

# Revista Nordestina de Zoologia

Volume 8

Número 1

jan/jun 2014



ISSN 1808-7663

Revista da Sociedade Nordestina de Zoologia  
[www.revistanordestinadezoologia.com](http://www.revistanordestinadezoologia.com)

**COMPARATIVE ANALYSIS OF THE CRANIAL OSTEOLOGY AND  
EVOLUTIONARY TRAITS OF *Micrastur gilvicollis*, *Micrastur ruficollis* AND  
*Micrastur semitorquatus* (AVES: FALCONIFORMES)**

Anderson Guzzi<sup>1\*</sup>, Francisco C. V. Santos<sup>1</sup>, Guilherme J.B. C. Ferreira<sup>2</sup>, & Reginaldo J. Donatelli<sup>3</sup>

<sup>1</sup>Centro de Ciências do Mar, Universidade Federal do Piauí. Av. São Sebastião, 2819, Planalto Horizonte, 64202-020 Parnaíba, Piauí, Brasil. e-mail: guzzi@ufpi.edu.br

<sup>1</sup>Centro de Ciências do Mar, Universidade Federal do Piauí. Av. São Sebastião, 2819, Planalto Horizonte, 64202-020 Parnaíba, Piauí, Brasil. e-mail: fcovieira2@hotmail.com

<sup>2</sup>Departamento de Medicina Veterinária, Universidade Federal do Piauí. Br 135, Km 03, 64900-000 Bom Jesus, Piauí, Brasil. e-mail: guilherme.ferreira@ufpi.edu.br

<sup>3</sup>Departamento de Ciências Biológicas, Faculdade de Ciências, Unesp, Campus de Bauru, São Paulo, Brasil. e-mail: rjdonat@fc.unesp.br

\* Autor de correspondência

**ABSTRACT**

The cranial osteology of *Micrastur gilvicollis* (Vieillot, 1817), *Micrastur ruficollis* (Vieillot, 1817) and *Micrastur semitorquatus* (Vieillot, 1817) is comparatively and meticulously described to characterize each of the species and to determine which traits the species have in common and which are distinct. These traits will be used *a posteriori* for phylogenetic analysis. Our results indicate that *M. gilvicollis* and *M. ruficollis* are closely related, as they share a large number of traits, including a lacrimal bone with a distal portion that is approximately half as long as the proximal portion and a parasphenoid rostrum that covers 50% of the distance between the occipital condyle and pterygoid. Similarly, *M. gilvicollis* and *M. semitorquatus* both have a partially fused craniofacial flexion zone. In both *M. ruficollis* and *M. semitorquatus*, the symphyseal region of the mandible is 1/5 the total length of the mandible. The diagnostic traits for each of these species are as follows: a) in *M. gilvicollis*, the interorbital distance is 1/3 the length of the parietal, and the zygomatic process stretches 1/5 of the distance

from the orbital arch to the jugal arch; b) in *M. ruficollis*, the interorbital distance is 2/5 of the length of the parietal and the zygomatic process extends 1/4 of the distance from the orbital arch to the jugal arch; and c) in *M. semitorquatus*, the interorbital distance is 3/7 the length of the parietal and the distal portion of the lacrimal is 1/3 the length of the proximal portion. Among the three species, *M. gilvicollis* and *M. ruficollis* share the most traits, which leads us to infer that these species are more closely related to one another than they are to *M. semitorquatus*. Phylogenetic analysis performed *a posteriori* may confirm the relationship between these three species.

**Keywords:** Anatomy, skull, Falconidae.

## RESUMO

A osteologia craniana de *Micrastur gilvicollis* (Vieillot, 1817) *Micrastur ruficollis* (Vieillot, 1817) e *Micrastur semitorquatus* (Vieillot, 1817) é descrita de forma detalhada e comparada visando caracterizar cada uma das espécies e interpretar os caracteres comuns e particulares que serão utilizados *a posteriori* em uma análise filogenética. Os resultados evidenciaram uma proximidade entre as duas primeiras espécies por compartilharem um grande número de caracteres, tais como a parte distal do lacrimal com cerca de 1/2 da proximal e o rostro paraesfenóide alcançar 50% da distância do côndilo occipital e o pérs pterigoide. Por outro lado, *M. gilvicollis* e *M. semitorquatus* compartilham a condição parcialmente fundida da zona flexória craniofacial. Entre *M. ruficollis* e *M. semitorquatus* a parte sinfisial da mandíbula ocupa 1/5 do comprimento total da mandíbula. Os caracteres diagnósticos cada uma dessas espécies são: a) em *M. gilvicollis* a largura interorbital é 1/3 da parietal e o processo zigomático atinge 1/5 da distância a partir do arco da órbita à barra jugal; b) em *M. ruficollis* a largura interorbital tem 2/5 da parietal e o processo zigomático atinge 1/4 da distância a partir do arco da órbita à barra jugal; c) em *M. semitorquatus* a largura interorbital é 3/7 da parietal e a parte distal do lacrimal tem 1/3 da largura da proximal. *Micrastur gilvicollis* e *M. ruficollis* compartilham um maior número de caracteres, o que permite inferir que tais espécies estão mais próximas entre si quando comparadas a *M. semitorquatus*. Uma análise

filogenética *a posteriori* poderá ou não confirmar essa relação entre essas três espécies.

**Palavras-chave:** Anatomia, crânio, Falconidae.

## INTRODUCTION

Falconidae is currently the only family in the Falconiformes order (CBRO, 2011). The makeup of this order was altered as a result of recently conducted genetic studies using molecular markers that showed that Falconidae is not closely related to Accipitridae (Ericson *et al.*, 2006).

The genus *Micrastur* comprises seven species of exclusively Neotropical forest falcons that replace *Falco* species in densely forested areas, that are distributed in the lowland and mid-elevation humid forest of Central and South America (Sick, 1997; Fuchs *et al.*, 2011): *Micrastur ruficollis* (Vieillot, 1817), *Micrastur gilvicollis* (Vieillot, 1817), *Micrastur semitorquatus* (Vieillot, 1817), *Micrastur plumbeus* (Sclater, 1918), *Micrastur mintoni* Whittaker, 2002, *Micrastur mirandollei* (Schlegel, 1862) and *Micrastur buckleyi* (Swann, 1919). The latter three are

well characterized, but more detailed anatomical studies are needed for the others to confirm whether the three taxa are subspecies or independent species.

For several decades, the taxa of the *M. ruficollis* complex were the topic of much debate, especially concerning their taxonomic status. The taxon *M. gilvicollis* was thought to be a subspecies of *M. ruficollis* with a wide distribution in the Amazon Basin (Amadon, 1964; Brow & Amadon, 1968).

Schultz (1972) analyzed the external morphology and vocalizations of the taxa in the *M. ruficollis* complex, especially those found in the Amazon Basin (*M. gilvicollis*, *M. concentricus*, *M. ruficollis* and *M. pelzelni*). Schultz (*op. cit.*) found that *M. gilvicollis* specimens had long wings and short tails. By contrast, *M. concentricus* and *M. pelzelni* had short wings and long tails, suggesting that they are synonymous and that *M.*

*concentricus* has priority over *M. pelzelni*. Therefore, Schuartz (*op. cit.*) validated the *M. gilvicollis* species with its wide distribution in the Amazon Basin and classified *M. concentricus* as a subspecies of *M. ruficollis* that is sympatric and syntopic with *M. gilvicollis* in some regions of the Amazon.

According to Sick (1997), *M. gilvicollis*, commonly known as the Lined Forest Falcon, inhabits Neotropical forests of the Amazon from the equator to Mato Grosso (Teles Pires River), Bahia and northern Espírito Santo (Doce River). The range of *M. ruficollis*, known as the Barred Forest Falcon, extends from Mexico to Argentina, Bolivia and the central-equatorial and eastern Brazilian Amazon, including Mato Grosso (Upper Xingu River, *M. ruficollis concentricus*), Rio de Janeiro and Rio Grande do Sul (*M. ruficollis ruficollis*). *M. semitorquatus*, known as the Collared Forest Falcon, inhabits the edges of forests and low, sparse and dry forests. It is distributed from Mexico to Argentina and is found throughout Brazil. The most comprehensive studies on *Micrastur*

were performed by Thorstrom (2000), who studied the food habits of *M. ruficollis* and *M. semitorquatus*.

Therefore, we sought to make a detailed comparative description of the cranial osteology of *M. gilvicollis*, *M. ruficollis* and *M. semitorquatus* to clarify the current composition of the complex as three distinct species. We also sought to identify shared and distinct traits for these species to support a future phylogenetic analysis of the genus.

## **MATERIALS AND METHODS**

The study focused on the cranial osteology of *M. gilvicollis* (USNM 621697, male, Acari Mountains, Guyana), *M. ruficollis* (USNM 621387, male, Baramita, Guyana) and *M. semitorquatus* (USNM 245788, female, Paraguay River, Mato Grosso, Brazil; USNM 013493, unknown sex, Costa Rica; USNM 289773, male, Magdalena, Colombia) using specimens in the osteological collection at the Division of Birds of the Smithsonian Natural History Museum (USNM), Washington, DC, USA.

The studied specimens were previously prepared (dry crania and mandibles). Cranial osteology descriptions were comparative and are illustrated by photos of the dorsal, ventral, caudal and lateral sides accompanied by legends to facilitate observation of the structures. Nomenclature for describing the osteological and other structures followed the *Nomina Anatomica Avium* (Baumel *et al.* 1993), and classifications followed the Brazilian Ornithological Records Committee recommendations (CBRO, 2011).

## RESULTS

### Ossa cranii

The frontal region (os frontale – F, Figs. 1, 8 and 15) makes up a large part of the skull roof and covers approximately half the length of the braincase. The interorbital distance is approximately 1/3 the length of the parietal region in *M. gilvicollis* (Fig 1), 2/5 in *M. ruficollis* (Fig 8) and 3/7 in *M. semitorquatus* (Fig 15). The frontal region articulates with the nasal region rostrally via the craniofacial flexion zone. This zone is partially fused

medially in *M. gilvicollis* (Fig 1) and *M. semitorquatus* (Fig 15), is not fused in *M. ruficollis* and has a frontal depression (DF) in all three species (Figs 1, 8 and 15).

The distal region of the lacrimal is approximately 1/2 as long as the proximal region in *M. gilvicollis* and *M. ruficollis* and 1/3 as long in *M. semitorquatus*. It terminates in a rounded shape in all three species and extends 1/5 of the distance from the orbital arch to the jugal arch in *M. gilvicollis*, 1/4 in *M. ruficollis* and 1/7 in *M. semitorquatus*.

The large parietal region (os parietale – P, Figs 1, 3, 8, 10, 15 and 16) borders the squamosal region lateroventrally via an inconspicuous superior temporal crest in *M. gilvicollis* (CrTS, Figs 2 and 3) and *M. ruficollis* (CrTS, Figs 9 and 10) and a conspicuous superior temporal crest in *M. semitorquatus* (CrTS, Figs 16 and 17). The ratio of the interorbital region length to the parietal region length is 3 in *M. gilvicollis*, 2.5 in *M. ruficollis* and 2.35 in *M. semitorquatus*.

The squamosal region (os squamosum) is bordered laterodorsally by the superior temporal crest (CrTS, Figs 2, 3, 9, 10, 16 and 17); the external acoustic meatus accounts for a large portion of the lateral cranium caudal of the postorbital process, ventrocaudal to the pronounced suprameatic process present in all three species (proc. suprameaticus – PrSM, Fig 3). The temporal fossa (fossa temporalis – FT, Figs 2, 3, 9, 10, 16 and 17) is deeper rostrally and shallower caudally and is longer than it is wide. The temporal fossa is bordered dorsally by the superior temporal crest (CrTS, Figs 2, 3, 8, 9, 16 and 17) and ventrally by the transverse nuchal crest.

The squamosal region projects rostrally to form the zygomatic process (proc. zygomaticus – PrZ, Figs 3, 10 and 17). This process is long and wider at its base, forming a characteristic triangle slightly twisted around itself and extends approximately 25% of the distance between its origin in the cranium and the jugal arch in *M. gilvicollis* and 30% of the distance in *M. ruficollis* and *M. semitorquatus*.

The zygomatic process has well-defined dorsal, ventral, lateral and medial surfaces where the adductor mandibulae externus, rostralis, lateralis and medialis muscles attach, respectively.

In the parasphenoid bone (os parasphenoidale) region, the parasphenoid rostrum projection (rostrum parasphenoidale – RP, Figs 4, 11 and 18) is noteworthy, as it extends 50% of the distance from the occipital condyle to the pterygoid in *M. gilvicollis* and *M. ruficollis* and 40% of the distance in *M. semitorquatus*, articulates rostrally with the palatine and rostrally with the pterygoid, fuses dorsally with the interorbital septum and contacts the vomer rostrally via the facies articularis vomeralis.

The ectethmoid (os ectethmoidale – E, Figs 3, 10 and 17) is fused to the lacrimal along its entire length and has a pronounced process in all three studied species. Interestingly, the medial portion of the orbit, the dorsomedial portion of the laterosphenoid region, contains an orbitocranial fonticle in the caudal portion of the interorbital septum

(septum interorbitale – SIO, Figs 3, 10 and 17).

### **Ossa Maxillae**

The superior maxilla (MS, Figs 1, 3, 8, 10 and 15) is approximately 1/3 as long as the cranium in *M. gilvicollis* and *M. ruficollis* and 2/5 as long in *M. semitorquatus*. The nasal aperture (NA, Figs 3, 10 and 17) is circular and is holorhinal-type. The craniofacial flexion zone is only found in the medial portion between the frontal and nasal regions. There is a clear fusion between the regions in all three species.

### **Palati**

The palatine region is formed by the palatine, pterygoid and vomer bones. The maxillopalatine process (proc. maxillopalatinum – PrMP, Figs 4, 11 and 18) connects the caudolateral palatine lamella to the base of the superior maxilla. The extension of this process is long and narrow in all three studied species. The caudolateral palatine lamina (lamella caudolateralis) of the pars lateralis is bordered medially by the prominent ventral palatine crest

(crista ventralis – CrV, Figs 4, 11 and 18) of the pars choanalis and laterally by the long lateral palatine crest (crista lateralis – CrL, Figs 4, 11 and 18). There is a deep ventral palatine fossa between the lateral and ventral crests (fossa ventralis – FV, Figs 4, 11 and 18). Thus, the ventral palatine fossa is short, wide, deep and makes up the majority of the caudolateral palatine lamella. The ventral palatine crests are long, very prominent and found in the parasphenoid articulating region in all three species. The medial palatine crests (crista medialis) are prominent, have a tapered end, are located more medially and border the fossa choanalis. The pars choanalis is narrow and more developed compared to the pars lateralis described above.

The vomer (V, Figs 4, 11 and 18) has a long and wide blade in *M. gilvicollis* and a long narrow blade in *M. ruficollis* and *M. semitorquatus*.

The quadrate orbital process (proc. orbitalis – POrQ, Figs 3 and 10) is short and wide in all three species, tapering slightly at the distal end and terminating in a bulb. It is clearly situated obliquely in the



orbit. The otic process of the quadrate (proc. oticus), extending from the corpus ossi quadrati, is long and enlarged in these three species. It articulates with the braincase in two locations: 1) via the external otic process (capitulum squamosum) supported on the ventrocaudal surface of the zygomatic process and 2) via the internal otic process (capitulum oticum) that is present in all three species and articulates with the cotylae quadratae otici of the prootic and opisthotic bones.

The pterygoid (pterygoideum – PT, Figs 4, 11 and 18) articulates with the palatine dorsolaterocaudally via a structure called the pes pterygoidei. The pterygoid generally has a relatively flattened blade that is obliquely situated in the orbit and lacks a dorsal process in all three species.

### **Ossa mandibulae**

The pars symphysialis mandibulae (PSI, Figs 5, 12 and 19) extends approximately 1/6 of the total length of the mandible in *M. gilvicollis* and 1/5 the length in the other two species studied. The pars

intermedia has a well-developed but shallow mandibular fenestra along its entire length (FecM, Figs 6 and 13). The coronoid process 1 is clear in all three analyzed *Micrastur* species (Figure 20).

Through a detailed and comparative description of the cranial osteology of *M. gilvicollis*, *M. ruficollis* and *M. semitorquatus*, we recorded the following traits shared among all three species: the distal portion of the lacrimal bone ends in a round shape; the suprameatic process is present; the postorbital process is long, robust and well-developed with a wide base; the ecthemoid is fused to the lacrimal along its entire length; the frontal region has a lacrimal process; the maxillopalatine process is long and narrow; the ventral palatine fossa is short, wide, deep and covers the majority of the caudolateral palatine lamella; the pterygoid process from the palatine is short; and the otic process of the quadrate is long and enlarged.

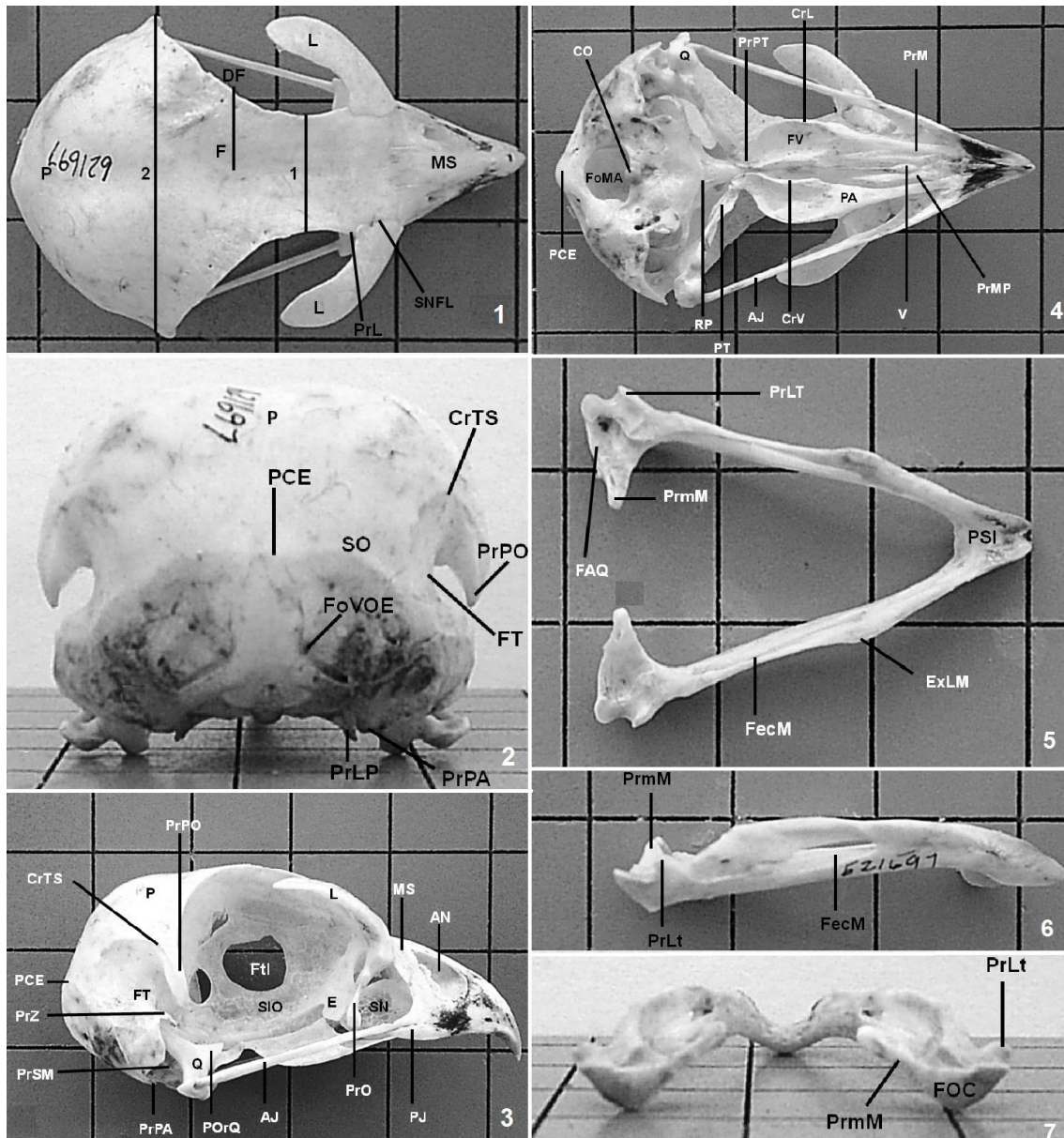
The unique traits of *M. semitorquatus* are as follows: the interorbital distance is approximately 3/7 of the width of the parietal

region; the distal end of the lacrimal is approximately  $1/3$  the width of the proximal end; the zygomatic process extends  $1/7$  of the distance from the orbital arch to the jugal arch; the ratio between the interorbital diameter and the width of the parietal region is at least 2.35; the parasphenoid rostrum extends 40% of the distance from the occipital condyle to the pterygoid feet; the narrowing of the interorbital distance is noteworthy, and the superior maxilla is approximately  $2/5$  as long as the cranium.

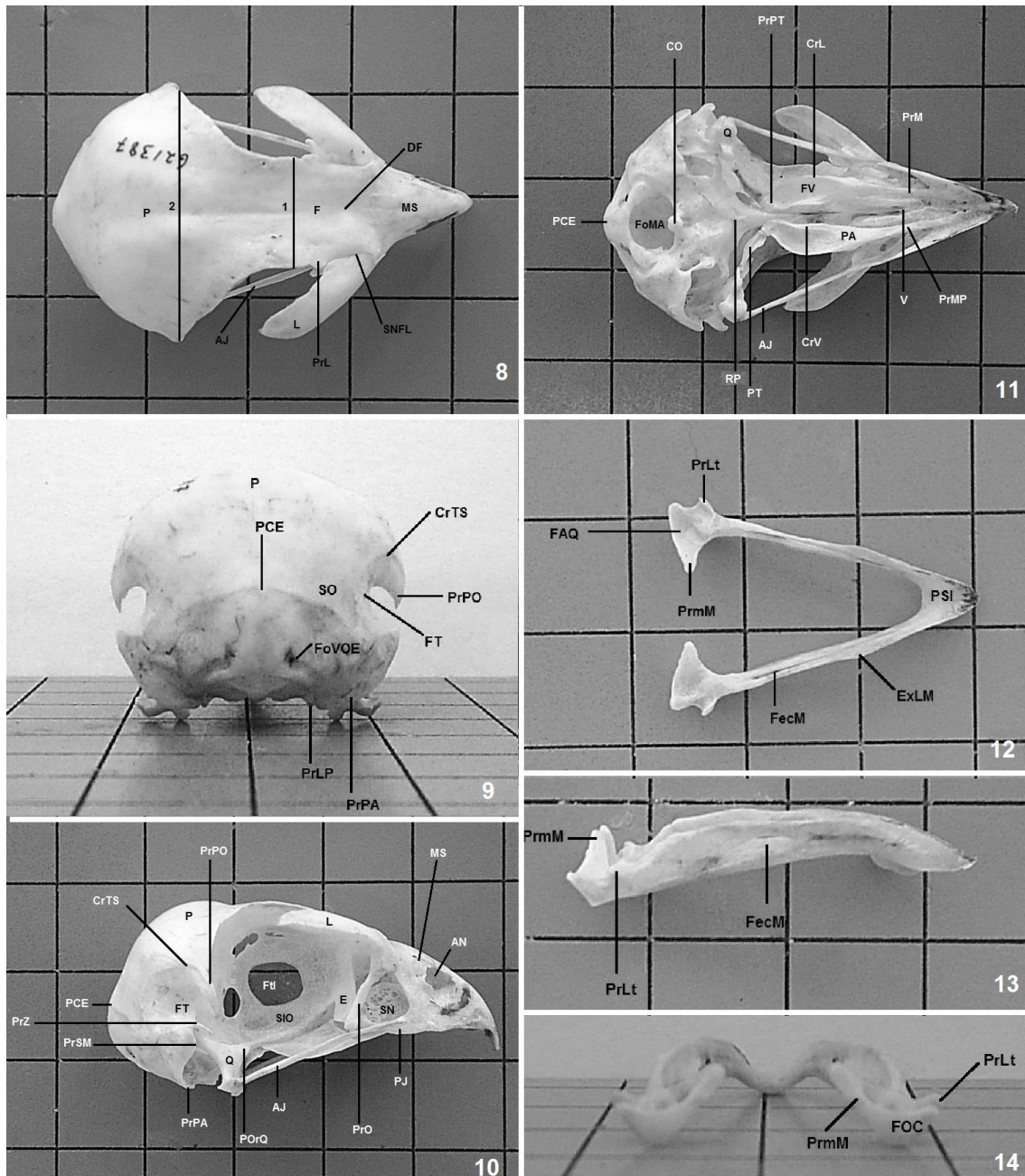
The unique traits of *M. gilvicollis* are as follows: the interorbital distance is approximately  $1/3$  the width of the parietal region; the zygomatic process extends  $1/5$  of the distance between the orbital

arch and the jugal arch; the ratio of the interorbital diameter and the width of the parietal region is 3; the zygomatic process extends approximately 25% of the distance from its origin in the cranium to the jugal arch; the vomer is a longer, wider blade than in the other studied species; and the symphyseal portion of the mandible is approximately  $1/6$  of the total length of the mandible.

The traits exclusive to *M. ruficollis* are as follows: the interorbital distance is  $2/5$  the width of the parietal region; the craniofacial flexion zone is unfused; the zygomatic process extends  $1/4$  of the distance from the orbital arch to the jugal arch; and the ratio of the interorbital diameter to the width of the parietal region is 2.5.

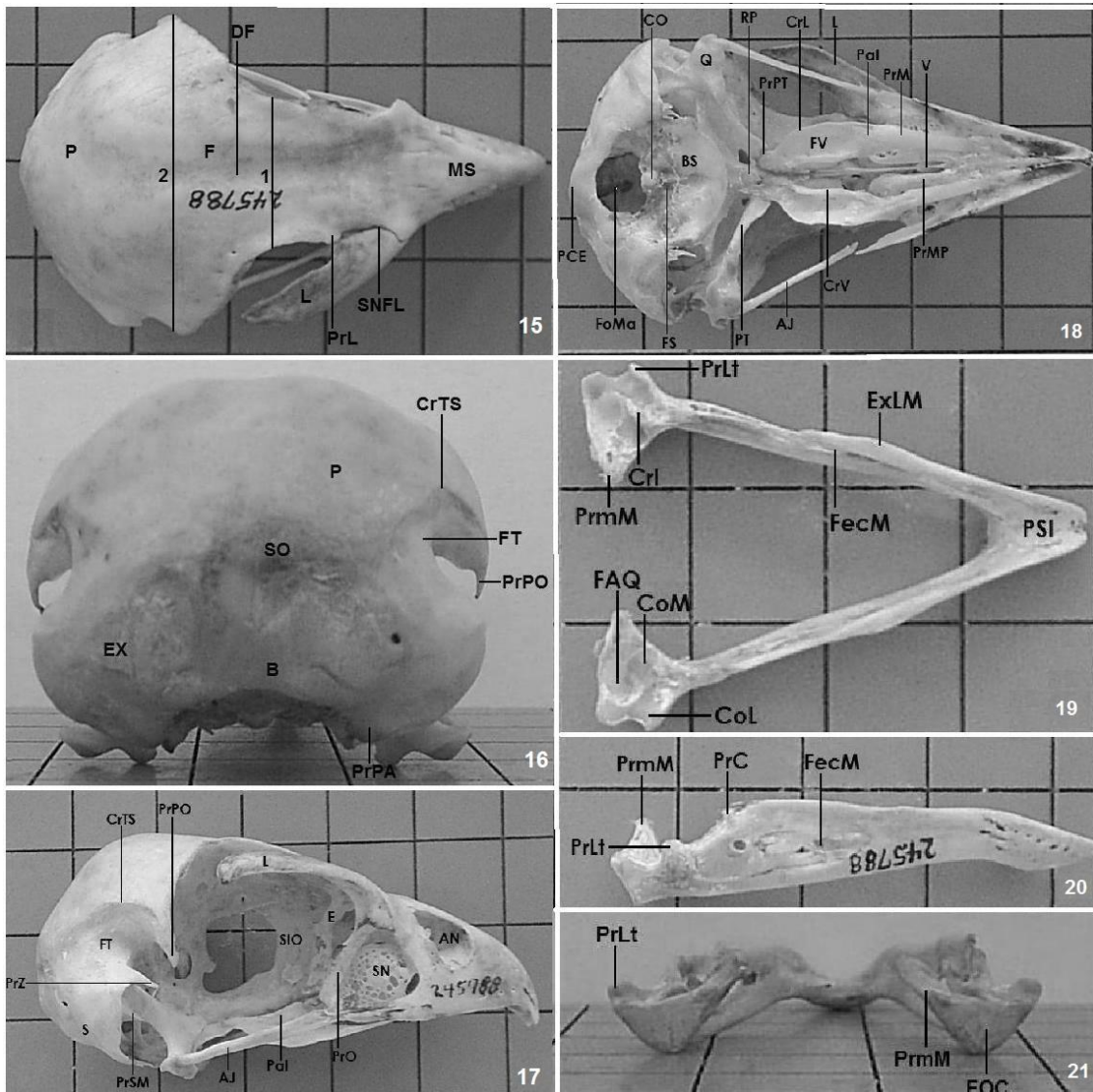


**Fig 1-7.** Photographs of the cranium and mandible of *M. gilvicollis* (USNM 621697). The grid underneath represents 1-cm squares. **1.** Dorsal view of the cranium. **2.** Caudal view of the cranium. **3.** Lateral view of the cranium. **4.** Ventral view of the cranium. **5.** Dorsal view of the mandible. **6.** Lateral view of the mandible. **7.** Caudal view of the mandibular branches. **LEGEND:** **1** - interorbital distance, **2** - parietal distance, **CEP:** cerebral prominence, **CF:** caudal fossa, **CFeM:** caudal fenestra of the mandible, **CrL:** lateral palatine crest, **CrV:** ventral palatine crest, **E:** ectethmoid, **ExLM:** lateral mandibular extension, **F:** frontal region, **FAQ:** quadrate articular fossa, **FD:** frontal depression, **FoEOV:** foramen of the external occipital vein, **FoMA:** foramen magnum, **FT:** temporal fossa, **FV:** ventral palatine fossa, **IFt:** interorbital fonticulus, **JA:** jugal arch, **JP:** jugal process, **L:** lacrimal bone, **NA:** nasal aperture, **NFLS:** nasofrontalacral suture, **NS:** nasal septum, **OC:** occipital condyle, **P:** parietal, **PA:** palatine bone, **PrL:** frontal lacrimal process, **PrLP:** lateral parasphenoid process, **PrLt:** lateral process of the mandible, **PrM:** maxillary process of the palatine, **PrmM:** medial mandibular process, **PrMP:** maxilopalatine process, **PrO:** orbital process of the lacrimal, **PrPA:** paraoccipital process, **PrPO:** postorbital process, **PrPT:** pterygoid process of the palatine, **PrSM:** suprameatic process, **PrZ:** zygomatic process, **PT:** pterygoid, **Q:** quadrate, **QOrP:** quadrate orbital process, **RP:** parasphenoid rostrum, **SIO:** interorbital septum, **SM:** superior maxilla, **SO:** supraoccipital region, **STCr:** superior temporal crest, **SYP:** symphyseal region of the mandible, **V:** vomer.



**Fig 8-14.** Photographs of the cranium and mandible of *M. ruficollis* (USNM 621387). The grid underneath represents 1-cm squares. **8.** Dorsal view of the cranium. **9.** Caudal view of the cranium. **10.** Lateral view of the cranium. **11.** Ventral view of the cranium. **12.** Dorsal view of the mandible. **13.** Lateral view of the mandible. **14.** Caudal view of the mandibular branches. **LEGEND:** **1** - interorbital distance, **2** - parietal distance, **CEP:** cerebral prominence, **CF:** caudal fossa, **CFeM:** caudal fenestra of the mandible, **CrL:** lateral palatine crest, **CrV:** ventral palatine crest, **E:** ectethmoid, **ExLM:** lateral mandibular extension, **F:** frontal region, **FAQ:** quadrate articular fossa, **FD:** frontal depression, **FoEOV:** foramen of the external occipital vein, **FoMA:** foramen magnum, **FT:** temporal fossa, **FV:** ventral palatine fossa, **IFt:** interorbital fonticulus, **JA:** jugal arch, **JP:** jugal process, **L:** lacrimal bone, **NA:** nasal aperture, **NFLS:** nasofrontalacrimonal suture, **NS:** nasal septum, **OC:** occipital condyle, **P:** parietal, **PA:** palatine bone, **PrL:** frontal lacrimal process, **PrLP:** lateral parasphenoid process, **PrLt:** lateral process of the mandible, **PrM:** maxillary process of the palatine, **PrmM:** medial mandibular process, **PrMP:** maxilopalatine process, **PrO:** orbital process of the lacrimal, **PrPA:** paraoccipital process, **PrPO:** postorbital process, **PrPT:** pterygoid process of the palatine, **PrSM:** suprameatic process, **PrZ:** zygomatic process, **PT:** pterygoid, **Q:** quadrate, **QOrP:** quadrate orbital process,

**RP:** parasphenoid rostrum, **SIO:** interorbital septum, **SM:** superior maxilla, **SO:** supraoccipital region, **STCr:** superior temporal crest, **SYP:** symphyseal region of the mandible, **V:** vomer.



**Fig 15-21.** Photographs of the cranium and mandible of *M. semitorquatus* (USNM 245788) (Silva *et al.* 2012). The grid underneath represents 1-cm squares. **15.** Dorsal view of the cranium. **16.** Caudal view of the cranium. **17.** Lateral view of the cranium. **18.** Ventral view of the cranium. **19.** Dorsal view of the mandible. **20.** Lateral view of the mandible. **21.** Caudal view of the mandibular branches. **LEGEND:** **1** - interorbital distance, **2** - parietal distance, **CEP:** cerebral prominence, **CF:** caudal fossa, **CFem:** caudal fenestra of the mandible, **CrL:** lateral palatine crest, **CrV:** ventral palatine crest, **E:** ectethmoid, **ExLM:** lateral mandibular extension, **F:** frontal region, **FAQ:** quadrate articular fossa, **FD:** frontal depression, **FoEOV:** foramen of the external occipital vein, **FoMA:** foramen magnum, **FT:** temporal fossa, **FV:** ventral palatine fossa, **IFT:** interorbital fonticulus, **JA:** jugal arch, **JP:** jugal process, **L:** lacrimal bone, **NA:** nasal aperture, **NFLS:** nasofrontalacrimonal suture, **NS:** nasal septum, **OC:** occipital condyle, **P:** parietal, **PA:** palatine bone, **PrL:** frontal lacrimal process, **PrLP:** lateral parasphenoid process, **PrLt:** lateral process of the mandible, **PrM:** maxillary process of the palatine, **PrmM:** medial mandibular process, **PrMP:** maxilopalatine process, **PrO:** orbital process of the lacrimal, **PrPA:** paraoccipital process, **PrPO:** postorbital process, **PrPT:** pterygoid process of the palatine, **PrSM:** suprimeatic process, **PrZ:** zygomatic process, **PT:** pterygoid, **Q:** quadrate, **QOrP:** quadrate orbital process, **RP:** parasphenoid rostrum, **SIO:** interorbital septum, **SM:** superior maxilla, **SO:** supraoccipital region, **STCr:** superior temporal crest, **SYP:** symphyseal region of the mandible, **V:** vomer.

## DISCUSSION

*Micrastur* species have a better-developed orbit when compared to scavengers' birds (Hertel, 1995; Sustaita & Hertel, 2010). Among *Micrastur* species, *M. gilvicollis* shows the smallest interorbital width, which might increase its vision in relation to other species that show greater interorbital width. As the twilight and nocturnal owls, *M. semitorquatus* has its eyes and ears faced forwards and relatively small interorbital width enabling a binocular vision (Silva *et al.*, 2012). Scavengers, on the other hand, show a larger interorbital width than raptors (which chase mobile preys), and are thus related to eat immobile prey (Hertel, 1995; Sustaita & Hertel, 2010).

The large parietal region borders the squamosal region lateroventrally via an inconspicuous superior temporal crest in *M. gilvicollis* and *M. ruficollis* and a conspicuous superior temporal crest in *M. semitorquatus*. The increase of body mass in the Falconidae is related with skull increase and both are associated with muscle insertion

on the neck region, enabling mechanical advantage on feeding (Sustaita, 2008). Scavengers have narrower skulls when compared with raptors. However, the distance between the occipital and opisthotic crests is greater than seen in raptors, being the magnum foramen more caudally housed on the skull. This arrangement enables a more linear housing with the vertebral column, which makes lateral movements easier and also increases the force to remove meat from a carcass (Hertel, 1995; Sustaita & Hertel, 2010). According to Fuchs this generalist/scavengering behavior arise in the Falconidae (Polyborinae) between 14 and 6.7 millions of years (ma) back. This behavioral distinction might be associated with the arid climate in open areas and the increase of grazing mammals, scavenger's food source. *Micrastur* speciation (23 to 5.3 ma), on the other hand, was clearly distinct from Polyborinae, and might be related to habitat use as secondary growth and humid forests. The most basal taxa considered from *Micrastur* species,

*M. semitorquatus*, might have started its diversification from other species of the genera about 3.6 ma; and *M. ruficollis* around 2.5 ma from *M. gilvicollis* (Fuchs *et al.*, 2011, 2012). Of the unique traits of *M. ruficollis*, the craniofacial flexion zone is especially interesting. High levels of cranial kinesis are normally associated with less capacity of force-generating as seen in insectivorous falcons (*Falco berigora*). However this may be directly associated with the speed of beak's gripping and also with the skill for insect capture in flight in contrast with bird eating falcons (*Falco peregrinus*), which have greater crushing and grinding force for prey immobilization (Sustaita, 2008).

*Micrastur* species have a well-developed adductor muscle more rostrally inserted on the mandible and together with beak's curvature enables grasping and killing their preys (Hertel, 1995; Sustaita & Hertel, 2010). This structure medially joins the squamosal bone region to the parietal. Similarly, Silva *et al.* (2012) found that *M. semitorquatus* has a well-developed superior temporal

crest that borders the squamosal region laterocaudally.

Silva *et al.* (2012) found that the cranial adaptations of *M. semitorquatus* may be related to its life habits and behavior, including the robustness of the *pila supranasalis* and the prokenesis of the cranium, which provide resistance for the superior maxilla during predation; a developed postorbital process that houses the powerful mandibular adductor muscles and protects the eyes; and an expanded palatine that can protect the ventral portion of the eyes from the impacts of prey on the palatine region. *Micrastur* species show the cutting edge of the beak smaller than other raptors and larger upper jaws (Accipitridae, Pandionidae and Vulturinae) (Hertel, 1995; Sustaita & Hertel, 2010). The increasing size of the skull provides also an increasing of clamping force in the Falconidae when compared with Accipitridae (associated with prey type and size) (Sustaita, 2008).

Although they have the same length, the position of the zygomatic process in *M. semitorquatus* is different than the position in *M. ruficollis* and *M. gilvicollis*, which is

more angular. This trait is important from a systematic point of view. The zygomatic process is also one of four synapomorphies that support the Buteoninae subfamily composed of the genera *Buteo*, *Geranoaetus*, *Harpyhaliaetus*, *Leucopternis* and *Parabuteo*. Marceliano *et al.* (2007) found that the zygomatic process is reduced in *Penelope superciliaris*, corroborating the results of Zusi & Livezey (2000), who reported that this process is reduced or absent in adults of Galliformes species.

The quadrate orbital process is short and wide in all three species, tapering slightly at the distal end and terminating in a bulb. The quadrate, pterygoid and *m. pterygoideus* are responsible for force transmission to the thomial tooth used by Falconidae to kill and dismembering prey with back and forwards head movements (Sustaita & Hertel, 2010). Moreover mandible adductors and *pseudotemporalis* muscles are associated with the prevention of mandible disarticulation (Sustaita, 2008).

The symphyseal portion of the mandible is approximately 50% of the total length of the mandible in species of the subfamily Cerylinae

(Méndez & Höfling, 2007), whereas the symphyseal portion in *M. momota* is slightly more than 1/3 of the total length of the mandible (Pascotto *et al.*, 2006). The coronoid process 1 is clear in all three analyzed *Micrastur* species, is related to mandibular adductor insertion area and increasing gripping beak's force (Sustaita & Hertel, 2010). Mandibular symphysis is smaller than in other species and together with mandibular muscle insertion, thickness of mandibular rami and length of the mandibular symphysis are the main variables related to gripping force. Thus the greater the distance among muscle insertion, the larger mandibular rami and mandibular symphysis, the greater gripping force. Thus falcons kill by delivering powerful bites to the neck, which disarticulates the cervical vertebrae, and damage the spinal cord 64% more effectively (2.7 to 24.5N) than Accipitridae (1.4 to 5.4N) (Sustaita, 2008; Sustaita & Hertel, 2010). The Accipitridae, Pandionidae and Vulturidae have longer mandibles and larger mandibular symphysis which enable them to explore more food items (as mammals, reptiles, fishes, and also



decomposing carcasses) than Falconidae (Hertel, 1995).

According to Zusi (1993), the external surface of the cranium in birds can be many shapes to support the muscles and ligaments of the mandible. The shape observed in *M. semitorquatus* was a deep temporal fossa, indicating that the mandibular adductor muscle is well developed to aid with hunting for prey much larger than itself in terms of size and weight (Antas, 2005).

Through a detailed and comparative description of the cranial osteology of *M. gilvicollis*, *M. ruficollis* and *M. semitorquatus*, we recorded the following traits shared among all three species: the distal portion of the lacrimal bone ends in a round shape; the suprameatic process is present; the postorbital process is long, robust and well-developed with a wide base; the ecthemoid is fused to the lacrimal along its entire length; the frontal region has a lacrimal process; the maxillopalatine process is long and narrow; the ventral palatine fossa is short, wide, deep and covers the majority of the caudolateral palatine lamella; the pterygoid process from

the palatine is short; and the otic process of the quadrate is long and enlarged. These data corroborate *Micrastur* monophyly and agrees with Griffiths *et al.* (2004) who worked with combined molecular and morphological data (syrinx) and also with Fuchs *et al.* (2012) who used molecular data as a phylogenetic tool.

## CONCLUSION

Our comparative study of *Micrastur gilvicollis*, *M. ruficollis* and *M. semitorquatus* showed that the first two species are more closely related, as they share a number of cranial osteological traits that the third species does not have (as the distal part of the lacrimal bone has about half of the width of the proximal part; the superior temporal crest is not conspicuous; the patesphenoid rostrum reaches 50% from the distance of the occipital condyle and *pes pterygoidei*; and the upper jaw shows about 1/3 of the total length of the skull), which corroborates Fuchs' *et al.* (2011) phylogenetic hypothesis with molecular data.

## ACKNOWLEDGMENTS

We are very indebted to curators from the following institutions: National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., U.S.A, for allowing us to visit their collection and to study the Falconidae; and we are very grateful to Leonardo Moura dos Santos Soares (Emilio Goeldi Museum) for invaluable contributions for our study.

## REFERENCES

- AMADON, D. 1964. Taxonomic notes on birds of prey. New York, America Museum Novitates, 24p.
- ANTAS, P.T.Z. 2005. Pantanal guide to birds: species of the Brazilian Natural Heritage Private Reserve of the SESC Pantanal, Rio de Janeiro. SESC, National Department, 225p.
- BAUMEL, J.J. & L.M. WITMER. 1993. OSTEOLOGIA, p. 45-132. In: Baumel, J.; A.S. King; A.M. Lucas; J.E. Breazile & T.H.E. Evans (Eds). Handbook of Avian Anatomy: Nomina anatomica avium. London, Academic Press, 637p.
- BROWN, L. & D. AMADON. 1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill Book Co., 531p.
- CBRO (Comitê Brasileiro de Registros Ornitológicos) 2011. List of Brazilian Birds. 10<sup>th</sup> Edition, Disponível na World Wide Web em: <http://www.cbro.org.br/CBRO/listabr.html> [23/04/2012].
- ERICSON, P.G.P.; C.L. ANDERSON; T. BRITTON; A. ELZANOWSKI; U.S. JOHANSSON; M. KÄLLERSJÖ; J.I. OHLSON; T.J. PARSONS; D. ZUCCON & G. MAYR. 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters*, London, 2: 543-547.
- Fuchs, J.; S. Chen; J.A. Johnson & D.P. Mindell. 2011. Pliocene diversification within the South American Forest falcons (Falconidae: *Micrastur*). *Molecular Phylogenetics and Evolution*, Detroit, 60: 398-407.
- FUCHS, J.; S. CHEN; J.A. JOHNSON & D.P. MINDELL. 2012. Molecular systematics of the

- caracaras and allies (Falconidae: Polyborinae) inferred from mitochondrial and nuclear sequence data. *Ibis*, London, 154: 520-532.
- GRIFFITHS, C.S.; G.F. BARROWCLOUGH; J.G. GROTH & L. MERTZ. 2004. Phylogeny of the Falconidae (Aves): a comparison of the efficacy of morphological, mitochondrial, and nuclear data. *Molecular Phylogenetics and Evolution*, Detroit, 32: 101-109.
- HERTEL, F. 1995. Ecomorphological indicators of feeding behavior in recent and fossil raptors. *The Auk*, Washington, 102 (4): 890-903.
- MARCELIANO, M.L.V.; S.R. POSSO. & R.J. DONATELLI. 2007. Cranial osteology of *Penelope superciliaris* Temminck, 1815 (Galliformes: Cracidae). *Boletim do Museu Paraense Emílio Goeldi*, Belém, 2 (1): 55-67.
- MÉNDEZ, A.C. & E. HÖFLING. 2007. Cranial Osteology of Ceryinae (Coraciiformes: Alcedinidae). *Boletim do Museu Paraense Emílio Goeldi*, Belém, 2 (1): 155-182.
- PASCOTTO, M.C.; E. HÖFLING. & R.J. DONATELLI. 2006. Cranial Osteology of Coraciiformes (Aves). *Revista Brasileira de Zoologia*, Curitiba, 23 (3): 841-864.
- SCHWARTZ, P. 1972. *Micrastur gilvicollis*, a valid species sympatric with *M. ruficollis* in Amazonia. *The Condor*, Los Angeles, 74: 399-415.
- SICK, H. 1997. *Ornitologia Brasileira*. Rio de Janeiro, Editora Nova Fronteira. 912p.
- SILVA, A.G.; G.J.B. FERREIRA; R.J. DONATELLI & A. GUZZI. 2012. Cranial osteology of *Micrastur semitorquatus* Vieillot, 1817 (Falconiformes: Falconidae). *Comunicata Scientiae*, Bom Jesus, 3 (1): 64-71.
- SUSTAITA, D. 2008. Musculoskeletal underpinnings to differences in killing behavior between North American accipiters (Falconiformes: Accipitridae) and falcons (Falconidae). *Journal of Morphology*, New Jersey, 269: 283-301.

SUSTAITA, D. & F. HERTEL. 2010. *In vivo* bite grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). The Journal of Experimental Biology, Cambridge, 213: 2617-2628.

THORSTROM, R. 2000. The food habits of sympatric forest-falcons during the breeding season in northeastern Guatemala. Journal of Raptor Research, Boise, 34: 196-202.

ZUSI, R.L. & B.C. LIVEZEY. 2000. Homologies and phylogenetic implications of some enigmatic cranial features in galliform and anseriform birds. Annals of Carnegie Museum, Pittsburgh, 69: 157-193.

ZUSI, R.L. 1993. Patterns of diversity in the avian skull, p. 391-437. In: Haken, J. & B.K. Hall. (Eds). The skull, patterns of structural and systematic diversity. Chicago, University of Chicago Press, v. 2. 580p.