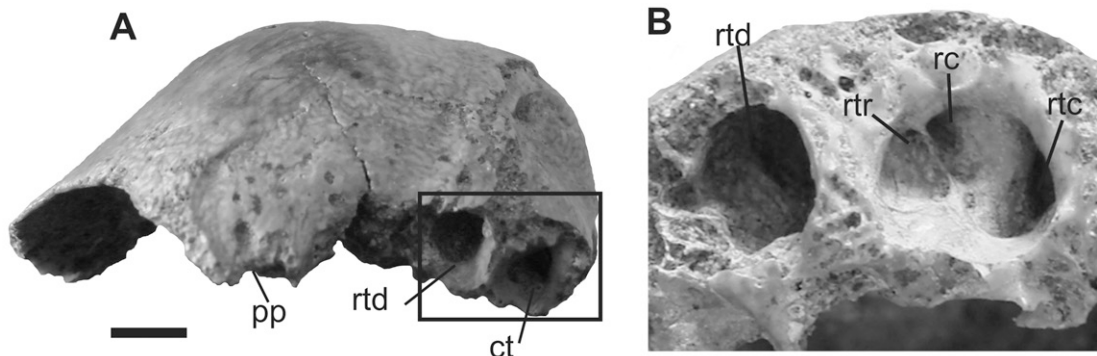

FIGURE 3. **A**, Accipitridae specimen MPEF-PV- 2523 showing the cavum cranii. The rectangles indicate the areas shown in B and C. 1. fossa cranii rostralis, 2. impressio eminetia sagittalis, 3. sulcus sinus sagittalis dorsalis, 4. venae cerebralis dorsocaudalis, 5. fossa cranii media, 6. crista marginalis. Arrow in B indicates the location of crista vallecularis. Arrow in C indicates the location of the sulcus sinus transversalis. Scale bar equals 10 mm.

FIGURE 4. **A**, View of left cavum tympanicum area. The rectangle indicates the area shown in B. Scale bar equals 10 mm.

rostralis (Fig. 3B). The fossa cranii media (Fig. 3A, C) are narrow and elongated with the major axis oriented transversally with respect to the rostro-caudal axis. The deep and strongly concave fossa cerebelli (Fig. 3C) extends from the caudalmost portion of the sulcus sinus sagitalis dorsalis almost to the dorsal edge of the foramen magnum. The fossa cerebelli and the fossae cranii rostralis are separated by the cristae marginalis. The paired kidney-shaped fossa auriculae cerebelli can be distinguished on the lateral walls of the fossa cerebelli (Fig. 3C).

The fossae cranii rostralis, cranii media, and cerebelli shows impressions that be correspond to the cranial dural venous sinuses and some cerebral vessels (Fig. 3B), i.e. the sinus sagitalis dorsalis between both fossae cranii rostralis, the sinus tranversus over both fossae cranii media and, the vena cerebralis dorsocaudalis over the caudal margin of impressio eminentiae sagittalis (see below for more descriptive details).

Endocast—In extant birds (as in mammals) the brain approximately fills the cranial cavity, so that the internal surface of the cranial bones closely reflects brain anatomy and shows the

impressions left by blood vessels (Edinger, 1951; Elzanowski and Galton 1991; Iwaniuk and Nelson, 2002; Osmólska, 2004; Evans, 2005 and literature cited therein).

In dorsal view, the MPEF-PV- 2523 endocast (Fig. 5A) show the hemispherium telencephali, which are narrow anteriorly and expands toward its caudal end. Its surface shows the eminentiae sagittalis, which are separated from the hemispherium telencephali by a shallow vallecula. The tectum mesencephali is visible in dorsal view and is laterally elongated. The lateral wall of the cerebellum bears paired prominences, the auriculae cerebelli. The surface between both hemispherium telencephali and over each tectum mesencephali show broad impressions that probably correspond to the sinus sagittalis dorsalis and to the sinus transversus respectively. Likewise, the impression over the cerebellum would represent the sinus occipitalis. In addition, several winding vascular marks can be distinguished: a rostrocaudal one that is interpreted here as the venae cerebralis dorsorostralis (Baumel, 1993) and one at the caudal limit of eminentiae sagittalis that would correspond to the venae cerebralis dorsocaudalis
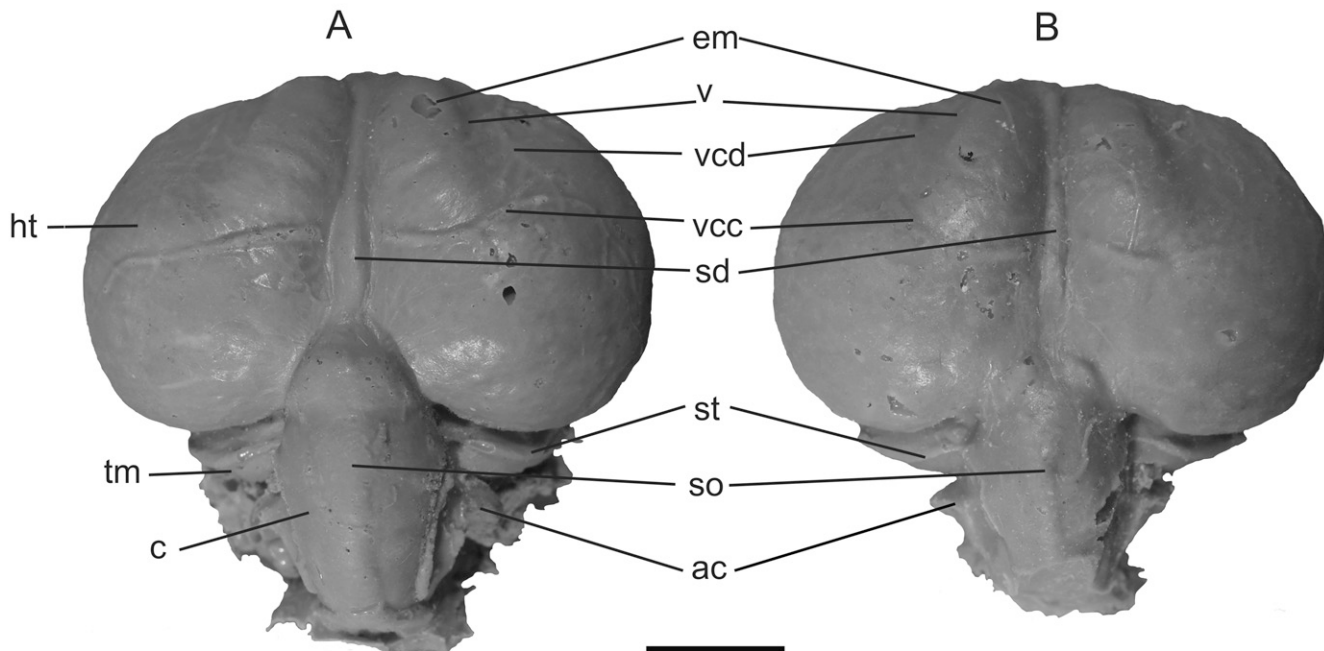

FIGURE 5.   Brain endocast in dorsal view. **A**, Accipitridae specimen MPEF-PV- 2523; **B**, *Geranoaetus melanoleucus* MLP-PV-OR 843. Scale bar equals 10 mm.

(Baumel, 1993). Finally, the MPEF-PV-2523 endocast lacks a bulbus olfactorius.

COMPARISON AND DISCUSSION

Neurocranium

Pycraft (1900) characterized the Falconiform skull on the basis of the presence of prominentia cerebellaris, a supraforaminal ridge and a shallow and linguiform fossa temporalis, which does not extend on the dorsal surface of the skull. Jollie (1976) noted that the presence of cerebral bulges with a shallow median groove (the frontal sulcus) was a constant feature in the Falconiform skulls that he analyzed. These features are present in both the fossil and the skulls of living species used for comparison. In particular, the accipitrid skull shows elongated-triangular shape of the cranial roof, vast separation between the processus postorbitalis and between both fossae temporalis, and narrow and acuminate outline of the fossa temporalis (Jollie, 1976). These features are shared with the MPEF-PV- 2523 and also are similar to Falconidae skull, according to the same author. Nevertheless, the comparisons of the dorsal and lateral aspects of all the available Falconidae and Accipitridae specimens analyzed for this work, allowed to distinguish between them by the shape of the area of attachment for the musculus adductor mandibulae externus. In the skulls of MPEF-PV- 2523 and accipitrids (Fig. 2A, D) this region has a rounded outline and flat surface. In contrast, in the falconids here analyzed this region is elliptical in outline and presents a concave surface (Fig. 2E).

Endocast

The endocast obtained from MPEF-PV-2523 showed a laterally displaced tectum mesencephalii and a great development of the hemispheria telencephali and cerebellum. These general features are shared with extant birds (Pearson, 1972). Furthermore, there were striking similarities between the endocast from MPEF-PV-2523 and those obtained from the extant *Geranoaetus melanoleucus* (Fig. 5B), as well as with the natural endocasts of Accipitridae from the Early Miocene of Bohemia (Mlíkovský, 1980:fig. 2). The endocast of MPEF-PV-2523 also shows the presence of eminentiae sagittalis. In extant birds this portion consists of dorsal protuberances of the hemispherium telencephali formed by hyperpallium (Reiner et al., 2005) which is involved in features such as visual integration, learning and cognition (Reiner et al., 2005). The size of the eminetiae sagittalis varies: it is large in the Emu (*Dromaius novaehollandiae*) (Martin et al., 2007) and in birds with binocular vision like strigiforms and some caprimulgiforms (Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008). They are moderate in the Pigeon (*Columba livia*) and reduced in the Kiwi (*Apteryx mantelli*) (Martin et al., 2007). The presence and development of eminentiae sagittalis in extinct birds seems to be somewhat different. In Mesozoic birds such as *Archaeopteryx* (Dominguez Alonso et al., 2004) of the Late Jurassic and ?Enantiornithes of the Late Cretaceous (Kurochkin et al., 2006) the eminetiae sagittalis are not evident. Paleogene birds show yet a different scenario: the eminetiae sagittalis are not evident in *Numenius gypsorum* from the Upper Eocene of Paris (Dechaseaux, 1970:fig. 70) whereas they are poorly developed in *Odontopteryx* and *Propheton* from the Lower Eocene of England (Milner and Walsh, 2006). These authors concluded that these latter taxa represent the earliest fossil records of eminentiae sagittalis. In contrast, the natural endocasts of Neogene birds described so far (Early and Middle Miocene and Pliocene birds from Europe described by Mlíkovský, 1980, 1981, 1988) and the specimen here studied, possess noticeable eminetiae sagittalis.

CONCLUSIONS

The osseous anatomy of MPEF-PV-2523 allows it assignation to Falconiformes Accipitridae. The similarity between the endocast of the fossil, the natural endocast decribed by Mlíkovský (1980) and that of the recent Accipitridae *Geranoaetus* reinforce this assignation. The presence of eminetiae sagittalis in the MPEF-PV-2523 is a significant feature because this area is responsible for important abilities that could have been present in this extinct bird.

MPEF-PV- 2523 was a large eagle (perhaps similar in size to the extant Black Chested Buzzard Eagle *Geranoaetus melanoleucus*) and it is the only carnivore known for the association recovered at the Estancia La Pastosa locality until now. Other Miocene associations of the Patagonian coast include phorusrhacids (terror birds) and marsupials as dominant predators (Tambussi and Noriega, 1996; Picasso et al. 2007).

More than twenty years ago, Olson (1985:112) stated that "the greatest handicap to understanding the fossil records is the lack of a modern anatomical revision of the genera and subgroups of the Accipitridae." Unfortunately, this situation has not changed significantly since then. Our results also show the need for further comparative studies of the brain anatomy, intracranial vascular system and its correlation with the cavum cranii of recent avian skulls. In this regard, the importance of works such as that of Sedlmayr (2002) on the vascular system of archosaurs becomes evident. Future research in this area can potentially lead to new insights into the evolution of the brain and blood vessels in these raptors. The last decade has brought important progress in the understanding of various features of the avian brain, while at the same time it has highlighted the increasing need for more descriptive and functional information.

ACKNOWLEDGMENTS

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